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Editorial Board

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Research Article

Differences in Reef Fish Assemblages between Populated and Remote Reefs Spanning Multiple Archipelagos Across the Central and Western Pacific

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Comparable information on the status of natural resources across large geographic and human impact scales provides invaluable context to ecosystem-based management and insights into processes driving differences among areas. Data on fish assemblages at 39 US flag coral reef-areas distributed across the Pacific are presented. Total reef fish biomass varied by more than an order of magnitude: lowest at densely-populated islands and highest on reefs distant from human populations. Remote reefs (<50 people within 100 km) averaged ~4 times the biomass of "all fishes" and 15 times the biomass of piscivores compared to reefs near populated areas. Greatest within-archipelagic differences were found in Hawaiian and Mariana Archipelagos, where differences were consistent with, but likely not exclusively driven by, higher fishing pressure around populated areas. Results highlight the importance of the extremely remote reefs now contained within the system of Pacific Marine National Monuments as ecological reference areas.

1. Introduction

Recent studies of isolated coral reefs, as well as of historical records, have contributed to a growing awareness of how substantially altered reef fish communities now are around human population centers [1–6]. The greatest difference between populated areas and what are assumed to be largely intact reef systems, at extremely remote locations, tends to be in the abundance and size of large predatory fishes such as sharks and jacks. Those groups often comprise a large portion of total fish biomass estimated from visual surveys at remote coral reefs [1, 2, 7], but are infrequently encountered and/or constitute a small portion of biomass on reefs close to even fairly small human populations [8]. Human impacts can also be substantial at lower trophic levels, particularly among species targeted by coral reef fisheries [8], and the depletion of predators can also lead to what appear to be cascading effects on prey species [7, 9, 10]. There is substantial evidence that relatively low levels of fishing can have profound impacts on coral reef fish assemblages, and that fishing is very likely a major contributor to the differences in reef fish communities between remote and populated coral reefs [8, 11–15], but anthropogenic impacts can also manifest themselves through habitat or environmental degradation which in turn reduces the capacity of affected reefs to support abundant marine life [16, 17].

While there is a developing consensus that reef fish populations around human population centers tend to be substantially different to those found on isolated reefs, there remains some uncertainties about the generality and normal extent of such differences. To date, studies involving extremely isolated reefs have either been at or below the scale of a single archipelago [1, 2, 7], or relied on data acquired from multiple studies using a range of sampling methods, survey habitats, and personnel [4]. This study utilizes data on coral reef fish assemblages gathered by a single large-scale program, NOAA's Pacific Reef Assessment and Monitoring Program (Pacific RAMP), that surveys coral reefs at the majority of US flag islands and atolls in the Pacific with shallow water coral reef habitat. The Pacific RAMP therefore spans a spatial range of thousands of kilometers as well as large gradients of potential human impact, from the heavily populated, urbanized, and developed islands of Oahu, Guam, and Saipan, to some of the most isolated reefs in the Pacific such as the uninhabited Howland and Baker Islands which are >500 km from the nearest populated area. A particular focus of this study was to quantify the extent of differences in reef fish assemblages between populated and remote reefs at Pacific-wide and within-archipelago scales for a range of trophic, taxonomic, and size-based groupings, and therefore to determine the generality of patterns corresponding with the presence of local human populations. In addition, this study provides information on the status of reef fish assemblages in four US Pacific Marine National Monuments (MNM) surveyed by the Pacific RAMP.

2. Methods

2.1. Survey Locations and Survey Program. The Pacific RAMP, conducted by the NOAA Pacific Islands Fisheries Science Center's Coral Reef Ecosystem Division (NOAA-CRED) and local partners, surveys coral reefs in the Hawaiian and Mariana Archipelagos, American Samoa, and the Pacific Remote Island Areas (PRIA, i.e., Johnston and Wake Atolls and the US Line and Phoenix Islands), and therefore encompasses the majority of all US Pacific islands and territories with shallow coral reef habitats (Figure 1). The 39 island and atolls (henceforth "reef-areas") included in this study (Table 1) comprise all reef areas surveyed by the Pacific RAMP between 2008 and April 2010; that is, after the Pacific RAMP survey design was changed to one based around stratified random sampling of <30 m hardbottom habitats, with the additional requirement that survey sites were always separated by at least 100 m. To increase comparability among reef areas, only data from fore reef sites were used. Data from 1,021 sites, constituting around 1,200 hours of underwater observation, were included in this study.

Recognizing that reef fish assemblages at lightly or unpopulated areas can be significantly affected by nearby population centers over scales of at least several tens of kilometers [12], reef areas were classified as either "populated" or "remote" based on a combination of local human population density (measured in terms of human population per unit area of reef, Table 1), proximity to larger population centers, and management status. The intention was to limit the classification of "remote" to reef areas where there was a reasonable expectation that direct human impacts were very low to negligible. All Pacific RAMP survey locations that might feasibly be considered as remote by that definition were over 100 kilometers from the nearest human settlement comprising more than a handful of people. It seems likely that the greatest near-term threat to reef fish assemblages at those locations would come from occasional visitation by fishing operations. Brewer and colleagues found evidence that depletion of fish stocks was related to proximity to provincial capitals (and presumably the larger markets for fish at those mini population centers) over scales of >50 km in the Solomon Islands [12]. Given that provincial capitals in the Solomon Islands have much smaller populations than several of the islands included in this study, it seemed plausible that the impacts, in terms of increased fishing pressure, of those larger population centers could be nontrivial over larger distances. Therefore, the criteria for a reef area to be classified as remote were set as (i) local population of <50 people; (ii) located >100 km from the nearest larger human settlement. Two exceptions were Midway and Wake Atolls, where human population was marginally above 50 but where there were significant restrictions on fishing activities, as described below.

Within the Hawaiian Islands there was a very clear divide between the southern main Hawaiian Islands (MHI: Hawaii Island to Kauai, Figure 1) and the Northwestern Hawaiian Islands (NWHI: French Frigate Shoals to Kure, Figure 1). While there are substantial differences in population density and apparently also in human impacts on reef fish assemblages among the main islands [8], all of the MHI are relatively close to large population centers (Table 1). For example, Niihau, the least populated of the MHI, is little more than 30 km from Kauai which has a population of >50,000. We therefore classified all of the MHI as populated (Table 1). In contrast, French Frigate Shoals, the most southerly of the NWHI covered by this study is >600 km from the nearest MHI (Figure 1). Midway Atoll, the only permanently inhabited reef area in the NWHI, with a resident population of around 60 management staff, researchers, and contractors, was a US Navy base until 1993 and has been a US Fish and Wildlife Service (FWS) National Wildlife Refuge (NWR) since 1988. A study based on surveys in 2000–2003 noted that, although sharks were abundant at Midway, jack populations were depleted compared to other reef areas in the NWHI, perhaps due to lingering effects of the four decades that Midway was a military base together with possible impacts of a catch and release sport fishery for jacks that operated between 1996 and 2000 [18]. Because of substantial local restrictions on fishing, it was assumed that overall human impacts to the reef fish assemblage would have been relatively minor by the time of our surveys in 2008. While other of the NWHI are intermittently inhabited by a small number of scientists or managers, the very strong likelihood is that, by virtue of their isolation, direct human impacts on reef fish assemblages in the NWHI have been very limited for a considerable period. In 2005 the State of Hawaii established the NWHI Marine Refuge which closed all state waters to fishing. Protection was further enhanced by the establishment of the Papahānaumokuākea Marine National Monument (PMNM) in 2006. Therefore all of the NWHI, including Midway, were classified as remote (Table 1).

Similarly, the Mariana Archipelago is comprised of a group of mostly inhabited southern islands (Guam to Saipan) and a series of unpopulated or virtually unpopulated northern islands (Sarigan to Farallon de Pajaros [FDP]). All of the southern islands were classified as populated, including Aguijan, which has no resident human population but is nine kilometers from Tinian, and less than 35 km from the densely populated island of Saipan (Table 1). All of the northern islands from Sarigan to FDP were classified as remote on the basis of no, or extremely small, resident human populations (highest population being six people at Alamagan, Table 1), and that the most southerly of those, Sarigan, is ∼150 km from the nearest population center, Saipan (Figure 1). While it is reasonable to assume that the Mariana reef areas classified as remote were much less directly impacted by human activities than those in the southern part of the archipelago, there is evidence of some intermittent commercial fishing operations in the northern islands and of unquantified levels of poaching by foreign vessels [19]. In addition, geological and physical differences between the southern and northern islands, which include a relatively recent history of volcanic activity at several of the northern islands, have resulted in distinct habitat differences between those two subregions [20], which have the potential to confound differences due to human impacts. In 2009, presidential proclamation 8335 established the Mariana Trench Marine National Monument (MTMNM) which contains the waters around the three northernmost of the Mariana Islands (FDP, Maug, and Asuncion, Figure 1).

The Pacific Remote Island Areas (PRIAs) are made up of US sovereign islands not within the jurisdiction of any US state or territory [21]. The PRIA therefore constitute a diverse and widely separated group of reef areas, including islands and atolls in the Marshall, US Line, and Phoenix Islands (Figure 1). All of the PRIA except Wake Atoll, which is a US Air Force installation, have been managed as NWR by the FWS since 1974 (Howland, Baker, Jarvis), 2001 (Kingman and Palmyra), or 2004 (Johnston Atoll). Five of the PRIA (Johnston, Kingman, Howland, Baker, and Jarvis) are unpopulated, and one, Palmyra, has a research station operated by the Nature Conservancy, which supports a small staff, scientists and visitors. As the coral reefs of Palmyra are within the NWR, harvesting of reef fishes is prohibited. In addition, the PRIA are distant from human population centers: the least remote being Jarvis and Palmyra, which are both around 350 km from, respectively, Kiritimati and Tabuaeran in the Line Islands chain. The US Air Force installation at Wake Atoll is staffed by ∼100 personnel at any one time. Although the population level at Wake was slightly higher than the criteria we used for “remote” areas, fishing is restricted at Wake by a ban on commercial fishing, the use of traps, most nets, and automated spear guns, and a prohibition on the take of sharks, rays, bumphead parrotfishes (*Bolbometopon muricatum*) and napoleon wrasse (*Cheilinus undulatus*). In 2009, all of the PRIA were designated by the Pacific Remote Islands MNM, and all are classified as remote for this study.

Survey data from five reef areas in American Samoa are used in this study (Figure 1). Tutuila is by far the largest and most densely populated (Table 1). Approximately 100 km east of Tutuila are the Manu’a Islands of Ta’u, and Ofu and Olosega (Figure 1, Table 1). The other two locations are Swains Island and Rose Atoll (Figure 1). While there are indications that commercial fishing of reef fishes has declined around Tutuila in the recent past, fishing continues to be an important part of the local culture and is a common recreational and subsistence activity [22]. Population density and, likely, levels of fishing are considerably lower on Ta’u and Ofu and Olosega, but fishing remains an important source of food on those islands. A recent study estimated that 1,400 kg of fish (excluding scad) and invertebrates were harvested annually per km of shoreline at Ofu and Olosega [23]. Therefore, Tutuila, Ta’u, and Ofu and Olosega were classified as “populated.” Rose Atoll is 130 km east of Ta’u and has been a FWS NWR since 1973. In 2009, waters around Rose were designated as the Rose Atoll Marine National Monument (RAMNM). Swains Island, which is part of the Tokelau chain, is located approximately 300 km north of the populated Samoan Islands. It is a private island inhabited by a small number of resident caretakers: 37 people in 2000 (Table 1), but population levels since then have dwindled to fewer than ten. Given their zero or low population densities, and remoteness from significant human population centers, both Swains and Rose were classified as remote.

2.2. Survey Design and Methodology. Fish data come by means of visual surveys conducted on SCUBA. Survey design and sampling domain were identical at all locations, but two visual surveys methods were used. In the Mariana Archipelago, American Samoa, and PRIA, surveys were conducted using stationary point counts (SPCs), but surveys in the Hawaiian Archipelago were conducted using belt transects. Details of those methods are given below. Pacific RAMP now uses only SPC but transition to that method had not yet occurred at the time of the Hawaii surveys. As part of that methods transition, 332 paired surveys were conducted (sites where both belt transect and SPC surveys were carried out), and those were distributed across all survey regions. Analysis of that data indicates that the two methods give very similar estimates of total biomass and planktivores biomass (mean difference between methods <5%) but that relative to SPC, belt transects tend to underrepresent piscivore biomass (23% lower in belts) and overrepresent herbivore

Table 1: Study Areas, Regions, and Status. MNM: Marine National Monument. NWR: US Fish and Wildlife Service National Wildlife Refuge. Shaded areas are those classified as remote. *N*: no. of sites surveyed.

Reef-area	*N*	Lat	Long	Human Pop^1	Area of Reef^2 (km^2)	Pop/km^2 Reef	*P*/*R*	Notes
Hawaiian archipelago								
Kure	13	−178.33	28.42	0	90.2	0	*R*	Papahānaumokuākea MNM established 06/2006 From 09/2005 NWHI Marine Refuge (state of Hawaii) banned extraction of reef fishes except by permit (mostly for research) at all islands other than Midway. Midway a NWR since 1988
Midway	8	−177.38	28.23	~60	85.4	~0.7	*R*	
Pearl & Hermes	20	−175.85	27.86	0	374.5	0	*R*	
Lisianski	14	−173.95	26.01	0	215.6	0	*R*	
Laysan	11	−171.73	25.78	0	26.4	0	*R*	
Maro	12	−170.58	25.41	0	217.5	0	*R*	
French Frigate	12	−166.21	23.79	0	469.4	0	*R*	
Kauai	24	−159.57	22.09	58,303	178.8	326.1	*P*	
Niihau-Lehua	20	−160.15	21.90	160	6.7	23.9	*P*	
Oahu	14	−158.00	21.49	876,151	374.8	2,337.6	*P*	
Molokai	16	−157.09	21.14	7,404	161.6	45.8	*P*	
Lanai	16	−156.92	20.82	3,193	46.3	69.0	*P*	
Maui	34	−156.40	20.82	117,644	164.6	714.7	*P*	
Hawaii	62	−155.42	19.53	148,677	193.7	767.6	*P*	
Mariana archipelago								
Farallon de Pajaros	7	144.89	20.55	0	0.8	0	*R*	Mariana Trench MNM, containing Asuncion, Maug, and Farallon de Pajaros, established 01/2009
Maug	21	145.22	20.02	0	2.1	0	*R*	
Asuncion	13	145.40	19.69	0	0.5	0	*R*	
Agrihan	14	145.66	18.76	0	8.6	0	*R*	Several were populated prior to volcanic activity in recent past (e.g., at Pagan in 1981). Alamagan population low but variable in recent years
Pagan	21	145.76	18.11	0	11.1	0	*R*	
Alamagan	6	145.83	17.60	6	3.2	1.9	*R*	
Guguan	6	145.84	17.31	0	1.1	0	*R*	
Sarigan	7	145.78	16.71	0	1.9	0	*R*	
Saipan	22	145.75	15.19	62,392	56.8	1,098.5	*P*	
Tinian	14	145.63	14.99	3,540	14.7	240.7	*P*	
Aguijan	6	145.55	14.85	0	2.6	0	*P*	
Rota	14	145.21	14.16	3,283	12.1	271.3	*P*	
Guam	25	144.79	13.46	154,805	91.3	1,695.6	*P*	
Pacific remote island areas (PRIA)—all within PRIA MNM (established 01/2009)								
Wake	29	166.62	19.30	~100	22.9	~4.4	*R*	US Air Force base
Johnston	11	−169.52	16.74	0	150.1	0	*R*	Marine waters in NWR since 2004
Kingman	26	−162.38	6.40	0	20.9	0	*R*	NWR Jan 2001 to 12 nautical miles (nm)
Palmyra	66	−162.10	5.54	~10–20	47.2	0.2–0.4	*R*	
Howland	26	−176.62	0.80	0	3.0	0	*R*	NWR 1974 -to 3 nm
Baker	25	−176.48	0.20	0	5.2	0	*R*	
Jarvis	49	−160.00	−0.37	0	3.0	0	*R*	
American Samoa								
Swains	41	−171.08	−11.06	37	2.4	15.4	*R*	Human pop ~10 in recent years
Ofu & Olosega	43	−169.65	−14.17	505	3.6	140.3	*P*	
Tau	36	−169.47	−14.24	380	3.8	100.0	*P*	
Tutuila	171	−170.70	−14.30	55,876	35.8	1,560.8	*P*	
Rose	46	−168.16	−14.55	0	7.9	0	*R*	RA MNM est. 01/09. NWR since 1973

Notes. (1) Population data from US Census 2000 (http://www.census.gov/main/www/cen2000.html) [21]; (2) area from shoreline to 10 fathom line [24].

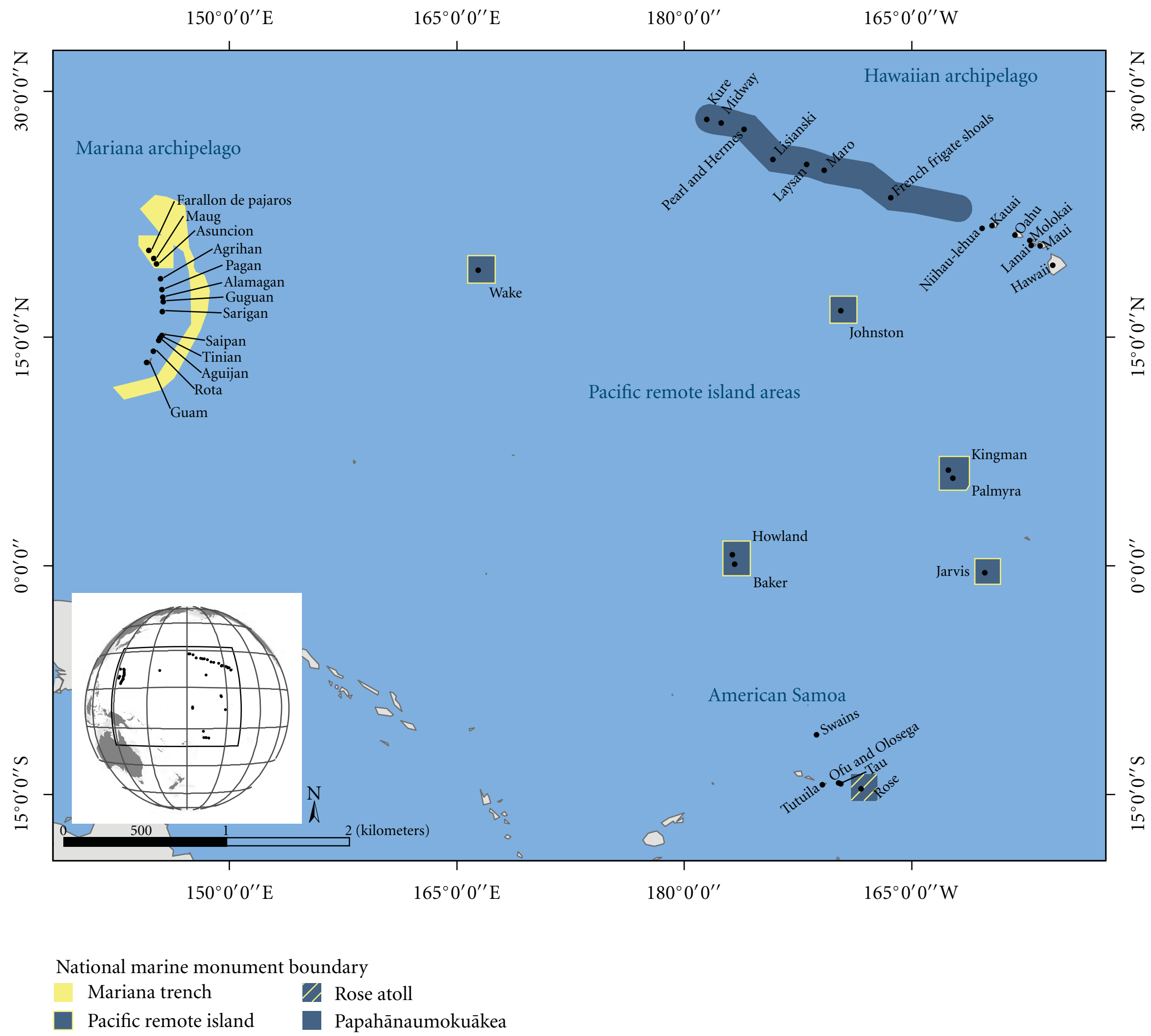

Figure 1: Locations of the reef-areas (i.e., islands and atolls) surveyed by NOAA CRED for Pacific RAMP between 2008 and April 2010. Boundaries of US Pacific Marine National Monuments are indicated. Note that labels are only shown for reef-areas that were surveyed by the Pacific RAMP in that period. The number of sites surveyed per reef-area is given in Table 1.

and secondary consumer biomass (by 19% and 34%, resp., CRED unpublished data).

The SPC protocol closely follows that used by Ault and colleagues [25], and involved a pair of divers conducting simultaneous counts in adjacent visually estimated 15 m-diameter plots extending from the substrate to the limits of vertical visibility. Prior to beginning each SPC pair, a 30 m line was laid across the substratum. Markings at 7.5 m, 15 m, and 22.5 m enabled survey divers to locate the mid point (7.5 m or 22.5 m) and two edges (0 m and 15 m; or 15 m and 30 m) of their survey plots. Each count consisted of two components. The first of those was a 5-minute species enumeration period in which the diver recorded all species observed within their cylinder. Following that was the tallying portion, in which the diver systematically worked through their species list successively recording the number and size (total length, TL, to nearest cm) of all fishes on the species list. The tallying portions were conducted as a series of rapid visual sweeps of the plot, with one species grouping counted per sweep. To the extent possible, divers remained at the center of their cylinders throughout the count. However, small and cryptic species, which will tend to be underrepresented in counts made by an observer remaining in the center of a 7.5 m radius cylinder, were left to the end of the tally period, at which time the observer swam through their plot area carefully searching for those species. In cases where a species was observed during the enumeration period but was not present in the cylinder during the tallying period, divers recorded their best estimates of size and number observed in the first encounter during the enumeration period and marked the data record as “noninstantaneous.” Surveys were not conducted if horizontal visibility was <7.5 m; that is, when observers could not distinguish the edge points of their cylinder.

For belt transect surveys, a pair of divers swam in parallel recording the species, number, and size (TL to nearest cm) of all fishes encountered on replicate 25 m long belt transects per site. Each transect was surveyed on two passes: an outward swim in which observers counted fishes ≥20 cm on adjacent nonoverlapping 4 m-wide belts (total transect width for the survey pair of 8 m) and a return swim in which fishes <20 cm were counted on 2 m wide belts (total transect width for survey pair on return swim of 4 m). Transects extended upwards to limits of vertical visibility.

2.3. Data Handling and Analysis. Replicate SPC and belt-transect counts were always pooled at the site level prior to analysis (i.e., to the mean of the replicate belt transects or SPCs conducted at a site by a dive team in a single dive). The core measure used for this study was estimated mass of fishes per unit area (hereafter "biomass"). Mass of individual fishes was calculated using length to weight (LW) conversion parameters, and, where necessary, length-length (LL) parameters (for example, to convert TL to fork length [FL] for species with LW parameters based on FL). LW and LL conversion parameters were taken from a range of published and web-based sources [26, 27].

Species data were pooled into "all fishes," and into a number of trophic, taxonomic, and size groupings. The four trophic groupings used were "primary consumers" (herbivores and detritivores); "secondary consumers" (omnivores and benthic invertivores); "planktivores;" and "piscivores," (see http://escholarship.org/uc/item/5394f7m3 for species classifications), based on diet information taken largely from FishBase [26].

It was not possible to perform meaningful species level analyses because study locations are spread across a range of biogeographic regions, and because, even within regions, few species were encountered frequently enough to be analyzed at that level. Therefore, the taxonomic groupings used were based largely on family, while taking account of trophic group and body size. For example, Serranidae includes both "groupers" (medium to large-bodied ambush predators that are often fishery targets) and also anthias (small-bodied and generally schooling planktivores that are rarely fished in most locations) [28]. Similarly, Carangidae include large-bodied taxa such as *Caranx ignobilis* and *Seriola dumerili* as well as smaller-bodied schooling planktivorous scad (*Decapterus* spp., *Atule mate*, and *Selar crumenophthalmus*). Therefore, the main jack group analyzed was "nonplanktivorous jacks" (i.e., all species other than scad), which seems a more appropriate functional grouping than "all jacks." Additionally, excluding such heavily clumped highly mobile and rarely encountered taxa will tend to improve data quality, as biomass of those are likely to be poorly estimated by visual surveys of small-area plots, such as were used for this study.

Taxonomic groupings considered to be commonly targeted by fishers or vulnerable to fishery depletion were (i) reef sharks (Carcharhinidae and Ginglymostomatidae); (ii) jacks (Carangidae) excluding planktivores; (iii) parrotfishes (Scaridae); (iv) groupers (Serranidae excluding Anthiinae); (v) snappers (Lutjanidae); (vi) emperors (Lethrinidae); (vii) surgeonfishes (Acanthuridae); (viii) goatfishes (Mullidae). Three species of introduced fish (two snapper: *Lutjanus kasmira, L. fulvus*, one grouper: *Cephalopholis argus*) were excluded from Hawaiian target fish groups. Hawaii has few native grouper or snapper species, which led to their deliberate introduction by the state government in the 1950s in the hope of developing new fisheries [29]. To date, they have not become preferred target species and in fact are often considered to be pests by local fishers [29]. In addition, the within archipelagic distributions of those species are likely still influenced by the fact that founder populations were released in the main islands. For example, although *Cephalopholis argus* is abundant in several places in the MHI, only four individuals have been recorded during Pacific RAMP belt surveys in the NWHI since the program began in 2000, and those were all at the most southerly reef areas of the NWHI chain.

Fishes were also pooled into six taxonomic groupings which were considered to be lightly or negligibly fished across the majority of reef areas in this study: (i)angelfishes (Pomacanthidae); (ii) nonplanktivorous butterflyfishes (Chaetodontidae), that is, all species other than *Hemitaurichthys* spp., *Chaetodon kleinii*, *Chaetodon miliaris,* and *Heniochus* spp.; (iii) small wrasses (Labridae), being all species with maximum length <20 cm; (iv) small hawkfishes (Cirrhitidae), as above limited to species with maximum length <20 cm; (vi) planktivorous damselfishes; (vi) all other damselfishes. Hawkfish and wrasse species with maximum length >20 cm TL were excluded from these nontarget groupings because larger-bodied taxa such as *Bodianus* spp., *Cheilinus undulatus*, and *Cirrhitus pinnulatus* are targeted in some locations. A size-based threshold was used because, given the spatial scale of this study, it was not possible for us to make reliable judgments regarding the fishery desirability of all species at each location. Small hawkfishes and wrasses, as defined here, made up 86% and 65%, respectively, of counts of fishes in those families.

Finally, as it is widely recognized that large-bodied species and large individuals tend to be preferentially targeted by reef fisheries [10, 30, 31], remote-populated differences among different size classes were explored, with fishes pooled into six size-based categories: TL < 10 cm; 11–20 cm; 21–30 cm; 31–40 cm; 41–50 cm; >50 cm.

Pacific-wide comparisons of mean fish biomass between the 15 reef-areas classified as "populated" and the 24 classified as "remote" were made using Wilcoxon tests [32].

2.4. Quantifying Differences between Remote and Populated Portions of Each Archipelago. As described above, all the PRIA were classified as "remote." The three other island groups, the Mariana and Hawaiian Archipelagos and American Samoa, contained both "remote" and "populated" subregions. For these three islands groups, the primary goal of the analysis was to quantify the extent of differences in biomass between the 'remote' and "populated" subregions for the fish groupings described above. More details of the analytical methods are given below, but, in brief, the mean difference in biomass between remote and populated subgroups within an archipelago was calculated, and a bootstrapping approach was used to estimate 2.5% and 97.5% quantiles (i.e., a range covering the middle 95% of the distribution = 95% quantile range [95%QR]) of those differences. Differences were normalized by dividing by mean biomass of populated reef areas to generate biomass ratios (BRs). 95%QR of a biomass ratio not overlapping 1 was interpreted as being evidence of difference between archipelagic subregions, with 95%QR > 1 indicating *higher* biomass at remote reef areas, and 95%QR < 1 as evidence of *lower* biomass at remote areas.

For parametric data, it is relatively easy to calculate means and confidence intervals of differences between data sets. However, as is not uncommon for coral reef fish visual survey data, biomass densities of several fish groups of interest were highly nonnormally distributed both within reef areas and within archipelagos. Transforming the data to make it conform to the requirements of parametric analyses was not attempted because of the difficulty in meaningfully interpreting backtransformed biomass ratios. Therefore, in order to apply a consistent analytical approach across all groupings, a bootstrapping method was used to calculate distributions of biomass ratios. Bootstrapping involves repeated resampling with replacement from an existing data set, in this case, from the biomass densities of all sites at a reef area, to generate pseudo samples of the same size as the original data set [33]. Multiple such bootstrap samples provide the basis for calculating distribution statistics that are based on the actual distribution of the survey data, rather than having to rely on assumptions about the form of that distribution (e.g., that data are normally distributed). To illustrate this, for an archipelago with *m* reef areas there were *m* data sets—one for each reef area, each set being a random sample consisting of all site surveys at that reef area. For example, in the Hawaiian Archipelago there were 15 reef areas: eight classified as populated and seven as remote. Among those reef areas, sample sizes ranged from 8 to 62 (Table 1). For a reef-area i with n survey-sites, the original data set can be represented as $X^i = (x_1^i, x_2^i, x_3^i, \ldots, x_n^i)$. Random resampling of that data set with replacement gives a bootstrap sample also of length n: $X^{i*} = (x_1^{i*}, x_2^{i*}, x_3^{i*}, \ldots, x_n^{i*})$, with mean of $\overline{x^{i*}}$. Doing that for all reef areas within an archipelago gives bootstrap sample means for the m reef-areas of $\overline{x^{1*}}$ to $\overline{x^{m*}}$. Averaging the bootstrap sample means separately for remote and populated areas gives bootstrap means for the remote and populated portions of the archipelago. By repeating that process 10,000 times per archipelago and fish group of interest, we were able to generate the 2.5% and 97.5% quantiles of the distributions of differences in biomass between subregions. Analyses were performed using the R statistical program version 2.9.2 (R Development Core Team, http://www.r-project.org).

3. Results

3.1. Pacific Wide. Among the 39 reef areas, estimated mean total fish biomass ranged from <20 g m^{-2} at the heavily populated islands of Guam, Saipan, and Tinian (mean ± SE: 13.2 ± 1.5 g m^{-2}, 18.2 ± 1.7, 18.9 ± 1.5 g m^{-2}, resp.) to around 250 g m^{-2} and above at the unpopulated and extremely isolated reef areas of Jarvis and Kingman in the PRIA (246.8 ± 36.9, 296.2 ± 40.5 g m^{-2}) and Kure in the NWHI (347.9 ± 212.7 g m^{-2}, Figure 2).

While there was considerable variability among reef areas within the "remote" and "populated" classifications and among archipelagos, there was a clear tendency at both Pacific-wide and archipelagic scales for biomass to be higher at remote reef areas (Figure 2). At the Pacific-wide scale, the grand mean of estimated total biomass for the 15 populated reef areas (33.2 ± 3.4 g m^{-2}) was less than a quarter of that for the 24 remote reef areas (131.1 ± 16.3 g m^{-2}). Additionally, the highest biomass at any populated reef area, 59.2 ± 6.8 g m^{-2} at Niihau-Lehua, was less than half of the grand mean of remote areas. In stark contrast to the populated reef areas, 15 of 24 remote reef areas had mean total fish biomass >100 g m^{-2} (Figure 2).

At Pacific-wide scale, remote areas tended to have higher biomass in all trophic groups (Wilcoxon test $P < .05$ in all cases), but the scale of difference was greatest for piscivores (Figure 2). The estimated mean piscivore biomass at remote reef areas ranged from 9.4 g m^{-2} at Maug to 231.6 g m^{-2} at Kure (grand mean = 59.7 g m^{-2}), whereas at populated reef areas it varied from 0.8 g m^{-2} at Oahu to 9.8 g m^{-2} at Aguijan (grand mean = 4.2 g m^{-2}). Piscivores made up between 9% and 68% of the total estimated biomass at remote areas (grand mean = 40%) and were the largest component of total biomass at half of the remote reef areas (Figure 2). In contrast, piscivores were a small portion of total biomass at nearly all populated reef areas (grand mean = 13%; and 18% or less everywhere other than Aguijan where they made up 38%) and comprised as little as 3% of total fish biomass at Oahu, the most densely populated island in this study. At all 15 of the populated areas primary consumers (88% made up of surgeonfishes and parrotfishes) were the largest component of biomass (38 to 54%, grand mean = 50%, Figure 2).

3.2. Hawaiian Archipelago. Within the Hawaiian Archipelago, total fish biomass at remote reef areas was over four times that at populated islands (BR: 4.5, 95%QR: 3.3–6.3, Figure 3). Remote reef-areas had higher biomass in all trophic groups (i.e., BR > 1 and 95%QR did not overlap 1), but the scale of differences was considerably larger for piscivores (BR: 22.1, 10.3–44.2), than for other trophic groups, which had biomass ratios between two and three (primary consumer BR: 3.0, 2.5–3.6; secondary consumer BR: 2.1, 1.7–2.8, planktivore BR: 2.6, 1.7–3.5).

Biomass of all target groups was higher at remote Hawaiian reef areas than at populated areas (Figure 3). The largest such differences were for sharks and large jacks, which had biomass ratios > 50 (shark BR: 50.9, 16.3–101.0; jack BR: 131.5, 49.2–291.1), and for emperors (BR: 13.4, 4.1–29.6). Remote area biomass of parrotfishes and native snappers was, respectively, 3.6 (2.9–4.3) and 4.2 (2.7–5.7) times that at populated reef areas. Among target groups, the smallest

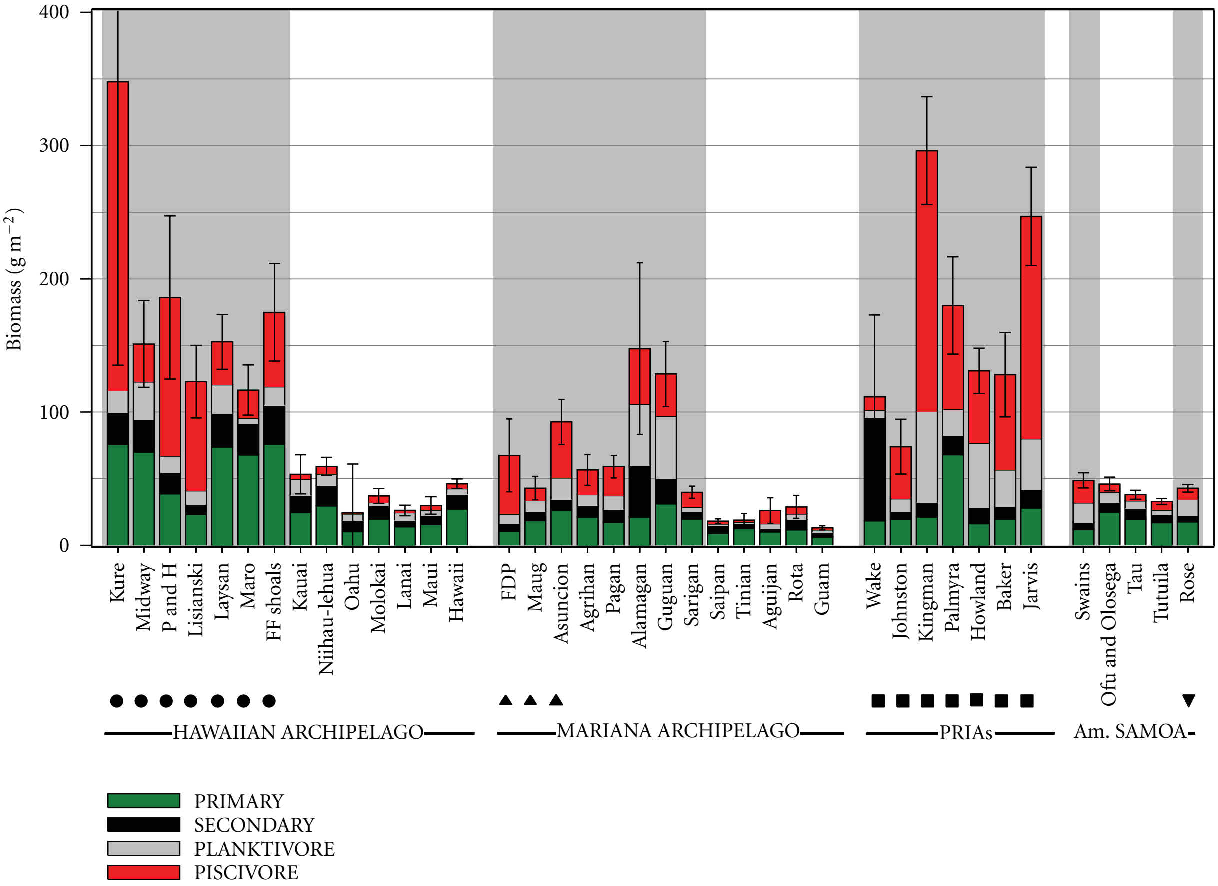

Figure 2: Mean biomass per reef-area by trophic grouping. Vertical bars indicate ± 1 SE (for total biomass) with all fore reef sites per location as replicates. Reef-areas are grouped by region (Hawaiian and Mariana Archipelagos, PRIA, American Samoa). Within regions, reef-areas are ordered by latitude with most northerly reef-areas to the left. Shaded portions of the figures indicate "remote" reef-areas, as defined in Section 2. Reef-areas within Marine National Monuments (MNMs) are identified by circles for Papahānaumokuākea MNM; upright triangles for Mariana Trench MNM; squares for Pacific Remote Islands MNM; and inverted triangle for Rose Atoll MNM.

biomass ratios were for surgeonfishes (1.9, 1.5–2.3) and goatfishes (1.6, 1.03–2.2). Native groupers were not recorded at any Hawaiian Archipelago site during the survey period.

Nontarget groups also tended to have higher biomass at remote reef-areas than at populated areas within the Hawaiian Archipelago, but in no case was that difference as large as it was for some of the target groups (Figure 3). For three of the six nontarget groups there was either no clear difference between remote and populated reef areas (95%QRs for nonplanktivorous butterflyfishes and small hawkfishes overlapped one) or the difference was marginal (small wrasse BR: 1.4, 1.1–1.7). However, for three of six nontarget taxa, biomass at remote reef areas was between three and nearly five times that at populated reef areas: angelfish (BR 4.1, 2.9–5.6); benthic damselfishes (BR: 3.3, 2.7–4.1); planktivorous damselfishes (BR:4.6, 3.1–6.6).

For all size classes, biomass was higher at remote reef areas (Figure 3). The lowest biomass ratios, ranging from 1.7 to 3.3, were for the smallest size classes (i.e., fishes <31 cm, Figure 3). For the largest size classes, 41–50 cm and >50 cm, biomass ratios were, respectively, 7.5 (5.4–10.9) and 16.5 (8.0–31.5).

3.3. Mariana Archipelago. As with the Hawaiian Archipelago, remote Mariana reef-areas had total fish biomass around four times that of populated reefs (BR 3.8, 3.0–4.7, Figure 3). Mariana remote areas also had higher biomass than populated reef-areas for all trophic groups (Figure 3), with substantial differences for piscivores (BR: 6.8, 4.8–9.2) and planktivores (BR: 6.8, 4.4–9.5) but relatively small differences for primary and secondary consumers, which had biomass ratios of between two and three (primary consumer BR: 2.1, 1.7–2.4; secondary consumer BR: 2.8, 1.7–4.5).

Within the Mariana Archipelago, seven of eight target groupings had higher biomass at remote reef-areas than at populated reef-areas (Figure 3). The one exception was emperors, for which high variability among samples and reef-areas contributed to a wide range of bootstrap differences between remote and populated areas. Hence, although BR was 2.5, the 95%QR (0.9–3.7) overlapped one. Among target groups with highest biomass ratios were snappers (BR: 18.0, 11.7–26.6) and jacks (BR: 14.5, 8.6–22.8). Biomass of sharks and grouper was also considerably higher at remote reef-areas, being more than four times that observed at populated islands within the chain (shark BR: BR 4.1,

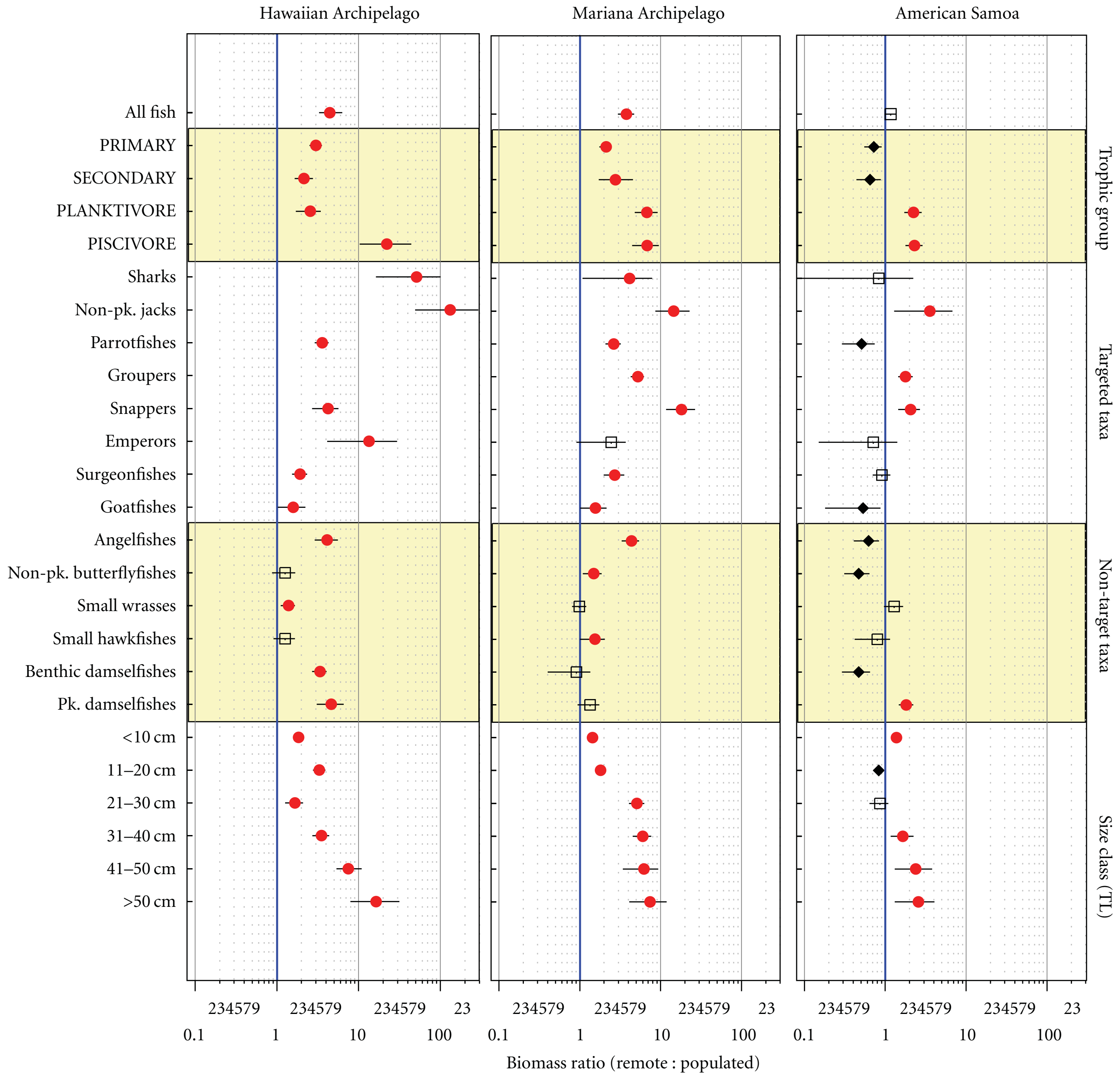

Figure 3: Differences in reef fish assemblages between remote and populated portions of US Pacific coral reef regions. Differences are given as the ratio of biomass between remote and human-populated portions of each region. The blue vertical line represents a ratio of one (i.e., no difference in biomass between remote and populated reef-areas). Horizontal bars indicate 95% quantile-range. Red circles: *higher* biomass at remote reef-areas; that is, positive biomass ratio and 95% quantile-range do not overlap one. Black diamonds: *lower* biomass at remote reef-areas; that is, ratio is negative and quantile-range does not overlap one. Open squares: 95% quantile-range overlaps one. Details of the analysis are given in Section 2.

1.1–7.8; grouper BR: 5.2, 4.3–6.2). While less substantial, biomass ratios of 2.7 (2.0–3.6) for surgeonfishes and 2.6 (2.1–3.2) for parrotfishes represent nontrivial differences, as even the low bound of the 95%QRs indicate greater than twice the biomass at remote reef-areas. As in the Hawaiian Archipelago, goatfishes had the lowest biomass ratio among target groups (BR: 1.6, 1.01–2.1).

Only one of the six nontarget groups, angelfishes, had substantially higher biomass at remote Mariana reef-areas than at populated areas (BR: 4.3, 3.3–5.4). For the other five nontarget groups there were either no clear differences between remote and populated reef-areas (i.e., 95%QRs overlap one, which was the case for small wrasses, and both damselfish groupings, Figure 3), or biomass was marginally higher at remote areas (nonplanktivorous butterflyfishes BR: 1.5, 1.1–1.9; small hawkfishes BR: 1.5, 1.004–2.0).

As in the Hawaiian Archipelago, fish biomass was higher at remote areas in all size classes and remote-populated differences were much greater for the larger size classes (Figure 3), which had biomass six or more times that at populated areas (e.g., 41–50 cm BR: 6.2, 3.4–9.3; >50 cm BR: 7.4, 4.1–11.8), than for the smaller size classes (1–10 cm BR: 1.4, 0.2–1.8; 11–20 cm BR: 1.8, 1.5–2.0).

3.4. American Samoa. Unlike the Mariana and Hawaiian Archipelagos, differences between the remote and populated reef-areas of American Samoa were less distinct. Neither of the two remote American Samoan reef-areas (the highest biomass of which was $48.8 \pm 5.8\,\mathrm{g\,m^{-2}}$ at Swains) had total fish biomass comparable to values found at remote reef-areas in other archipelagos (Figure 2). Overall, at American Samoa, there was no difference in total fish biomass between remote and populated reef-areas (BR: 1.2, 0.98–1.4). The two remote reef-areas had lower biomass of primary and secondary consumers than the three populated reef-areas (primary BR: 0.7, 0.6–0.9; secondary consumer BR: 0.6, 0.4–0.9), but higher biomass of planktivores (BR: 2.2, 1.7–2.8) and piscivores (BR: 2.3, 1.8–2.9).

Although target fish biomass was not consistently greater at remote reef-areas of American Samoa: there were clear differences for 5 of the 8 target fish groups: biomass of jacks, snappers, and groupers was higher at remote areas (BRs: 3.5, 1.3–6.8; 2.1, 1.5–2.7; and 1.8, 1.4–2.2); but remote areas biomass of parrotfish and goatfish was around half that at populated areas (BRs: 0.5, 0.3–0.7; and 0.5, 0.2–0.9, resp., Figure 3). There were no clear differences for emperors, surgeonfishes, or sharks (Figure 3). Similarly, among nontarget taxa, biomass of two of six groups—small wrasses and small hawkfishes—did not clearly differ between remote and populated reef-areas (Figure 3). However, remote areas had lower biomass of angelfishes, nonplanktivorous butterflyfishes, and benthic damselfishes (BRs: 0.6, 0.4–0.8; 0.5, 0.3–0.6; and 0.5, 0.3–0.6, resp.), and slightly higher biomass of planktivorous damselfishes (BR: 1.8, 1.5–2.2).

As at other island groups, biomass differences between remote and populated areas were least for the smaller size classes, but increased as size class increased, with both 41–50 cm and >50 cm size classes having biomass ratios of greater than 2 (41–50 cm BR: 2.4, 1.3–3.8; >50 cm BR: 2.6, 1.3–4.1).

4. Discussion

The 39 islands and atolls included in this study span wide ranges both geographically and in terms of potential human impact, from the heavily populated, urbanized, and physically altered islands of Oahu and Guam to the isolated reef-areas of Jarvis, Baker, and Howland, which are several hundred kilometers from the nearest human settlement. Clearly there are substantial physical, biological, and oceanographic differences among surveyed areas which likely influence standing biomass and structure of reef fish assemblages [34–38], and therefore limit the ability to draw definitive conclusions about the importance of single factors such as the presence of local human populations. Nevertheless, whatever the causes, this study robustly quantifies the extent of differences in reef fish assemblages between populated and remote reef-areas, and demonstrates the generality of those differences across large portions of the central and western Pacific. Such differences are clearly ecologically significant remote reef-areas having, on average, fish biomass around four times that found at populated areas. The magnitude of the differences between remote and populated islands was consistent with earlier smaller-scale studies of isolated reefs in the Pacific [1, 2, 4]. Also in common with those studies, the most striking difference we observed between remote and populated reefs was that large-bodied piscivores, such as sharks and jacks, were a conspicuous presence and made up a substantial portion of survey biomass at many of the remote reef-areas, but were rarely encountered around populated islands. For example, sharks were recorded during 101 of the 231 surveys in the PRIA, but on only two of 232 surveys at the four most densely populated islands: Oahu, Guam, Saipan, and Tutuila.

Because biogeographic differences among regions, such as low diversity of native groupers, snappers, and emperors on Hawaiian reefs, have the potential to confound Pacific-wide comparisons, we focused on within-archipelagic comparisons for the three island groups containing both remote and populated reef-areas: Hawaiian, Mariana, and American Samoa. At two of those—Hawaiian and Mariana—there were distinct and consistent differences between remote and populated reef-areas, with nearly all (21 and 19, resp.) of the 23 fish groupings having higher biomass at remote reef-areas, and no grouping having higher biomass around populated areas. The patterns of difference between remote and populated reefs within those archipelagos were similar to those at the Pacific-wide scale: total biomass at remote reefs was ~4 times that at populated reef-areas, and remote biomass was higher in all trophic groups but particularly so for piscivores (biomass ratios of ~22 and ~7, resp.). However, differences between remote and populated reef-areas in American Samoa were more complex: biomass of ten groups was higher at remote areas, but seven groups had lower biomass at remote reef-areas. This may reflect fundamental differences in oceanography, in types of human impact, or in ecological resilience at American Samoa. However, it seems more likely that it was due to a combination of (1) limited numbers of surveyed islands and atolls in American Samoa (only 5 in total: 2 nominally remote, 3 populated, compared to the 13 reef-areas in both Mariana and Hawaii chains, with 5–8 in each of remote and populated); (2) less distinct difference between the areas classified as remote and populated in American Samoa than within other archipelagos. Mariana and Hawaiian remote islands were nearly all uninhabited and distant from the nearest human population center (in the case of the NWHI, all were >600 km from the nearest population center). In contrast, of the two remote American Samoa areas, Rose Atoll is ~130 km from the populated Manu'a Islands, and the other, Swains Island, has a small resident population.

Also, both Rose and Swains have relatively small shallow nearshore habitats (7.9 and 2.4 km^2, resp., Table 1), so even low absolute levels of human activity have the potential to have tangible impacts there.

While we do not discount the importance of other anthropogenic impacts on habitat or environmental quality [17, 39], there is abundant evidence that increased fishing pressure is normally one of the main reasons for the depletion of coral reef fish populations, particularly of preferred target species, around populated areas, or in comparison to marine reserves that have had effective long-term protection [5, 8, 10–12, 40, 41]. Results from this study are consistent with fishing being among the main drivers of difference between remote and populated areas, particularly within the Hawaiian and Mariana Archipelagos. First, remote areas had higher biomass of virtually all target groups in those archipelagos, but for nontarget groups the remote-populated differences were mixed. Emperors in the Mariana were the only target group which did not have clearly higher biomass in remote areas. However, a biomass ratio of 2.5 but wide quantile range indicates that the lack of statistical significance for that group was more likely a consequence of high variability than small effect size. Most other target groups had remote areas biomass that was more than double that at populated areas. In contrast, five of the six nontarget groups in the Mariana were either not significantly different or had biomass ratios of 1.5 or below; and three of the six nontarget groups in Hawaii showed no or low difference between populated and remote areas. Secondly, among target groups, the remote-populated differences were greatest for larger size classes and for taxa which tend to be most vulnerable to fishery depletion, that is, jacks, sharks, snappers, and grouper [30, 42]. Remote-populated differences were less pronounced for goatfish and surgeonfishes, that is, taxa with life history characteristics, such as rapid growth to asymptotic size and early maturity, which tend to make them relatively resilient to fishing [43–45]. Lower remote-populated biomass ratios for those groups could also reflect lower fishing pressure on those groups, or in the availability of suitable habitat. Although remote-populated differences were less clear-cut among American Samoan reef-areas, remote reefs had around double or more biomass of groupers, snappers, jacks, and size classes larger than 40 cm. Those patterns are consistent with those areas being less impacted by fishing than populated areas. However, remote-populated biomass ratios significantly different from one for multiple nontarget groups within each archipelago emphasize that fishing pressure alone does not fully explain the differences we found between remote and populated archipelagic subregions. Localized human impacts other than fishing have the potential to have large and widespread impacts [16, 17]. In addition, over the scale of entire archipelagos there are large differences in both physical and oceanographic factors, and in habitat quality and availability, which are sufficient to affect local reef fish assemblages [20, 38].

One obvious difficulty for any comparison of extremely remote and heavily populated coral reef-areas is that medium to large land masses tend to be populated, but very small atolls and areas with limited emergent land tend not to be. Hence, some degree of confounding between island type and population status seems unavoidable. We believe it is useful to present robust information on large-scale patterns, but clearly there is a need for more detailed analysis of fish assemblages and standing stock in relation to a range of potential human, habitat, and environmental factors, particularly if that can be done at lower taxonomic levels, which are likely to be more closely tied to forcing factors than are functional groupings [39].

As with any study using data from underwater visual surveys, the presence of divers has the potential to alter fish behavior in ways that can lead to undercounting of species that tend to avoid divers [46], particularly if fishes have learned to associate divers with fishing [47]. Overcounting of species that are attracted to divers can also occur, as seems to be the case for sharks and jacks in the NWHI [48]. In general, underwater visual survey data gathered by divers are best treated as relative rather than absolute measures of density, particularly given the scope for differences in survey methods including dimensions, observer training and experience level, and survey design to impact densities derived from underwater counts [49–53]. For this study, survey design and sampling domain were common throughout (sites were randomized within 0–30 m hardbottom), and there were no systematic differences in observer training level or experience between regions or subregions, as the same survey personnel tended to survey remote and populated regions within the same archipelago on a single cruise. Although we do present some results as biomass densities (e.g., as g m^{-2}), we focused our analytical efforts on estimating relative biomass density (i.e., biomass ratios) between remote and populated reef-areas within archipelagos (i.e., where methods were consistent throughout), and on comparisons at Pacific-wide scale, where the divergence in methodology might have contributed to perceived differences between regions but was not plausibly an important factor in the clear disparity between remote and populated reef-areas at that scale.

The binary remote/populated classification scheme used in this study was rather crude. Human population density per reef-area varied by two orders of magnitude among “populated” reef-areas (least at Niihau-Lehua and highest at Oahu), which in turn meant that there are likely to be substantial differences in human impact on local reef fish populations among those areas [8]. Similarly “remote” reef-areas included extremely isolated reef-areas as Jarvis, Kingman, Baker and the NWHI, but also areas much closer to human population centers, such as Sarigan in the Mariana and Rose Atoll in American Samoa. Both Sarigan and Rose Atoll are within ~150 km of the nearest inhabited island, and are therefore much more accessible to and potentially impacted by human activities. Better understanding of the extent of human activities over medium to large distances—that is, scales of several tens to hundreds of kilometers—would allow for more sophisticated classifications than the simple “remote” and “populated” scheme used here. However, it is likely to remain difficult to reliably quantify human activities, including fishing, at isolated and uninhabited reef-areas, and we do not currently have the ability to make meaningful assessments of those at the study locations. While the simple classifications used likely underestimates the difference between the most remote and the most populated areas covered by Pacific RAMP, it was sufficient to highlight substantial differences in reef fish assemblages between those two broad categories. Notably, even with the low bar to being considered “populated” and the likelihood that some of the areas we classified as “remote” were fished to some degree, the highest reef fish biomass of the 15 populated areas, at Niihau-Lehua, was less than half of the average of all reef-areas classified as remote (and closer to a third of the average of the most isolated reefs). Although remoteness, as defined here, did not guarantee an area would support high fish biomass (e.g., six of 24 remote areas had lower mean biomass than Niihau-Lehua), the low upper limit to populated area biomass strongly suggests that even relatively low human population density and/or proximity to larger population centers is incompatible with anything resembling a pristine reef fish community structure. These results are consistent with studies showing that even low levels of exploitation can have substantial impacts on reef fish assemblages [6, 10, 11], and reinforces the importance, as biological and ecological reference areas, of the extremely isolated coral reef-areas now contained within the system of the US Marine National Monuments.

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Research Article

The Occurrence of Coral Species Reported as Threatened in Federally Protected Waters of the US Pacific

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A recent study reported that seventy-five species of reef-building corals, considered to be at elevated extinction risk when assessed by the criteria of the International Union for Conservation of Nature, occur in Pacific waters under United States jurisdiction. Closer examination substantiates records of occurrence for 66 species, while records for the other 9 species were based on misinterpretations or are otherwise uncertain. Of these, at least 55 have been reported from reef habitat under federal protection within National Parks, Marine National Monuments, National Marine Sanctuaries, and National Wildlife Refuges. The highest number of species (31) is found within the Ofu Island unit of the National Park of American Samoa, followed by Kingman Reef (24) and Palmyra Atoll (21), both within the Pacific Remote Islands Marine National Monument. Federally protected areas already in place serve as important habitats for resources whose stewardship needs and priorities may vary over time.

1. Introduction

The International Union for Conservation of Nature (IUCN) Red List of Threatened Species is a tool that is widely used for focusing attention on species of potential conservation concern [1, 2]. Assessments based on the IUCN Red List Criteria allocate species to categories of extinction risk using quantitative rules based on population sizes and decline rates, and range areas and declines. Categories range from "Least Concern" with very little probability of extinction to high risk "Critically Endangered". Three categories collectively considered "threatened" and representing increasing extinction risk (Vulnerable, Endangered, and Critically Endangered) are intended to serve as one means of setting priority measures for biodiversity conservation [3].

Corals and coral reefs in many regions of the world are reported to be in a state of decline due to numerous local and global anthropogenic stressors including coastal point source pollution, agricultural and land use practices, overutilization for commercial or recreational purposes, and climate change and ocean acidification [4–9]. In response to their declining condition, three workshops were conducted in 2006 and 2007 to apply the IUCN Red List Categories and Criteria [10] in assessing the extinction risk of all known zooxanthellate reef-building corals from the order Scleractinia plus reef-building octocorals and hydrocorals (families Helioporidae, Tubiporidae, and Milleporidae). Of the 704 species for which there were sufficient data to assign a category, 231 species (32.8%) were assigned to one of the three categories considered threatened [3]. Of these, 75 species were reported to occur in Pacific waters under US jurisdiction (Hawai'i, American Samoa, Guam, Northern Mariana Islands, Wake Atoll, Johnston Atoll, Howland Island, Baker Island, Jarvis Island, Palmyra Atoll, and Kingman Reef).

Throughout the US Pacific, substantial areas of coral reef habitat are under federal protection within the boundaries of National Wildlife Refuges, Marine National Monuments, National Marine Sanctuaries, or National Parks (Table 1). While the establishment of protected areas may be driven by one or several key resources (e.g., the safeguarding of breeding and calving habitat for the endangered humpback whale by the Hawaiian Humpback Whale National Marine Sanctuary), their legal mandate includes the comprehensive management of the ecological, historical, and aesthetic

Table 1: Marine National Monuments, National Marine Sanctuaries, National Wildlife Refuges, and National Parks with coral reef habitat in the US Pacific.

	General Location	Units
Marine National Monuments		
Papahānaumokuākea (PMNM)	Northwestern Hawaiian Islands	Nihoa*, Necker*, French Frigate Shoals*, Gardner*, Maro*, Laysan*, Lisianski*, Pearl and Hermes*, Midway NWR, Kure
Pacific Remote Islands (PRIMNM)	Central Pacific	Johnston Atoll NWR, Howland Island NWR, Baker Island NWR, Jarvis Island NWR, Palmyra Atoll NWR, Kingman Reef NWR, Wake Atoll NWR.
Rose Atoll (RAMNM)	American Samoa	Rose Atoll NWR
Marianas Trench, Islands Unit (MTMNM)	Northern Mariana Islands	Asuncion, Maug, Farallon de Pajaros
National Marine Sanctuaries		
Hawaiian Islands Humpback Whale (HIHWNMS)	Main Hawaiian Islands	Maui, Lana‘i, Moloka‘i, O‘ahu, Kaua‘i, Hawai‘i
Fagatele Bay (FBNMS)	American Samoa	Tutuila
National Parks		
NP of American Samoa (NPSA)	American Samoa	Tutuila, Ofu-Olosega, Ta’u
War in the Pacific NHP (WAPA)	Southern Mariana Islands	Guam
American Memorial Park (AMME)	Northern Mariana Islands	Saipan
Kalaupapa NHP (KALA)	Main Hawaiian Islands	Moloka‘i
Haleakalā NP (HALE)	Main Hawaiian Islands	Maui
Pu‘ukoholā Heiau NHS (PUHE)	Main Hawaiian Islands	Hawai‘i
Kaloko-Honokōhau NHP (KAHO)	Main Hawaiian Islands	Hawai‘i
Pu‘uhonua o Hōnaunau NHP (PUHO)	Main Hawaiian Islands	Hawai‘i
Hawai‘i Volcanoes NP (HAVO)	Main Hawaiian Islands	Hawai‘i
Other National Wildlife Refuges	Ritidian Point	Guam

A “unit” is here considered to be a geographically distinct island, atoll, or reef system. NWR: National Wildlife Refuge, *: unit within Hawaiian Islands NWR.

resources within them. As physical and biological resources continue to respond to environmental change driven by human enterprise, protected areas may provide an umbrella of shelter to habitats and communities not originally envisioned in need of refuge. However, some threats such as climate change are very widespread and challenge the ability of protected areas to limit their effects.

The purpose of this paper is to explore the currently known occurrence within federally protected waters of the 75 coral species assessed as threatened by the IUCN and reported by that body to occur within the US Pacific. The number of alleged threatened species occurring in each system of federal protection is reported and those species that are not presently known to occur within the boundaries of US federal protection are identified.

2. Materials and Methods

Assessments based on the IUCN Red List criteria were obtained from Carpenter et al. [3] Supporting Online Material. Peer-reviewed literature, published and unpublished reports, monitoring program databases, and local experts were consulted (Table 2) to corroborate the occurrence of the 75 species stated to occur within US Pacific waters by Carpenter et al. [3] and the IUCN Red List database [43]. Occurrences within the boundaries of federally protected waters were determined from a subset of this suite of sources. No data were available for Haleakalā National Park, Hawai‘i Volcanoes National Park, or American Memorial Park (Brown, pers. comm.).

3. Results

Of the 75 coral species stated to occur in the US Pacific in Carpenter et al. [3] and the IUCN database [43], substantiated records could be identified for 66 species. Six species (*Acanthastrea regularis, Acropora tenella, Anacropora puertogalerae, Anacropora spinosa, Pectinia alcicornis,* and *Physogyra lichtensteini*) are shown on distribution maps in Veron [33] as occurring in the Mariana Archipelago, which is the basis of their records in US waters in the IUCN database. However, these records were based on photos submitted to Veron by G. Paulay from Palau and elsewhere that were mistakenly attributed to Guam [31], (G. Paulay pers. comm. Veron pers. comm.), and these 6 species have not been authenticated by other reports from US waters. A seventh

Table 2: Data sources used to substantiate the occurrence of 75 IUCN Red List coral species in the US Pacific and in federally protected areas.

Location	References
Hawaiʻi	[11–25] NPS Pacific Islands Network monitoring database NOAA Pacific Islands Fisheries Science Center (PIFSC) Coral Reef Ecosystem Division (CRED) database
Pacific Remote Islands	[26, 27] Maragos unpubl. data 2000–2010 Kenyon and Bonito unpubl. data 2005
Rose Atoll	[28] Fenner unpubl. data 2010
Marianas Archipelago	[29–33] D. Burdick unpubl. data 2010 NOAA PIFSC CRED database G. Paulay, pers. comm.
American Samoa	[30, 34–42] Birkeland unpubl. data 1979–2007 Fenner unpubl. data 2010

species (*Acropora lokani*) was identified from photographs compared to Veron [33] but was reidentified as *A. caroliniana* based on the original description of *A. lokani* in Wallace [44] and the description of *A. caroliniana* in Wallace [30] (Fenner, pers. comm.). For 2 additional species (*Acropora dendrum* and *Caulastrea echinulata*), the initial tentative identifications from photographs are now uncertain (Fenner, pers. comm.).

Of these 66 species, records of occurrence in federally protected waters were identified for 55 species. Forty-three species were recorded within National Parks (NP), 39 species within Marine National Monuments (MNM) and National Wildlife Refuges within the MNM, and 18 within National Marine Sanctuaries (NMS) (Table 3, where data are reported as the number of discrete islands or atolls ("units") where each species has been recorded. Additionally, a supplementary online table incorporates data presented in Tables 3, 4 and 5 in a single matrix.) The most frequently occurring species, reported at 10 or more of the 26 major units afforded federal protection from which data have been reported (excluding the Hawaiian Islands Humpback Whale NMS where reported occurrence data were not attributed to the 6 component islands), were *Montipora patula* (15), *Cyphastrea ocellina* (13), *Montipora flabellata* (13), *Psammocora stellata* (13), *Pocillopora elegans* (12), *Leptoseris incrustans* (10), *Montipora caliculata* (10), and *Pocillopora danae* (10). Twenty species were recorded from 3 to 8 reef units, and 27 species were recorded at only 1 or 2 reef units.

Eleven of the 66 species with substantiated records of occurrence in the US Pacific have not been recorded within federally protected waters (Table 3). Of these, 5 species (*Acanthastrea hemprichii, Acanthastrea ishigakiensis, Acropora jacquelineae, Acropora pharaonis, and Euphyllia paradivisa)* have been reported from single locations at Tutuila, American Samoa, and were rare, represented by only 1 or 2 colonies (Fenner, pers. comm.). *Pachyseris rugosa* and *Turbinaria peltata* have been reported at several locations by several authors in American Samoa [36, 37, 40], (Birkeland unpubl. data, Fenner unpubl. data), indicating that they are relatively more abundant. Four species (*Alveopora fenestrata*, *Euphyllia paraancora*, *Millepora foveolata*, and *Seriatopora aculeata*) have been reported from Guam [34], (D. Burdick unpubl. data) though abundance data are not available. The occurrence of *P. rugosa* in the Mariana Archipelago as shown in Veron [33] has not been substantiated by other sources and is based on the misattribution of photographs as indicated previously for 6 other species (Veron pers. comm.).

Of the 39 species recorded within the Marine National Monuments and National Wildlife Refuges (NWR) (Table 4), the highest numbers of Red List threatened coral species have been recorded from Kingman Reef NWR (24) and Palmyra Atoll NWR (21) in the Pacific Remote Islands MNM followed by Rose Atoll NWR and MNM (17). In the Islands Unit of the Mariana Trench MNM, the highest number of Red List threatened coral species has been recorded at Asuncion Island (7). In the Papahānaumokuākea MNM covering the Northwestern Hawaiian Islands, the highest numbers of Red List threatened coral species (5) have been recorded at French Frigate Shoals, Maro Reef, Pearl and Hermes Atoll, and Midway Atoll.

Of all the federally protected locations, the highest number of Red List threatened coral species (31) has been recorded from Ofu Island in the National Park of American Samoa (Table 5). Fagatele Bay NMS and the Tutuila section of the National Park of American Samoa each host 12 Red List threatened coral species, despite the substantially smaller size of Fagatele Bay (0.65 km^2 and 4.9 km^2, resp.)[45, 46]. In Guam, War in the Pacific National Historical Park hosted

Table 3: IUCN Red List Categories for 66 species with substantiated records of occurrence in the US Pacific, ranked by number of units (geographically distinct islands, atolls, or reef systems) where found within federally protected waters.

	IUCN Red List Category	National Parks	Marine National Monuments	National Marine Sanctuaries	Total units
Montipora patula	VU	2	13	1	15
Cyphastrea ocellina	VU	2	11	1	13
Montipora flabellata	VU	1	12	1	13
Psammocora stellata	VU	0	13	1	13
Pocillopora elegans	VU	1	11	1	12
Montipora caliculata	VU	2	7	1	10
Pocillopora danae	VU	2	8	0	10
Leptoseris incrustans	VU	2	7	1	10
Acropora verweyi	VU	2	6	0	8
Acropora acuminata	VU	1	5	1	7
Acropora paniculata	VU	1	5	0	6
Turbinaria reniformis	VU	1	4	1	6
Acropora aspera	VU	2	3	0	5
Acropora retusa	VU	1	4	0	5
Acropora vaughani	VU	1	4	0	5
Pavona venosa	VU	3	2	1	5
Turbinaria stellulata	VU	1	4	0	5
Acropora aculeus	VU	1	3	0	4
Acropora globiceps	VU	1	3	0	4
Acropora microclados	VU	1	3	0	4
Acropora polystoma	VU	1	3	0	4
Cyphastrea agassizi	VU	2	2	1	4
Heliopora coerulea	VU	2	2	0	4
Acropora palmerae	VU	1	1	1	3
Alveopora verrilliana	VU	0	3	0	3
Isopora cuneata	VU	1	2	0	3
Montipora dilatata	EN	0	3	0	3
Montipora lobulata	VU	0	2	1	3
Acropora striata	VU	1	1	0	2
Astreopora cucullata	VU	1	1	0	2
Isopora crateriformis	VU	2	0	1	2
Leptoseris yabei	VU	1	1	0	2
Millepora tuberosa	EN	2	0	1	2
Montipora calcarea	VU	1	1	1	2
Pavona cactus	VU	1	1	0	2
Pavona decussata	VU	2	0	0	2
Acanthastrea brevis	VU	0	1	0	1
Acropora donei	VU	1	0	0	1
Acropora horrida	VU	1	0	0	1
Acropora listeri	VU	1	0	0	1
Acropora rudis	EN	0	0	1	1
Acropora speciosa	VU	0	1	0	1
Alveopora allingi	VU	1	0	0	1
Barabattoia laddi	VU	0	1	0	1
Euphyllia cristata	VU	1	0	0	1
Galaxea astreata	VU	1	0	0	1
Montipora angulata	VU	0	1	0	1

Table 3: Continued.

	IUCN Red List Category	National Parks	Marine National Monuments	National Marine Sanctuaries	Total units
Montipora australiensis	VU	1	0	0	1
Pavona bipartita	VU	0	1	0	1
Pavona diffluens	VU	1	0	0	1
Porites horizontalata	VU	1	0	0	1
Porites napopora	VU	0	0	1	1
Porites nigrescens	VU	1	0	0	1
Porites pukoensis	CR	0	1	0	1
Turbinaria mesenterina	VU	1	0	0	1
Acanthastrea hemprichii	VU	0	0	0	0
Acanthastrea ishigakiensis	VU	0	0	0	0
Acropora jacquelineae	VU	0	0	0	0
Acropora pharaonis	VU	0	0	0	0
Alveopora fenestrata	VU	0	0	0	0
Euphyllia paraancora	VU	0	0	0	0
Euphyllia paradivisa	VU	0	0	0	0
Millepora foveolata	VU	0	0	0	0
Pachyseris rugosa	VU	0	0	0	0
Seriatopora aculeata	VU	0	0	0	0
Turbinaria peltata	VU	0	0	0	0

"Total units" is not strictly additive, as Tutuila hosts both a National Park and a National Marine Sanctuary.

6 Red List threatened coral species. In Hawai'i, the highest number of Red List threatened coral species (5) was recorded in the Hawaiian Islands Humpback Whale NMS.

4. Discussion

This paper summarizes information drawn from publications, reports, museum voucher specimens, monitoring program databases, and coral expert records to the extent that species occurrence could be assigned to benthic habitat within the boundaries of federally protected waters of the US Pacific. However, not all sources provide detailed geographic information; see for example, [32], and not all benthic habitat within the boundaries of federal protection has been surveyed and assessed. Consequently, the extent to which IUCN Red List threatened coral species appear to occur within Marine National Monuments, National Wildlife Refuges, National Parks, and National Marine Sanctuaries of the US Pacific is likely underestimated.

Occurrence records are also likely confounded by problems inherent to current methods of species identification and to classifying corals solely on the basis of morphological criteria. Only relatively recently has coral taxonomy reached a sufficiently comprehensive stage to enable identification of many species over wide areas; see for example, [31, 33, 47]. Corals are highly variable at all scales, and many taxonomic problems remain. A generally accepted hierarchy of data quality, from highest to lowest, is species identification based on examination of voucher specimens, primarily skeletal remains; examination of photographs of both skeletons and living corals; visual field inspection. Even identification of voucher specimens requires resources that are often not available, such as the original description and the type specimen. Nevertheless, many publications and reports are based on visual field identification which for some taxa can be challenging even for veteran experts. In this study, though *Pocillopora elegans* and *P. danae* are considered valid species [33], they can be difficult to distinguish from *P. meandrina* and *P. verrucosa*, respectively, in the field where they co-occur, and consequently their representation within federally protected waters in the current analysis may be over- or underestimated. Similarly, *Porites pukoensis*, described from Vaughan [48] and said to be restricted to a single small site off the coast of Moloka'i Island in Hawai'i [3, 49], has been reported from Kingman Reef NWR in the Pacific Remote Islands Marine National Monument (Table 4) based on visual identification by a coral taxonomist (Maragos, unpubl. data 2010). *Porites pukoensis* has also been reported from American Samoa [34, 35], Indonesia [50], Tabuaeran Atoll in the Line Islands and Kanton Atoll in the Phoenix Islands [51, 52], Madagascar [53, 54], Mauritius [54], and Reunion [53, 54], demonstrating the difficulty of validating

Table 4: Occurrence of 39 IUCN Red Listed Coral Species in US Pacific Marine National Monuments, ranked by frequency of occurrence at reef units. “1” indicates presence; empty cell indicates no record of occurrence.

TAXON	Pacific Remote Islands							Rose	Marianas			Papahānaumokuākea										
	Johnston	Howland	Baker	Jarvis	Palmyra	Kingman	Wake	Rose	Maug	Asuncion	FDP	Nihoa	Necker	FFS	Gardner	Maro	Laysan	Lisinski	P&H	Midway	Kure	No. units
Montipora patula	1				1	1						1	1	1	1	1	1	1	1	1	1	13
Psammocora stellata	1	1			1	1						1		1	1	1	1	1	1	1	1	13
Montipora flabellata	1				1	1							1	1	1	1	1	1	1	1	1	12
Pocillopora elegans	1	1	1	1	1	1	1	1	1	1	1											11
Cyphastrea ocellina	1					1						1	1	1	1	1	1	1	1	1		11
Pocillopora danae		1	1	1	1	1			1	1	1											8
Leptoseris incrustans	1			1				1						1					1	1	1	7
Montipora caliculata		1	1	1	1	1			1	1												7
Acropora verweyi			1	1	1	1			1													5
Acropora acuminata		1	1		1	1	1															5
Acropora paniculata	1				1	1		1	1													5
Acropora retusa	1	1				1		1														4
Acropora vaughani		1	1		1	1																4
Turbinaria reniformis			1		1	1		1														4
Turbinaria stellulata					1	1		1		1												4
Acropora aculeus					1	1	1															3
Acropora aspera					1	1		1														3
Acropora globiceps					1	1		1														3
Acropora microclados			1	1		1																3
Acropora polystoma		1	1		1																	3
Alveopora verrilliana					1	1		1														3
Montipora dilatata					1	1										1						3

Table 4: Continued.

TAXON	Pacific Remote Islands							Rose	Marianas			Papahānaumokuākea										
	Johnston	Howland	Baker	Jarvis	Palmyra	Kingman	Wake	Rose	Maug	Asuncion	FDP	Nihoa	Necker	FFS	Gardner	Maro	Laysan	Lisinski	P&H	Midway	Kure	No. units
Cyphastrea agassizi					1					1												2
Heliopora coerulea									1	1												2
Isopora cuneata		1			1																	2
Montipora lobulata							1	1														2
Pavona venosa						1		1														2
Acanthastrea brevis								1														1
Acropora palmerae							1															1
Acropora speciosa						1																1
Acropora striata						1																1
Astreopora cucullata								1														1
Barabattoia laddi								1														1
Leptoseris yabei								1														1
Montipora angulata								1														1
Montipora calcarea								1														1
Pavona bipartita										1												1
Pavona cactus					1																	1
Porites pukoensis						1																1
# Red List species	8	9	9	6	21	24	5	17	6	7	2	3	3	5	4	5	4	4	5	5	4	

FDP: Farallon de Pajaros; FFS: French Frigate Shoals; P&H: Pearl and Hermes.

Table 5: Occurrence of 46 IUCN Red Listed Coral Species in US Pacific National Parks and National Marine Sanctuaries, ranked by total frequency of occurrence at reef units. See Table 1 for name codes.

	National Parks								Marine Sanctuaries		
TAXON	WAPA	KAHO	PUHE	PUHO	KALA	NPSA Tutuila	NPSA Ofu	Total park units	FBNMS	HIHWNMS	Total sanctuaries
Leptoseris incrustans				1	1		1	3		1	1
Pavona venosa	1					1	1	3	1		1
Cyphastrea ocellina		1	1		1			2		1	1
Cyphastrea agassizi		1			1			2		1	1
Isopora crateriformis						1	1	2	1		1
Millepora tuberosa						1	1	2	1		1
Montipora patula		1	1	1	1			2		1	1
Montipora caliculata						1	1	2	1		1
Turbinaria reniformis							1	1	1		1
Pocillopora elegans						1		1	1		1
Pocillopora danae	1						1	2			0
Pavona decussata	1						1	2			0
Montipora flabellata					1			1		1	1
Montipora calcarea						1		1	1		1
Heliopora coerulea	1						1	2			0
Acropora verweyi						1	1	2			0
Acropora palmerae							1	1	1		1
Acropora aspera	1						1	2			0
Acropora acuminata							1	1	1		1
Turbinaria stellulata							1	1			0
Turbinaria mesenterina							1	1			0
Porites nigrescens							1	1			0
Porites napopora								0	1		1
Porites horizontalata						1		1			0
Pavona diffluens						1		1			0

Table 5: Continued.

	National Parks								Marine Sanctuaries		
TAXON	WAPA	KAHO	PUHE	PUHO	KALA	NPSA Tutuila	NPSA Ofu	Total park units	FBNMS	HIHWNMS	Total sanctuaries
Pavona cactus							1	1			0
Montipora lobulata								0	1		1
Montipora australiensis							1	1			0
Leptoseris yabei							1	1			0
Isopora cuneata							1	1			0
Galaxea astreata							1	1			0
Euphyllia cristata	1							1			0
Astreopora cucullata							1	1			0
Alveopora allingi						1		1			0
Acropora vaughani							1	1			0
Acropora striata							1	1			0
Acropora rudis								0	1		1
Acropora retusa							1	1			0
Acropora polystoma							1	1			0
Acropora paniculata							1	1			0
Acropora microclados						1		1			0
Acropora listeri						1		1			0
Acropora horrida							1	1			0
Acropora globiceps							1	1			0
Acropora donei							1	1			0
Acropora aculeus							1	1			0
# Red List species	6	3	2	2	5	12	31		12	5	

species distributions even from peer-reviewed publications as the data quality underlying the classification is frequently not stated, and samples that can be used for later verification are rarely collected. Moreover, this species is similar to another species reported from Australia (*Porites stephensoni*), and molecular analysis may be needed to determine whether these are the same or different species. *Montipora dilatata* is considered a valid species based on morphological criteria [14, 33, 48, 55] and is thought to have a restricted and disjunct distribution in the Hawaiian Archipelago [3, 13, 14, 33, 56]; however, it has also been reported from Palmyra Atoll NWR [26] and Kingman Reef NWR (Maragos unpubl. data). Moreover, examination of a suite of molecular markers (mitochondrial and nuclear) in addition to a suite of measurements on skeletal microstructure suggest that *Montipora dilatata, M. flabellata,* and *M.* cf. *turgescens* reported from Hawai‘i may be morphological variants of the same biological species [57]. However, *Montipora turgescens* at its type locality in Australia may not be the same as those identified from Hawai‘i by Veron [33], which are separated by a distance of more than 5000 km, and as a result, the latter may still be a valid species. Occurrence records in this study are based on peer-reviewed literature and the reported observations of scientists widely considered as experts in their field, and therefore, they represent the most current reliable application of coral species identification.

Of the 75 petitioned Pacific species, all but four (*Montipora dilatata, M. flabellata, M. patula,* and *Porites pukoensis)* were evaluated under IUCN Red List subcriterion A4, an observed, estimated, inferred, projected, or suspected population size reduction of ≥50% (for Endangered, EN) or 30% (for Vulnerable, VU) over two generations in the past and one into the future, where the generation length for all but 2 species was considered as 10 years [3]. Species-specific population trend data were not available for the Pacific coral species across their global distributional range, so loss of coral cover within a species distribution in combination with life history traits were used as a surrogate for population reduction. For each species, a quantitative estimate of population reduction was calculated using the coral reef area within its distributional range in conjunction with an estimate of the percent of total coral cover loss or the combined percent of total coral cover loss and critically declining reef [3]. “Total coral cover loss” was operationally defined as the percentage of reef with >90% coral cover loss over at least the past 15 to 20 years, and “critically declining reef” was operationally defined as the percentage of reefs with 50%–90% coral cover loss and likely to join the total coral cover loss category within 10 to 20 years [6]. Three species (*Montipora flabellata*, *M. patula*, and *Porites pukoensis*) were evaluated under IUCN Red List Criterion D, which can be applied to very small populations, where “population” is defined as the total number of individuals of the taxon [10]. *Porites pukoensis* was listed as Critically Endangered as the population size was estimated to number fewer than 50 mature individuals. *Montipora flabellata* and *M. patula* were listed as Vulnerable because they are endemic to Hawai‘i and the number of locations for these species was less than five, where “location” is defined as “a geographically or ecologically distinct area in which a single threatening event can rapidly affect all individuals of the taxon present”. *Montipora dilatata* was evaluated under IUCN Red List Criterion B, which can be applied to very geographically restricted populations, and was listed as Endangered as its area of occupancy was less than 500 km^2 and it existed in less than 5 locations.

While widely viewed as a useful index in estimating extinction risk, the IUCN Red List of Threatened Species carries no weight of law. In October 2009 the nongovernmental organization Center for Biological Diversity petitioned the NOAA to list 83 species of corals under the US Endangered Species Act, including the 75 Pacific species addressed in this study. The Endangered Species Act does have the weight of law. As of this publication, the NMFS is currently leading the process to independently evaluate the extinction risk of these species, and if listed as endangered species, these corals would receive legal protection. Coral reef habitat presently under federal protection harbors at least 55 of the 66 species with validated occurrence records in the US, with three reef units—Palmyra Atoll NWR, Kingman Reef NWR, and the Ofu unit of the National Park of American Samoa—each hosting more than 20 Red List threatened coral species. Protected areas already in place serve as important habitats and may be models for other areas deserving protection because they harbor species at elevated risk.

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Review Article

Clade D *Symbiodinium* in Scleractinian Corals: A "Nugget" of Hope, a Selfish Opportunist, an Ominous Sign, or All of the Above?

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Clade D *Symbiodinium* are thermally tolerant coral endosymbionts that confer resistance to elevated sea surface temperature and bleaching to the host. The union between corals and clade D is thus important to management and coral conservation. Here, we review the diversity and biogeography of clade D *Symbiodinium*, factors linked to increasing abundances of clade D, and the benefits and drawbacks of associating with clade D for corals. We identify clade D *Symbiodinium* as uncommon pandemically distributed generalists found in higher abundances on reefs exposed to challenging sea surface temperatures and local stressors or with a history of bleaching. This distribution suggests that clade D *Symbiodinium* are mostly opportunistic endosymbionts, whereby they outcompete and replace optimal symbionts in health-compromised corals. We conclude by identifying research gaps that limit our understanding of the adaptive role clade D *Symbiodinium* play in corals and discuss the utility of monitoring clade D *Symbiodinium* as indicators of habitat degradation in coral reef ecosystems.

1. Introduction

Scleractinian corals form obligate endosymbioses with unicellular photosynthetic dinoflagellates in the genus *Symbiodinium* [1, 2]. The *Symbiodinium* translocates newly fixed organic carbon to the host coral and, in return, receive inorganic waste metabolites from host respiration and an environment free from predators [3]. This mutually beneficial symbiosis contributes to the productivity of coral reef ecosystems, promotes deposition of calcium carbonate skeletons, and creates the structural framework that protects coastlines and serves as habitat for the extraordinary biodiversity found in coral reef ecosystems [4]. A consortium of bacteria, archaea, viruses, and fungi also forms close associations with corals and contributes collectively to the overall function and environmental thresholds of corals (e.g., [5–8]). These coral-microorganism communities are collectively described as the coral holobiont.

Climate change and other anthropogenic impacts have already damaged an estimated 30% of the world's coral reefs, and further declines in the integrity of coral reef ecosystems are projected for the near future [9]. A suite of often synergistic factors are contributing to the declining health of corals including global stressors such as elevated sea water temperatures and ocean acidification and local stressors like increased nutrient loading, sedimentation, and pollution [9]. The best documented and arguably most acutely damaging environmental conditions for corals are anomalously high surface seawater temperatures (SSTs) [10, 11]. Corals live close to their thermal maxima, and when ocean temperatures elevate beyond a normal range for a given region, the thermal tolerance of the coral-*Symbiodinium* symbiosis can be exceeded [12, 13]. This deleteriously impacts the functional integration of the symbiosis, and the dinoflagellates are expelled or lost from the host tissues [14]. The breakdown of the symbiosis reflects in a paling of coral tissues, the phenomenon known as coral bleaching [13]. Depending on the duration and severity of the environmental disturbance and the extent of bleaching, a coral will either be repopulated with *Symbiodinium* and return to its characteristic brown coloration or die. However, corals that survive thermal challenges show a reduction in reproductive capacity, exhibit reduced growth rates and increased susceptibility to disease [15]. The thermal challenges for corals are predicted to intensify with climate change and will be compounded by ocean acidification [16, 17]. The latter, caused by the dissolution of atmospheric carbon dioxide into seawater, has the potential to reduce or inhibit calcification completely, effects that have profound implications for corals and reef accretion. In addition to these global stressors, local stressors such as sedimentation and pollution from coastal runoff, overfishing, bacterial infection, and salinity changes all impact coral health and is contributing to the deterioration of reef integrity worldwide [18–20].

Given the serious threat that climate change and local anthropogenic impacts pose to the world's coral reefs [9], management and conservation efforts are currently focused on understanding and monitoring the responses of coral reef ecosystems to these stressors with the ultimate goal of developing action strategies aimed at mitigating their damaging effects on coral health (e.g., [21]). The monitoring clearly shows that corals exhibit variation in their responses to stress with some species, and individuals within species, being more resistant (e.g., [22]). One factor that contributes to this resistance is the genetic identity of the endosymbionts hosted by a coral. Members of the genus *Symbiodinium* show variation in physiological characteristics that contribute to the overall performance of the coral holobiont [23]. For example, *Symbiodinium* clade D is thermally tolerant and increases the resistance of corals that harbor them to elevated SSTs [24, 25]. Given this context, it is not surprising that the jurisdiction-wide NOAA Coral Reef Research Plan highlights "the potential for coral reefs to adapt to future bleaching events through changes in clades of zooxanthellae in individual species and shifts in taxonomic composition of symbiotic organisms," as a key research area with the potential to contribute to the management objective of "minimizing the effects of climate change on coral reef ecosystems" [26]. The "changes in clades of zooxanthellae" described in the plan refers specifically to the ability of corals to acquire *Symbiodinium* clade D. Here, we synthesize the literature pertaining to clade D *Symbiodinium* to provide context for this research agenda. Specifically, we organize the discussion around six key themes: (1) the diversity and distribution of clade D *Symbiodinium*; (2) coral species known to associate with clade D; (3) reef environments and abiotic factors linked with increased abundances of clade D; (4) benefits and drawbacks of harboring clade D for corals; (5) research gaps limiting our understanding of the adaptive role that clade D *Symbiodinium* play in corals; and (6) advantages of using clade D *Symbiodinium* as a tool for monitoring coral reefs.

2. The Diversity and Distribution of Clade D *Symbiodinium*

Symbiodinium diversity is generally characterized using molecular markers because there is very little morphological differentiation within the genus [27]. Given their morphological uniformity, it is perhaps surprising that genetic distances among members of the genus *Symbiodinium* are comparable to different taxonomic orders in free-living dinoflagellate groups [28, 29]. *Symbiodinium* is currently divided into 9 divergent phylogenetic clades, named A-I [30], with each containing subclade genetic sequence types distinguished using faster evolving gene markers. In order to further resolve the taxonomy of *Symbiodinium* to species, molecular markers that clearly resolve genotypes correlated to biogeography, host, environment, or physiology need to be employed and, ideally, the putative species available in culture. The latter has proven very difficult for *Symbiodinium*, and the majority of diversity remains unculturable to date. In addition, the Internal Transcribed Spacer 2 (ITS2), a molecular marker frequently used to distinguish subclade sequence types for *Symbiodinium* is multicopy and intragenomically variable, and there are two major interpretational problems that stem from these characteristics. First, more than one ITS2 sequence can be found in an individual *Symbiodinium* cell and the differences among sequence types within a cell are often greater within a cell than between different *Symbiodinium* cells. As such, the relationship between individual *Symbiodinium* cells and the ITS2 sequences is not 1 : 1 [31, 32]. Second, a particular ITS2 sequence may be dominant (or abundant) in one *Symbiodinium* cell but represent a minor (or rare) sequence type in another *Symbiodinium* cell. These two issues combine to make it difficult to quantify the number of individual *Symbiodinium* cells present in a sample based on retrieval of ITS2 sequences alone and hence impossible to accurately delineate the number of species present.

Symbiodinium clade D is considered to be a relatively rare but pandemically distributed endosymbiont of corals (Figure 1), generally representing less than 10% of the endosymbiotic community in the host population (see Section 4 for exceptions) [33]. This contrasts with *Symbiodinium* clade C, which is the dominant lineage in corals throughout the Great Barrier Reef and other Pacific coral reef ecosystems [32, 34–38] and is codominant with clade B in corals from the Atlantic [35, 39]. Consistent with their very different abundances on reefs, clade C has over 100 subclade sequence types (based on the ITS2) and clade D just 10 [33, 34, 40]. In this paper we consider all available data on clade D *Symbiodinium* and discuss these data at the level of clade rather than the individual subclade sequence types. Our rationale for this approach is twofold: first, the different genetic markers used to identify clade D *Symbiodinium* subclade sequence types provide different levels of taxonomic resolution, making it difficult to identify parallels among studies (e.g., partial large ribosomal subunit DNA [41], versus the internal transcribed spacer 1 [42], versus ITS2 [33], versus cytochrome oxidase B [43]); second, no study has yet examined whether different clade D subclade

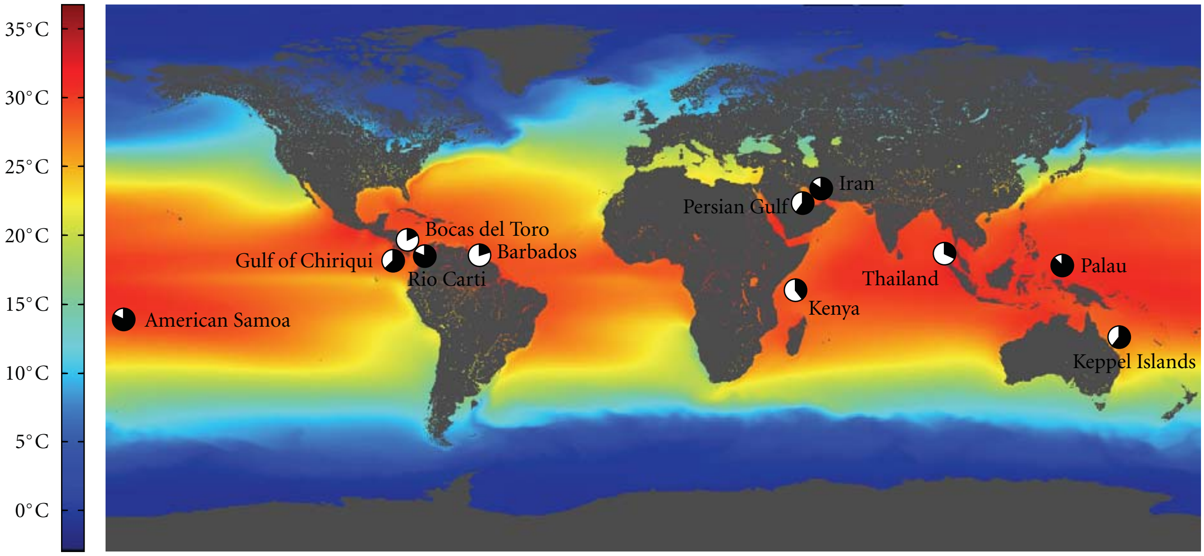

FIGURE 1: Global map showing mean sea surface temperatures between 1985–2005 from CoRTAD [47]. Black and white sections of pie charts represent the frequency of clade D and C, respectively, from the corresponding studies in Table 1.

sequence types exhibit differences in basic physiology or in their capacity to interact with coral hosts. Therefore, even though some studies have provided preliminary evidence for within clade D delineation (e.g., [33]), the ecological significance of these designated subclade D *Symbiodinium* is unknown.

3. Species of Coral Known to Associate with Clade D *Symbiodinium*

Clade D *Symbiodinium* are found in endosymbioses with a diverse range of coral species that encompass a variety of characteristics common in corals. For example, hosts include fast-growing branching coral species (e.g., *Acropora, Stylophora and Pocillopora*), slow-growing massive species (e.g., *Montastraea*), encrusting forms (e.g., *Montipora*) and solitary corals (e.g., *Fungia*) [25, 37, 41, 44–46]. Depending on the coral host, clade D *Symbiodinium* can be acquired vertically (passed from parent coral to offspring, e.g., *Pocillopora*, *Stylophora* and *Montipora*) or horizontally (acquired from the ocean environment, e.g., *Montastraea*, *Acropora* and *Fungia*). It is important to note that clade D *Symbiodinium* also associate with a taxonomically diverse group of other organisms including foraminiferans, soft coral, bivalves, and sponges [27]. Given their capacity to interact with such a broad array of hosts, Clade D *Symbiodinium* are described as generalist endosymbionts.

Although clade D *Symbiodinium* are considered relatively rare in comparison to clades B or C, they are the dominant endosymbionts in some host species, such as *Pocillopora* from the Gulf of California (Eastern Pacific), *Montipora patula* from Johnston atoll (Central Pacific), and *Oulastrea crispata* from Japan (Western Pacific) [32, 46, 48]. Interestingly, some of these hosts exclusively associate with other clades of *Symbiodinium* at different locations. For example, *Pocillopora* harbors clade C in the southern Great Barrier Reef [49, 50]. Further, the endosymbiotic communities of juvenile *Acropora tenuis* are dominated by clade D *Symbiodinium*, but the dominance hierarchy in these endosymbiont communities shifts during development to ones dominated by clade C *Symbiodinium* in adults [51]. The reason why corals show differences in the composition of their endosymbiotic communities among locations or with ontogeny of the host is not clearly understood but is attributed to some combination of local adaptation of the holobionts to abiotic conditions [27], delayed onset of symbiont specificity in juveniles [51] and, genetic radiation by both the host and *Symbiodinium* [34].

4. Reef Environments and Abiotic Factors Linked with Increased Abundances of Clade D *Symbiodinium*

Clade D *Symbiodinium* are present in higher abundances on some reefs than others, and these are often reefs exposed to relatively high levels of SSTs or local stressors such as sedimentation or reefs with a history of coral bleaching (Table 1, Figure 1). For example, clade D *Symbiodinium* are the most common endosymbionts in the Persian Gulf, where they associate with a wide range of coral genera [41, 52]. Corals in this region typically experience ocean temperatures exceeding 33°C [41], representing some of the warmest waters where corals are found in the world. This region also experiences high salinities (up to 40 ppt) and water temperatures as cool as 14°C [53, 54]. Clade D *Symbiodinium* are also more abundant in Acroporid corals from back-reef environments in American Samoa, where the SSTs reach higher maximum temperatures than the neighboring fore-reef environments, where *Acropora* primarily hosts clade C [43]. Likewise in Palau, corals in the lagoonal environment of Heliofungia Lake experience higher SSTs than the neighboring fringing and platform reefs and

Table 1: Distribution and factors associated with relatively high abundances of *Symbiodinium* clade D in corals.

Location	Host corals	Factors	References
American Samoa	*Acropora*	High Temperature	[43]
Thailand	*Fungia*	High temperature (mean, ≈29 –32°C)	[33]
	Platygyra	High turbidity (≈0.4 –0.6 mg/m^2 Chl a)	
	Symphyllia	Coastal habitat	
	Favites		
	Goniastrea		
	Pavona		
	Goniopora		
	Montipora		
	Oulastrea		
	Pocillopora		
Barbados	*Agaricia*	Bleaching	[56]
	Montastraea		
Gulf of Chiriqui	*Pocillopora*	Bleaching	[41]
Kenya	*Acropora*	Bleaching	[41]
	Astreopora		
	Pocillopora		
	Stylophora		
	Galaxea		
	Porites		
	Coeloseris		
	Pavona		
	Hydnophora		
	Echinopora		
	Favia		
	Goniastrea		
	Leptoria		
	Montastraea		
	Platygyra		
Keppel Islands	*Acropora*	Bleaching	[42]
Palau	*Hydnophora*	High temperature (mean, 28.5–31.8°C)	[45]
	Echinophyllia	Lagoonal habitat	
	Echinopora		
	Favites		
	Goniastrea		
	Montastrea		
	Fungia		
	Heliofungia		
	Merulina		
	Lobophyllia		
	Pectinia		
	Porites		
Boca del Toro	*Montastraea*	High turbidity (sedimentation)	[55]
		Coastal habitat	
Rio Carti	*Montastraea*	Coastal habitat (sedimentation)	[44]

Table 1: Continued.

Location	Host corals	Factors	References
Persian Gulf	*Acropora* *Pocillopora* *Goniopora* *Pavona* *Oxypora* *Acanthastrea* *Cyphastrea* *Favites* *Platygyra* *Turbinaria*	High temperature (summer >33°C) Bleaching (temperature >38°C)	[41]
Iran (Persian Gulf)	*Acropora* *Cyphastrea* *Favia* *Turbinaria* *Pavona* *Platygyra* *Porites* *Psammocora*	High temperature (summer, mean: 33°C, max: 33°C) Low temperature (winter, 13.2°C)	[52]

exclusively harbor clade D *Symbiodinium* [45]. Further, a diverse range of coral species host clade D *Symbiodinium* in coastal reef habitats in Thailand that experience higher levels of sedimentation, and warmer waters than offshore reefs [33]. In addition, the coral genus *Montastraea* associates with clade D *Symbiodinium* on reefs exposed to high levels of sedimentation where thermal stress is absent [44, 55]. Collectively, these data confirm that clade D *Symbiodinium* associate with a diverse range of coral species found in conditions that range from thermally challenging to polluted.

Mass coral bleaching events are often driven by higher than normal SSTs. For corals that survive the stress event, bleaching, or the loss of endosymbionts from host tissues, provides a potential opportunity for the host to modify its endosymbiotic communities by acquiring new *Symbiodinium* during recovery that are better optimized to the environment [57]. Given the range of challenging environments that clade D *Symbiodinium* are found in naturally, the repopulation of recovering bleached coral hosts with clade D *Symbiodinium* is thought to represent a survival mechanism or a “nugget of hope” for corals facing ocean warming with climate change [25]. Several studies have shown increases in the abundance of clade D *Symbiodinium* in corals following bleaching events (Table 1, Figure 1) [41, 42, 56]. For example, Baker et al. [41] showed a higher incidence of clade D in a diversity of hosts sampled from reefs with a history of bleaching. In more targeted studies aimed at understanding the timing of changes in *Symbiodinium* communities, a shift in the dominance hierarchy from clade C to D in endosymbiotic communities in *Acropora millepora* occurred within 3 months of a bleaching event [42] but leading up to bleaching as ocean temperatures increased in *Montastraea annularis* [56]. In contrast to these reports of change, a number of studies have also shown that the endosymbiotic communities of corals exposed to episodes of thermal stress remain stable and dominated by *Symbiodinium* belonging to clades other than D [58–61]. For example, clade D *Symbiodinium* have not yet been found in Fiji, a location that has had frequent thermal stress anomalies [43], and clade D is rare on offshore reefs in the Great Barrier Reef, a region where there have been a number of coral bleaching events [35, 36, 50]. The detection of clade D *Symbiodinium* in recovering bleached corals is, however, complicated by the fact that the endosymbiotic communities in these corals often revert to their original dominant *Symbiodinium* at some point during recovery (over 2-3 years postbleaching) [59]. Recent evidence suggests that these shifts in dominance hierarchy reflect changes in the relative abundance of endosymbiotic types found in the host colony (shuffling) rather than the acquisition of clade D *Symbiodinium* from the water column or sediments [25, 56]. The latter infers that only those corals that initially harbor cryptic clade D in their *Symbiodinium* community have the capacity to become dominated by them during or after a stress event. Such a scenario could help explain the patchy distribution of clade D and the inconsistencies in the literature that pertain to the composition of *Symbiodinium* in post-stressed corals (i.e., stable versus shift to clade D dominance). It is unknown what circumstances allow for the initial uptake of clade D in individual corals, but evidence points to life-stage and environmental conditions as important factors. Perhaps it takes several generations for clade D to integrate into a host endosymbiotic community, and it is an event that only occurs when stressful conditions occur at a specific point during the integration process.

5. Benefits and Drawbacks of Harboring *Symbiodinium* Clade D for Corals

The increased thermal tolerance of clade D *Symbiodinium* relative to the other *Symbiodinium* clades has understandably received a lot of attention. Rowan [24] showed that clade D *Symbiodinium* isolated from *Pocillopora damicornis* in Guam showed evidence of photoprotection at 32°C, while clade C isolated from the same host showed photoinhibition. These results provided the context to explain the thermal sensitivity and propensity of corals harboring clade C *Symbiodinium* to bleaching and the higher resistance of corals hosting clade D [41]. A shift in dominance to clade D *Symbiodinium* in *Acropora millepora* has since been shown to result in an acquired tolerance of 1–1.5°C [25].

These aforementioned studies clearly demonstrate that clade D *Symbiodinium* have a higher thermal tolerance than other clades of *Symbiodinium* and confer a higher level of resistance to thermal stress to the corals that host them. Although this is a very positive attribute, there are also drawbacks of harboring endosymbiotic communities dominated by clade D *Symbiodinium* for corals. For example, they grow more slowly than conspecifics harboring clade C *Symbiodinium* [62, 63]. Indeed, *Acropora millepora* harboring clade D grow 38% slower than colonies harboring clade C and bleaching reduces growth by 50% in this species regardless of the *Symbiodinium* clade hosted [63]. In reality, many of the circumstances where clade D *Symbiodinium* are found represent conditions that are stressful for the host and it is plausible that these conditions render the host more susceptible to invasion by opportunistic *Symbiodinium* present in the environment that exploit the host as a habitat rather than engage in an interactive and mutually beneficial partnership. In the short term, a coral may benefit from harboring clade D *Symbiodinium* allowing them to survive current bleaching conditions, but there are clearly fitness trade-offs associated with these shifts that may have major implications for the long-term growth and survival of coral reefs.

6. Research Gaps Limiting Our Understanding of the Adaptive Role That Clade D *Symbiodinium* Play in Corals

There are a number of significant gaps in our knowledge of clade D *Symbiodinium* and their interactions with corals. First, although the thermal tolerance of clade D *Symbiodinium* as a group has received a lot of attention, no information is available on the relative thermal tolerances of subclade sequence types within clade D. It is clear, however, that some subclade C *Symbiodinium* sequence types show evidence of increased thermal tolerance over others [42, 60, 64], and thus it is probable that variation also exists in clade D.

Second, our understanding of the endosymbiotic and free-living diversity and biogeography of *Symbiodinium* in general, and clade D specifically, is incomplete, with no information available from the majority of the world's reefs. A handful of studies have characterized *Symbiodinium* diversity in a wide range of marine invertebrates at a select location using a "snapshot" approach that most often distinguishes the dominant endosymbionts in corals (e.g., [32, 35–39]). More detailed analyses of corals at these locations often reveal additional *Symbiodinium* diversity and new patterns in their distribution [49]. The bulk of evidence suggests that clade D becomes more abundant in coral hosts via changes in the relative abundance of different *Symbiodinium* clades within existing endosymbiotic communities. As such, documenting the presence of clade D *Symbiodinium* as cryptic members of coral endosymbiont communities is important to predicting which corals have the innate capacity to potentially use this mechanism to survive thermal anomalies and bleaching events. Studies that have specifically addressed this issue show that there is considerable complexity in coral *Symbiodinium* communities and that clade D is often a cryptic member of endosymbiotic communities in corals [56, 65, 66].

Third, we have no information about the suite of biological and environmental characteristics that combine to initiate a shift in the dominance hierarchy to clade D. For example, no studies to date have evaluated whether corals have the ability to acquire *Symbiodinium* clade D from the environment as adults or examined the distribution and diversity of clade D *Symbiodinium* in the water column and sediments. If adult corals can acquire clade D *Symbiodinium* from the environment, this represents a mechanism to increase the pool of corals that can increase thermal resistance on the short term.

Lastly, the interactive physiology and fitness benefits/trade-offs for corals that host endosymbiotic communities dominated by clade D *Symbiodinium* are poorly understood. Only three studies focusing on a single coral genus (*Acropora*) at one location have compared the fitness of corals with endosymbiotic communities dominated by either clade C or D *Symbiodinium*, and these studies suggest that corals dominated by clade D *Symbiodinium* have reduced growth rates [23, 62, 63]. It is unknown how these changes in growth play out in terms of the long-term survival and reproductive fitness of the host colony, but understanding these trade-offs across host species and environments is critical to interpreting the overall contribution that shifts towards clade D will contribute to the long-term survival of coral reef ecosystems.

7. Advantages of Using Clade D *Symbiodinium* as a Tool for Monitoring Coral Reefs

Clade D *Symbiodinium* are useful from a management perspective because they are often found in increased abundance on coral reefs that are exposed to some combination of environmental stressors (challenging thermal regimes and/or land-based pollutants) that compromise coral health. As such, the presence of clade D *Symbiodinium* may represent a powerful biological indicator of negative changes in coral health that are driven by suboptimal conditions on reefs. Monitoring the abundance of *Symbiodinium* in corals in the field for shifts towards clade D provides valuable information on dynamic and sublethal changes in coral health states that reflect the condition of the ecosystem. The monitoring itself is relatively straightforward and cost effective and can be achieved by tagging colonies at the site to be monitored, taking small biopsies of coral tissues and surrounding ocean water on an annual or rapid response basis during/after bleaching events, and detecting *Symbiodinium* clade D using standard and quantitative PCR. Such monitoring systems can be implemented to follow corals in their environment and evaluate their responses to acute and/or chronic stressors, identify corals in populations and communities that are health compromised and susceptible to stress, and as an early indication of stress in the absence of bleaching or other visible signs of compromised health. Monitoring the occurrence of clade D *Symbiodinium* in corals, therefore, represents an additional tool that complements the current ecological methods used to monitor coral reef ecosystem health.

8. Conclusion

Clade D *Symbiodinium* are relatively uncommon pandemically distributed endosymbionts that associate with a diversity of coral and invertebrate hosts. *Symbiodinium* clade D generally occurs in higher abundance in corals from thermally challenging environments and/or reefs impacted by land-based pollution. In the short term, corals associating with clade D benefit from higher thermal tolerance and resistance to bleaching. However, corals hosting clade D exhibit lower growth rates than conspecifics harboring clade C *Symbiodinium*. In most cases, clade D *Symbiodinium* appear to be opportunistic and are found or become dominant in corals exposed to stressful abiotic conditions that negatively impact coral health. Increased abundance on reefs and/or shifts towards *Symbiodinium* communities dominated by clade D potentially represents a tool with which to monitor the health of a coral reef ecosystem with respect to changes in reef environments.

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Research Article

Small-Scale Spatial Analysis of *In Situ* Sea Temperature throughout a Single Coral Patch Reef

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Thermal stress can cause geographically widespread bleaching events, during which corals become decoupled from their symbiotic algae. Bleaching, however, also can occur on smaller, spatially patchy scales, with corals on the same reef exhibiting varying bleaching responses. Thus, to investigate fine spatial scale sea temperature variation, temperature loggers were deployed on a 4 m grid on a patch reef in Kāne'ohe Bay, Oahu, Hawai'i to monitor *in situ*, benthic temperature every 50 minutes at 85 locations for two years. Temperature variation on the reef was characterized using several summary indices related to coral thermal stress. Results show that stable, biologically significant temperature variation indeed exists at small scales and that depth, relative water flow, and substrate cover and type were not significant drivers of this variation. Instead, finer spatial and temporal scale advection processes at the benthic boundary layer are likely responsible. The implications for coral ecology and conservation are discussed.

1. Introduction

As one of the most biodiverse ecosystems in the world, coral reefs are generally limited to tropical, shallow waters and cover less than 0.1% of the Earth's surface [1]. Their restricted distribution, sessile adult stage, and narrow habitat preferences all point to corals as being vulnerable to global climate change and threatened by projected increases in sea temperature [2–4]. While corals, like many aquatic organisms, have physiological mechanisms for dealing with thermal stress [5, 6], the fact that they already inhabit waters that often are within a few degrees Celsius of their tolerance limits [7, 8] underscores the scientific and conservation urgency to understand how global climate change will affect sea temperatures and how corals will respond.

A major response to thermal stress exhibited by corals is the phenomenon known as bleaching, whereby intracellular symbiotic algae, *Symbiodinium* spp., either leave or are expelled from the coral host. For corals, bleaching has been shown to result in decreased skeletal growth and reproductive output [9], reduced resistance to disease [10–12], as well as local extirpation and shifts in community composition [13, 14]. While multiple environmental factors acting in concert result in bleaching [15], thermal stress causing protein damage and disrupting photosynthetic reactions in *Symbiodinium* spp., has been implicated as the primary stressor in recent mass bleaching events [16, 17]. It is also the most important parameter in predicting when events will occur [18]. One curiosity with regards to bleaching, however, is that it often appears as spatially patchy phenomena, such that bleached and unbleached corals of the same species can be found adjacent to one another on the same reef (Figure 1). Yet, despite observing variation among corals on the scale of a single reef, very little is known about how sea temperature may vary at the same scale. Thus, while the threat of climate change puts corals at risk on a global scale, their narrow range of environmental tolerance implies that habitat differences that exist on much smaller geographic scales may also prove to be biologically and ecologically significant. Indeed, one of the major challenges in understanding ecological processes is the quantification of physical and biological patterns at appropriate spatial scales [19].

On large geographic scales, mass bleaching episodes have been shown to correlate with anomalously high sea surface

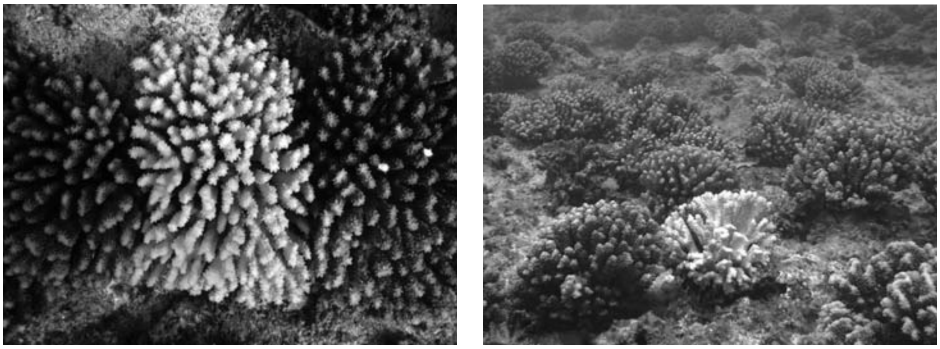

(a) (b)

Figure 1: Microspatial heterogeneity in degree of coral bleaching seen in *Pocillopora* sp. (photograph by K. Gorospe) (a) and *P. meandrina* (photograph by K. Tice) (b) on a reef at Kure Atoll, Hawai'i.

temperatures (reviewed in [20]). For example, the largest documented coral bleaching event occurred between mid-1997 and the end of 1998 and affected reefs in the Caribbean, Mediterranean, Persian Gulf, Red Sea, Indian Ocean, and throughout the Pacific Ocean. This event coincided with elevated sea temperatures caused by a strong El Niño-Southern Oscillation [7]. Such macrogeographic scale (e.g., ocean basin wide) bleaching events have captured the interests of conservation scientists because they offer possible clues as to how reefs will be affected by widespread rising sea temperatures caused by global climate change. This interest, combined with technological advances in satellite remote sensing of the marine environment [21], has driven scientific focus towards studying these ecosystems on broad geographic scales. Unfortunately, while a macrogeographic approach may be appropriate for the prediction of mass bleaching events, it may also inadvertently obscure smaller-scale ecological processes affecting individual reef organisms that are equally important.

Some attention has been turned to characterizing environmental variation among reefs and reef systems at a more regional scale [22]. This has provided insight into explaining mesoscale (i.e., 10s–100s km) patterns of coral bleaching in the field. For example, experimental evidence shows that high and intermediate water flow environments can help to increase coral resistance to bleaching, presumably by increasing diffusion rates between the coral and external environment and thus, preventing the build up of toxic free radicals [23]. Some field studies, however, point to the opposite effect, whereby low water flow may expose corals to greater thermal fluctuations, possibly allowing them to acclimatize to temperature extremes [24, 25]. Other studies have shown that the thermal history of a reef (e.g., lagoon versus fringing reefs) may produce colonies better able to cope with high temperature stress [24]. These studies of regional variability highlight some of the myriad of factors contributing to bleaching and point to the need for additional data to tease apart multiple, bleaching-related environmental factors. From a conservation standpoint, investigating bleaching on a variety of spatial scales may help to identify individual reefs that have proven to be more resistant to bleaching. Prioritizing such reefs as marine reserves could be the best, preemptive strategy for protecting reefs in the face of global climate change [26].

Identifying processes that affect individual reef organisms *within* reefs, however, requires that microspatial (i.e., on the scale of meters or centimeters) environmental variation be measured. For example, despite the observation that corals of the same species separated by just a few centimeters can exhibit variable bleaching responses (Figure 1), sea temperature variation in the context of bleaching potential has largely been ignored at this spatial scale. Furthermore, laboratory methods, from which our current models of bleaching thresholds are derived, have primarily been limited to prolonged, shock-based experiments that mimic the conditions of mass-bleaching episodes [7, 16, 17]. Rarely do these experiments take into account the temperature variability that corals are exposed to *in situ*. In addition, while numerous temperature indices have been described as good predictors of coral bleaching events [27], our understanding of temperature-sensitivity in corals has recently become more nuanced with the recognition that bleaching susceptibility may also be dependent upon the individual coral colony's past environmental experience and recent thermal history [15, 25, 28]. Thus, characterization of temperature variation as it relates to coral bleaching will require an investigation of not only spatial but temporal variation over a range of scales.

Here, we present a spatiotemporal analysis of a two-year, *in situ*, microspatial scale dataset of benthic sea temperature variation in the context of coral bleaching on a single patch reef in Kāne'ohe Bay, Oahu, Hawai'i. While some studies suggest the possible existence of microspatial environmental variability on reefs—even as a potential mechanism for explaining spatial patterns of bleaching [29]—here, we describe such variation in detail. Our goal is not to implicate microspatial sea temperature variation as the sole or even primary mechanism by which patchy bleaching may occur, but instead, to investigate whether or not biologically relevant variation in temperature exists on small spatial scales across a reef.

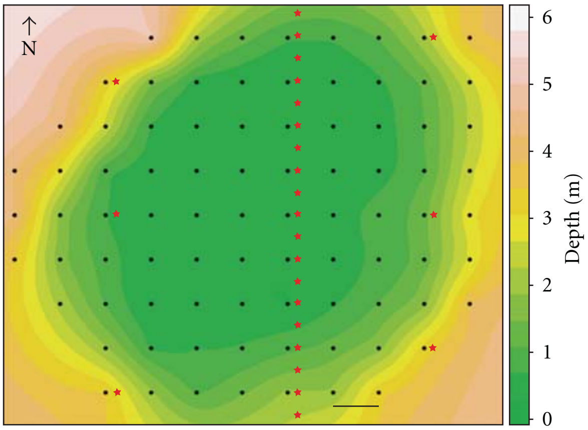


Figure 2: Ordinary kriging interpolation of depth across the reef. Small black dots are the locations of 85 temperature data loggers. Red stars are the locations of rebar placed for orientation. Scale bar in the lower right is 4 meters. Green areas are shallow, and peach ones are deep.

2. Materials and Methods

2.1. Study Site. A circular, patch reef in Kāne'ohe Bay, Oahu (21.45767°N, 157.80677°W) was selected for its accessibility (snorkeling depth between one and five meters), size (~40 m in diameter), and appropriateness to the spatial scale of interest. This reef is typical of the type of reefs found in Kāne'ohe Bay as well as at some of the atolls of Northwestern Hawaiian Islands (e.g., Pearl and Hermes). Labeled reinforcing bars were placed at 2 m intervals, running north to south down the center of the reef, as well as at several points on the reef edge to be used as orientation markers during deployment and recovery of temperature data loggers (Figure 2).

2.2. Temperature Data Collection. High-Resolution Thermochron iButton temperature and time data loggers (model DS1921H; Maxim Integrated Products, Inc., Sunnyvale, CA, USA) were used to monitor spatiotemporal temperature at the study site. The iButton has a manufacturer-specified temperature range of 15°C to 46°C, an accuracy of ±1°C, a resolution of 0.125°C, and a lifetime of seven to eight years (when used in 20°C–30°C environments and at a sampling rate of 10 minutes).

A total of 85 sites, situated 4 m apart in a grid pattern, were monitored for temperature (Figure 2). The loggers were waterproofed using liquid electrical tape and secured to the benthic substrate—rock, sand, rubble, or dead coral—using either an aluminum wire or nail. Before each deployment, all loggers were time-synchronized and programmed to begin to take temperature readings simultaneously at a user-defined time delay and sampling rate. Each logger is capable of storing 2048 temperature readings after which, data must be downloaded and cleared from memory before redeployment. Thus, loggers were collected every two to eight weeks and replaced with newly programmed loggers to ensure a virtually continuous time series. Due to the need to redeploy loggers on a regular basis throughout the study period, small gaps in the temperature time series were inevitably created. In order to minimize the duration of these time series gaps, the reef was divided into a western and eastern half, and loggers from each half were set to different redeployment schedules. As a result, time series gaps due to redeployments only lasted between one and four hours (i.e., from 1 to ~5 readings). Two other sources of time series gaps in the data resulted from (1) data saturation of the loggers occurring *in situ* before they could be replaced and (2) when individual loggers were lost or damaged during deployment.

Before their first deployment, all loggers were calibrated at room temperature for at least 24 hours by placing them in a sealed plastic container, free from air circulation. To account for any systematic logger-to-logger differences, we determined a calibration coefficient for each logger by dividing the individual logger's average calibration temperature by the global average temperature over all loggers. Field-recorded temperatures then, were adjusted by multiplying the raw temperature by the logger-specific calibration coefficient. As loggers were lost in the field, new loggers were calibrated in batches as described above on an as-needed basis. Midstudy and poststudy calibration tests also were conducted on loggers that had previously been deployed. Furthermore, each logger has an internal counter that tallies the total number of sampled points it has recorded over its lifetime. This data was used to determine if there was any significant drift in the loggers' measurements over the course of the study period.

Temperature recordings began in June 2007 for the western-half and October 2007 for the eastern-half of the reef and continued until October 2009. Initially, the sampling rate was set to 25 minutes (June 2007 to July 2008 for the western-half and October 2007 to May 2008 for the eastern-half). Subsequently, and for the remainder of the study period, the sampling interval was increased to 50 minutes to allow for longer deployments and greater flexibility in the logger redeployment schedule.

2.3. Other Environmental Variables. Depth, relative water flow, and substrate type and cover were measured for each of the 85 monitoring sites as potential explanatory variables to be used in modeling spatial variation in temperature. For the shallow portions of the reef, a metric-labeled PVC pipe and a bubble level were used to measure depth. A standard dive computer depth gauge (IQ700, Tabata Co., Ltd., Tokyo, Japan) was calibrated using a pressurized instrument test chamber with 0.25% accuracy to 90 m of sea water (no. 48310, Global Manufacturing Company, West Allis, WI, USA) and used to measure the deeper portions of the reef.

To obtain estimates of relative water flow, half-sphere casts of plaster of Paris (100 mL of water per 250 mg of calcium sulfate hemihydrate) were deployed at each temperature-monitoring site and allowed to dissolve. This "clod card" approach [30], although limited, is an elegant field method that provides time-averaged measurements of multidirectional, water flow. Clod cards were deployed on the reef for several days on each of two occasions (October 2009 and May 2010). The mass of each clod card was weighed

Table 1: Categories and abbreviations used in benthic characterization.

Category	Abbreviation
Coral	
Porites compressa	PCO
Montipora sp.	MSP
Pocillopora damicornis	PDA
other corals	OCOR
Macroalgae	
Dictyosphaeria sp.	DSP
Eucheuma sp. or *Kappaphycus* sp.	EKSP
other macroalgae	OMAC
Other substrates	
dead coral with algae	DCA
recently dead coral	RDC
rubble	RUB
sand	SAN
Miscellaneous	
other invertebrates	OINV
unknown	UNK

before and after deployment in the field, and the percent loss in mass due to dissolution, averaged between the two deployments, was used as a measure of relative water flow between sites.

Finally, characterizing benthic coverage was accomplished by taking digital photographs of 30 cm × 30 cm quadrats centered at each temperature-monitoring site. The program CPCe [31] was used to generate 90 spatially, stratified random points on each photograph and to calculate percent coverage statistics at each location. There were four major benthic cover categories: coral, macroalgae, other substrates (e.g., dead coral, rubble, or sand), and miscellaneous (Table 1). Each category was subdivided into subcategories along taxonomic lines or substrate composition (Table 1). The two miscellaneous subcategories were other invertebrates (OINV), which primarily consisted of sponges and feather duster worms (*Sabellastarte sanctijosephi*), and "unknown" (UNK) for substrates that could not be identified. A Shannon diversity index was calculated for each temperature-monitoring site.

2.4. Data Analysis. All spatiotemporal analyses of temperature variation were accomplished using the open source computer programming languages, Python (Python Software Foundation, http://www.python.org/) and R (R Development Core Team, http://www.R-project.org/). After logger calibration, the time series data for each monitoring site was smoothed by calculating the average hourly temperature. This created a more consistent dataset since the data consisted of both the initial 25- and subsequent 50-minute sampling intervals. In addition, this allowed for a simpler comparison of eastern versus western reef data loggers, which were not time-synchronized to each other due to different deployment schedules. Since temperature generally remained stable over the course of several hours (within the 0.125°C resolution of the iButton data loggers), it is unlikely that small-scale temporal variation is being lost as a result of smoothing.

Fourier transforms were used to decompose time series data into a linear combination of sinusoids each representing different frequencies present in the original signal [32]. There were a total of 15 monitoring sites that had complete time series datasets (see Results for details), thus making it possible to investigate the various periodicities of temperature variation and compare across sites. Before spectral analysis, each dataset was detrended (i.e., linear trend and mean removed) and smoothed by twice applying a modified Daniell kernel (bandwidth [L/n] = 0.000689; [32]). The resulting time series was then used to perform a Fourier Transform and create a scaled periodogram. The periodogram can be regarded as a measure of the squared correlation between the original time series data and sinusoids oscillating at all possible frequencies between 0.0 and 0.5 (for our data, frequency represents cycles per hour). The powers of the dominant frequencies as well as the 95% confidence intervals associated with each frequency were calculated. Furthermore, the same calculations described above were performed on a time series of standard deviation across all monitoring sites. Finally, to increase our resolution at low frequencies (i.e., between seasonal and diurnal periods), spectral analysis was repeated after daily averaging both the mean temperature and standard deviation across all monitoring sites.

Since the goal is to look for biologically relevant temperature variation, a series of temperature indices were developed to encompass one or more of the following temperature characteristics that have previously been implicated as potential thermal stress indicators in corals: (1) absolute temperature stress (e.g., temperature above some threshold), (2) duration at a particular temperature or cumulative stress, and (3) temperature variability or rate of change in temperature. In addition, some of the analyses performed here were modeled after techniques developed by the National Oceanic and Atmospheric Administration as part of Coral Reef Watch's satellite observation and coral bleaching monitoring program. Two products developed by them—Hotspots and Degree Heating Weeks [33]—were modified slightly in our analysis. We define relative Hot- and Coldspots as any monitoring site whose temperature is more than one standard deviation above or below, respectively, the average temperature for the entire reef at a given hour. We define relative Hot- and Coldhours for each site as any hour the temperature is one standard deviation above or below, respectively, the average temperature experienced at that particular location in the past twelve hours. Twelve hours were chosen because this was the smallest cyclical period of temperature variation indicated in the spectral analysis. Thus, relative Hot- and Coldspots are based on spatially averaged temperatures, while relative Hot- and Coldhours are based on site-specific temporally averaged temperatures. The number of times that each site was a Hot- or Coldspot or a Hot- or Coldhour was tallied and normalized by the total number of logged hours for that site. Furthermore, the dataset was truncated to exactly two years (31 October 2007 to 31 October 2009) to minimize any seasonal bias by avoiding the pre-October 2007 (i.e., summer) data.

The approach described above of summarizing temperature variation over two years effectively obscures our ability to look for temporal variation. Thus, to assess temporal variation, the Hot- and Coldspot and Hot- and Coldhour analyses were repeated for the following seasonal subsets: Winter 2007 (22 November 2007 to 13 January 2008), Summer 2008 (13 June 2008 to 13 August 2008), Winter 2008 (22 November 2008 to 13 January 2009), and Summer 2009 (13 June 2009 to 13 August 2009). Sites whose loggers were lost or broken during these seasonal data subsets were excluded from subsequent analysis and small, redeployment gaps linearly interpolated. In addition, the seasonal subsets were used in calculating average daily maximum and minimum temperatures, average daily temperature ranges, as well as overall average temperature.

Finally, the Degree Heating Hours (DHHs in units of °C-hour) were used to simultaneously characterize both the duration and intensity of heating. DHHs are calculated by tallying the number of hour equivalents the temperature at a site exceeds the maximum monthly mean (MMM) sea surface temperature of 27°C (as defined for Hawaii by Coral Reef Watch's Degree Heating Weeks Index; http://www.osdpd.noaa.gov/ml/ocean/cb/virtual_stations.html). Thus, for example, 2°C-hours are equivalent to two hours at 28°C or one hour at 29°C. The number of DHHs was summed per monitoring site for Summer 2008 and Summer 2009.

Overall, there were a total of 9 temperature indices: Hotspot, Coldspot, Hothour, and Coldhour (two-year and four seasonal subdatasets); overall, daily minimum, daily maximum, and daily range temperature averages (four seasonal subdatasets); DHHs (Summer 2008 and Summer 2009).

Ordinary kriging using gstat [34], an extension package of R, was used to create spatially interpolated maps of the various temperature summary indices and environmental predictors. Kriging is a geostatistical spatial interpolation method that models the relationship between distance and variance of sampled points to predict values at unsampled locations. Depth, water flow, and benthic coverage data were tested for correlation with each temperature summary index using Dutilleul's modified t-test. The modification corrects for spatial autocorrelation in the data by adjusting the variance of the test statistic as well as the degrees of freedom. This correction is necessary because tests of significance using an unmodified t-test are subject to inflated rates of type I error when both the response and explanatory variables are spatially autocorrelated [35].

Furthermore, in order to explain spatial variation in each temperature summary index, spatial filters were generated by performing principal coordinates of neighbor matrices analysis (PCNM, also known as spatial eigenvector mapping or SEVM) on the distance matrix of the temperature monitoring sites. The resulting eigenvectors serve as spatial descriptors of the temperature monitoring sites [36]. Finally, the eigenvector-based spatial filters that were statistically significant at a $P < .1$ level were used, along with the potential explanatory environmental variables as part of a partial regression model in determining the relative contributions of pure environmental, pure spatial, and shared (i.e., environmental and spatial) variation in explaining temperature variation on the reef. Incorporating location as an explanatory variable in the partial regression model also reduces or eliminates spatial autocorrelation among the residuals, thus minimizing type I error rates. For each of the temperature summary indices, five models were tested: (1) a regression of the temperature summary index on depth, (2) temperature on location, (3) temperature on depth and location, (4) temperature on depth and substrate, and (5) temperature on depth, location, and substrate. Models were chosen based on minimizing Akaike's Information Criterion. Both the principal coordinates and the partial regression analyses were performed in the computer program, Spatial Analysis in Macroecology (SAM, ver. 3.1; [37]).

3. Results

3.1. Calibration Data. Over the course of the study period, a total of 201 loggers, or approximately 16.5% of the data, were lost in the field. For any given location on the reef, the percent of missing data (not including saturation or redeployment gaps) ranged from 0.3% to 49.1%. Fifteen of the sites, however, had only 0.3% missing data entirely due to the unavoidable gaps during redeployment and are considered to be complete data sets.

Calibration tests revealed that among logger variation in recorded temperatures ranged from 0.79 to 1.35°C ($\overline{x}$ = 0.80°C) and calibration coefficients ranged from 0.97868 to 1.01991 ($\overline{x} = 1.00004$). Comparing pre-, mid-, and poststudy calibration tests showed that the mean change in calibration coefficients across 171 possible comparisons was 0.00021, indicating that loggers did not show significant drift in their calibration coefficients. A linear regression, however, indicated a small but significant relationship between the magnitude of the change in calibration coefficient (i.e., with no regard to the direction of change) and the number of sampled points between calibration tests ($r^2 = 0.03$; $P < .05$). The amount of change, however, is negligible with a regression slope of 2.666×10^{-8}. Thus, the maximum possible calibration drift a logger could have experienced (i.e., 10 data-saturated deployments with 2048 sampled points per deployment) would be 0.00287. To put this into perspective, using the maximum observed calibration coefficient of 1.01991, the difference in pre- and postdrift calibration of a 25°C raw data point would only be 0.07°C. Therefore, we think that drift can be safely ignored.

3.2. Spectral Analysis. Figure 3 shows the temperature time series, averaged daily and across all monitoring sites, with shaded bars indicating the various data subsets used in creating the temperature summary indices described above. Figure 4 shows a representative scaled periodogram for the hourly averaged temperature time series at a single monitoring site. The periodograms point to five dominant frequencies corresponding to both solar- and lunar-driven

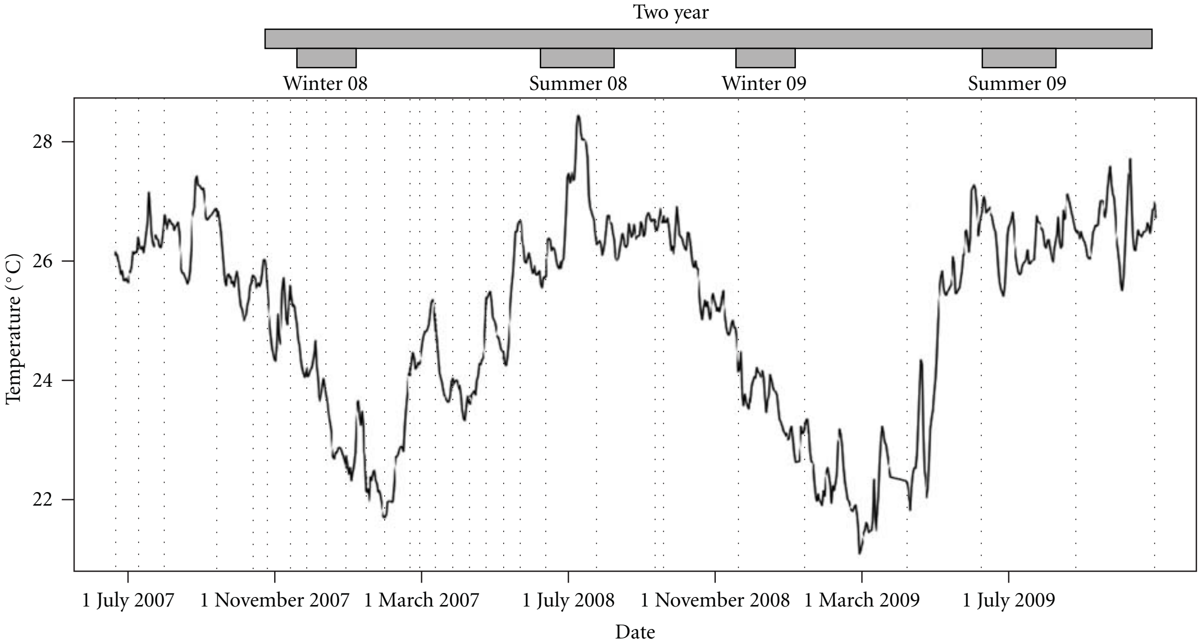


Figure 3: Temperature graph for the entire temperature data set (June 2007 to October 2008). Dashed vertical lines indicate deployment days when temperature data loggers in the field were collected and replaced. Bars above graph indicate the two-year and seasonal subsets that were used in the analyses.

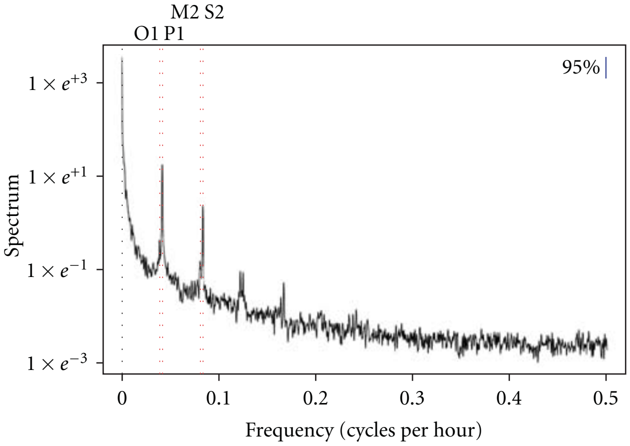
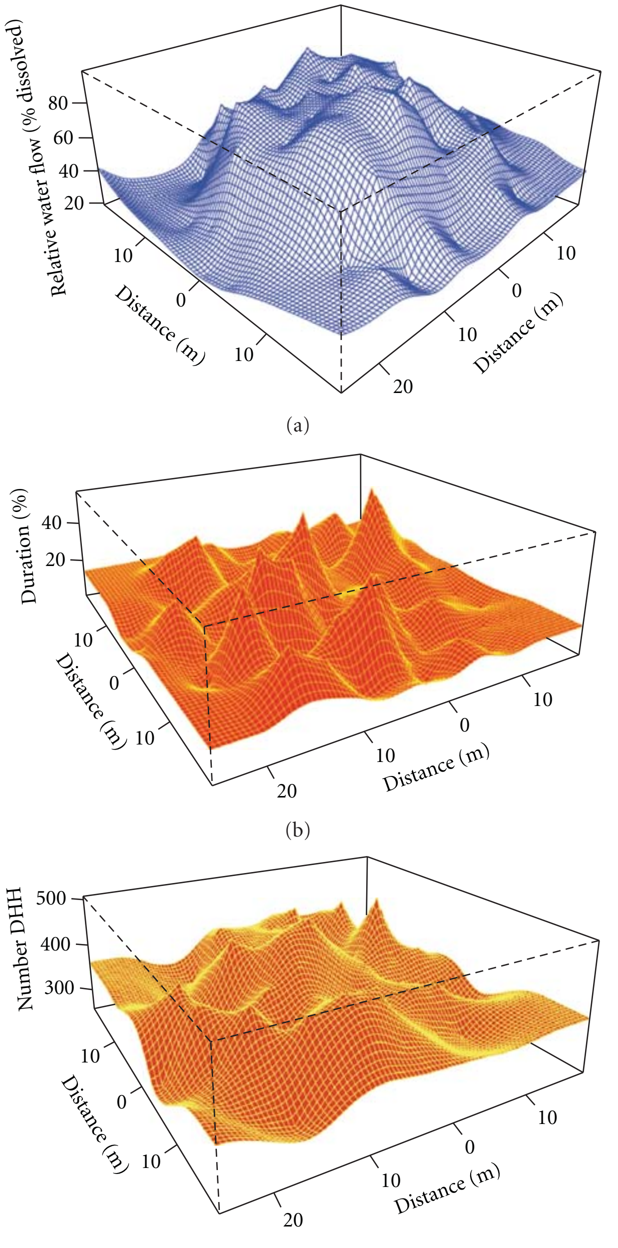


Figure 4: Fourier transform scaled periodogram of two years of temperature data at one monitoring site. Principal frequencies are marked with vertical, dashed lines and correspond to (from left to right) seasonal (365 days), lunar (O1, 25.82 hours), solar (P1, 24 hours), lunar semidiurnal (M2, 12.42 hours), and solar semidiurnal (S2, 12 hours). Other peaks between 0.1 and 0.2 cycles per hour are likely echoes of O1 and P1. Scale bar in the upper right corner is the 95% confidence limit.

periodicities: seasonal (365 days), principal lunar diurnal or O1 (24.83 hours), principal solar diurnal or P1 (24 hours), principal lunar semidiurnal or M2 (12.42 hours), and principal solar semidiurnal or S2 (12 hours). Peaks at eight- and six-hour periods (between 0.1 and 0.2 cycles per hour) most likely are harmonics of the principal lunar (O1) and solar diurnal (P1) components. Most notable, an expected ~28 day lunar monthly periodicity (between the seasonal and O1 peaks) is not present. Repeating the spectral analysis for the daily averaged temperature across all monitoring sites revealed no additional periodicities. Furthermore, comparing the periodograms for each of the 15 monitoring sites with complete time series datasets revealed that the relative distribution of power over the major driving periodicities was the same across the reef (seasonal signal ≫ P1 ≫ S2 > O1 > M2). Finally, the scaled periodogram for the hourly standard deviation time series revealed the same five periodicities as well as an additional periodicity at 2.5 hours (frequency = 0.4 cycles per hour; see Figure 1S in Supplementary Material available on line at doi:10.1155/2011/719580.) Smoothing by calculating daily averages, as above, failed to reveal additional periodicities.

3.3. Modeling Spatial Variation. Ordinary kriging interpolation of depth (Figure 2) shows a smooth transition from the center, shallow areas of the reef to the outer, deeper areas and, as such, can be regarded as a representation of the reef's bathymetry. The map of water flow shows broad similarities with depth such that high and low relative flows correspond to shallow and deep sites, respectively (Figure 5(a)). In fact, depth also correlated with many of the substrate variables (discussed below). On the other hand, maps for the various temperature summary indices ranged from being visually consistent with depth, such as the proportion of time spent as a Coldhour and Winter 2008 range in daily temperature (Figures 2AS and 2BS, resp.), to being strikingly patchy as is seen for the proportion of time spent as a relative Hotspot and Summer 2008 DHHs (Figures 5(b) and 5(c), resp.).

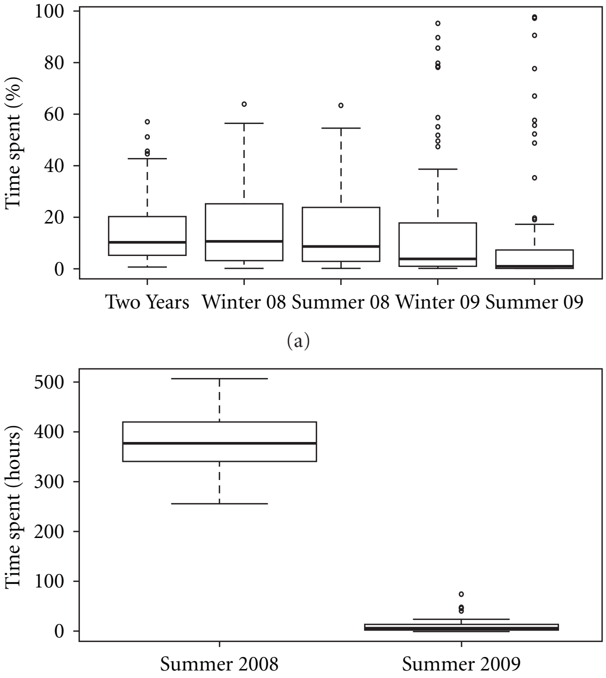


(a)

(b)

(c)

Figure 5: Ordinary kriging interpolation of water flow (a), percent of time spent as a relative Hotspot over two years (b), and number of Degree Heating Hours for Summer 2008 (c).



(a)

(b)

Figure 6: Tukey boxplots of the seasonal and annual variation in the proportion of time spent as a relative Hotspot (a) and total Degree Heating Hours for Summer 2008 and 2009 (b). The rectangle represents the interquartile range (i.e., the 25th percentile, median, and 75th percentile), the "whiskers" represent all values that are within 1.5 times the interquartile range, and the open circles represent outliers, defined as data points that lie outside the whiskers. Paired Welch's t-tests were used to test for statistically significant temperature differences between seasonal subdatasets. One-tailed tests were used for comparing winter versus summer or two-year versus summer or winter datasets. Two-tailed tests were used for comparing winter versus winter or summer versus summer datasets.

Tukey boxplots of the temperature summary indices reveal considerable microspatial temperature variation on the patch reef. For example, sites ranged from spending 0% to nearly 60% of the two years of temperature monitoring as a relative Hotspot (Figure 6(a)). In addition to the expected temporal variation seen in average daily minimum and maximum temperatures (Figure 3S), the boxplots also indicate seasonal and annual variation with regards to Hothours and Coldhours (Figure 4S), with a greater proportion of time being spent as a Hothour or Coldhour in the summer as opposed to the winter months (Figures 4S). Finally, Summer 2008 resulted in a considerably larger number of DHHs as compared to Summer 2009 (Figure 6(b)).

Spatial correlation analyses of substrate type using Dutilleul's modified t-test revealed that depth was significantly correlated ($P < .1$) with PCO, EKSP, RUB, SAN, and OINV (Table 1S). In addition, depth correlated with all coral (all subcategories combined) and all macroalgae (all subcategories combined). Variables that correlated significantly with depth were excluded from the PCNM and partial regression analyses to avoid colinearity among variables. The results of the partial regression analyses—reported as the percent of variation explained by location, environment (i.e., depth and/or substrate), and shared environment and location—can be found in Table 2S. For each temperature summary index, only the best model (i.e., the one with the lowest AIC value) is reported. Thus, if a standard linear regression model (i.e., models with no shared component) fits better than a partial regression model (i.e., models that include a shared environmental and location component), then only the standard linear regression model is reported. Among the competing models, location, as described by the PCNM-generated eigenvector filters, was a component of the best model in 35 out of the 38 temperature index regressions and was the dominant (i.e., greatest explanatory power) component in 25 (Table 2S). The percent of temperature variation explained by purely spatial factors ranged from 4.6% to 48.9% (Table 2S). On the other hand, environmental variables (i.e., depth, substrate, etc.) were included in the model for 22 regressions (Table 2S). Compared with location, environmental variables had a much greater range in explanatory power (from 2.3% to 75.5%) when comparing across temperature datasets, but was a dominant component only five times (Table 2S). Finally, while depth was always included among the 22 regressions with environmental variables, AIC-based model comparisons only included substrate as part of the best model for two temperature summaries: DHHs and average daily temperature range for Summer 2009.

4. Discussion

4.1. Temperature Variation in Time and Space. It is often stated that the environment is neither perfectly regular nor entirely random and that spatial patterns are, therefore, a common characteristic of the natural world [38]. Visual inspection of our spatially interpolated maps of water flow, depth, and by extension, most substrate variables, which correlated significantly with depth, reveal that our choice of environmental variables cannot by themselves account for our observed variation in temperature across the reef. Furthermore, results from the regression analyses indicate that location was the most ubiquitous statistically significant explanatory variable and, when compared to the environmental variables, was more commonly found to be the dominant component. Thus, location was the most important explanatory variable in accounting for temperature variation at the spatial scale of this study. To many, our finding that location was a significant predictor of observed temperature will not be surprising. What is unexpected, however, is how the explanatory power of location compared with that of the other environmental variables were tested. Depth, water flow, and substrate were chosen specifically because they incorporate one or several processes and characteristics that should affect benthic sea temperature (i.e., advection, insolation, light absorption and reflection of the substrate, etc.). Yet, most of the temperature summary indices were not significantly predicted by these environmental explanatory variables or, when they were included in the model, were only a small fraction. In other words, these results indicate that at microspatial scales, two locations as little as 4 m apart on a reef may have similar depth, water flow, and substrate coverage and yet still exhibit different temperature profiles. Conversely, two locations that differ with respect to depth, water flow, and substrate coverage may in fact have very similar temperature profiles. Thus, while temperature variation at large spatial scales might be explained by certain intuitive environmental variables, the importance of these variables at much smaller spatial scales is diminished and in fact eclipsed by microspatial considerations.

It is important to note, however, that even though the calibrations applied were small (i.e., no more than 0.07°C), calibration can only correct any systematic bias present. The reported accuracy of the loggers is ±1.0°C, and it is possible that some of the among site temperature differences that were found were due to poor logger accuracy. We doubt, however, that this is a major factor because all sites had at least two different loggers due to alternating deployments and logger loss. It is also difficult to imagine a stochastic process favoring specific sites and asymmetrically erring either too high or too low for long periods of time (e.g., up to 60% of the two-year recording period for the relative Hotspot analysis). The absolute temperature also is unimportant to many of our temperature indices because they are relative measures. If spatially patchy temperature variation were being caused by stochastic, among logger inaccuracies, we would expect all of our temperature indices to be affected equally by this. Each temperature index, however, exhibited distinct overall spatial patterns, with some indices (e.g., Coldhour and Winter 2008 range in daily temperature; Figures 2AS and 2BS, resp.) even exhibited nonpatchy patterns.

Although we present data from only a single reef, we have no reason to suspect that our findings are particular to this reef. Overall diversity and coral cover vary from reef to reef in Kāne'ohe Bay (as elsewhere), but the monitored reef is typical of what is found in the bay and at some of the atolls in the Northwestern Hawaiian Islands. It is located in the center of the bay and does not appear to be uniquely influenced by external inputs (e.g., river outflow, oceanic currents, etc.). Even so, further testing on other reefs is necessary to indicate how universal our results are.

Interpreting location as an explanatory variable can be abstract. Environmental variables themselves have an inherent spatial structure, which is why in a partial regression analysis, there is a distinction made between pure environment, pure location, and shared environment and location components. In other words, the pure location component is separate from the common spatial structure that is shared by the environment and response variable (i.e., the shared environment and location component). This does not exclude the possibility, however, that the pure location component in our analysis is comprised of other environmental features that were not captured by our choice of explanatory variables [36]. It is also possible that our choice of environmental variables is sound, but that the spatiotemporal scale at which they were measured was too large, and thus, limited their explanatory power. This is most likely to be true for our measurement of water flow, since relative depth and substrate cover measurements are less likely to significantly change at finer spatiotemporal scales. That location helps to explain sea temperature variation at a microspatial scale simply means that locations that are close together in space have more similar temperature characteristics than points farther apart. Thus, the most parsimonious explanation here is that location, in this study, likely refers to microscale water flow processes that were not captured by the clod card measurements.

Relative water flow was negatively correlated with depth (high flow in the shallow portions of the reef and low flow in the deeper portions)—a pattern that is consistent with the decay of oscillatory wave-driven flow with increasing depth. Water flow in the benthic boundary layer, or the layer of water at which flow is influenced by reef structure [39], can be very different from wave- or tide-driven flow seen in the water column in terms of direction and magnitude as well as net transport, and these microscale differences can be lost as a result of time-averaging [40, 41]. Thus, finer-scale processes (spatial or temporal) not captured by our clod card measurements should not be excluded as a driver of temperature variation at this scale. For example, water flow velocity influences the thickness of the coral thermal boundary layer, which in turn influences the rate of heat transfer between the substrate and the surrounding water [42]. Coral pigmentation can also affect temperature such that darker-pigmented corals experience greater temperatures, but the effect is mediated by differences in water flow [43]. Furthermore, temporally stable temperature variation, such as that observed in this study, points to the possible influence of reef bathymetry in channeling warm or cold water across a reef (e.g., from internal waves) [44]. Finally, small-scale temperature heterogeneity may be influenced by the movement of water into and through the interstitial structure of whole reefs, as evidenced by dye transport experiments (Koehl, Cooper, and Hadfield, unpublished data). All of these studies suggest that fine-scale water flow heterogeneity could be a potential driver of fine-scale temperature heterogeneity. That our observed temperature differences could not be explained by wave-driven water flow as measured by clod cards highlights the need for future research to focus on even finer spatial and temporal scale flow patterns across reefs in explaining microspatial temperature variation at the benthos.

The results of spectral analysis also lend insight into the temporal scale of the processes that are driving temperature variation. Scaled periodograms of the 15 monitoring sites with complete time series datasets reveal the same power distribution pattern across the same lunar- and solar-associated periodicities. This suggests that large temporal scale processes such as tides are not causing the observed temperature difference among sites. Interestingly, in addition to the lunar- and solar-associated signals, the periodogram for the time series of standard deviation of temperature data revealed a high frequency peak at 0.4 cycles per hour corresponding to 2.5-hour periodicity. Unfortunately, it is beyond the scope of this study to identify the specific processes involved, but other studies have pointed to high-frequency internal waves and internal tides as being potential drivers of high-frequency, subsurface temperature variation [44, 45].

If depth, relative water flow, and substrate composition are not significant predictors of temperature variation within a single coral reef, then what is? Our results suggest that benthic temperature differences on microspatial scales are likely due to finer spatial and temporal scale advection processes. Specifically, these advection processes are on a spatial scale finer than oscillatory wave-driven flow and a temporal scale finer than tide-associated frequencies. Furthermore, our finding that biologically significant, benthic temperature variation exists on a microspatial scale demonstrates the need for future research to further explore the physical drivers of this variation as well as its ecological significance for benthic organisms.

4.2. Implications for Corals. Since the 1970s, research on coral reef ecosystems has been shifting from small-scale research focused on ecological processes (e.g., competition and herbivory) to large-scale conservation and management driven research. This expansion in spatial scale was also accompanied by a paradigm shift, from one that viewed coral reefs as stable ecosystems to one that began to emphasize the vulnerability and decline of coral reefs due to a host of environmental stressors [46]. As our understanding of coral reefs progresses, it is important to acknowledge the rapid pace of these shifts and consider the possibility that coral reef scientists may have been pushed to scale up prematurely, obscuring the importance of ecological processes that may be occurring more locally and creating a knowledge gap in our understanding of these threatened ecosystems. It should be acknowledged, however, that high-density studies at much smaller geographical scales may involve a considerable amount of effort and expense and in some cases prohibitively so. It also is important to note that reliable, accurate data loggers for other important and interesting parameters (salinity, current, irradiance, etc.), which are necessary for this type of study, often do not exist. Even so, it is clear from this study that even reasonable outputs of money and effort can result in interesting and unexpected findings and deepen our understanding of coral reefs.

Our study demonstrated the existence of microscale temperature heterogeneity on a single patch reef based on temperature summary indices that were developed specifically to investigate different aspects (e.g., absolute temperature, duration of temperature, and temperature variability) of coral thermal stress. But what relevance do microscale studies have in helping conservationists to better understand coral biology? For example, remotely sensed sea surface temperature (SST) data have been crucial to providing the first evidence of thermal stress as a primary environmental driver of bleaching. Even so, satellite-derived SST data are spatially and temporally averaged and are based on the reflective properties of just the top few mm of the water column. They therefore do not reflect thermal stress levels experienced by individual coral colonies [47]. We suspect that the finer scale processes occurring at the boundary layer are important.

As mentioned above, our current understanding of coral bleaching thresholds are based on either correlations between macrogeographic bleaching episodes and SST data or on laboratory-based experiments that ignore the actual temperature variability experienced by corals *in situ*. The former hides finer-scale variability that may be important for refining our bleaching models, while the latter suffers from temporal isolation that may obscure the importance of long-term acclimatization of corals to environmental conditions.

In both cases, *in situ* temperature data at the scale of the individual colony can provide the environmental context for interpreting results and gaining a more comprehensive understanding of the spatial heterogeneity seen in bleaching patterns and thresholds of thermal stress for coral.

A full understanding of the spatial patterns of bleaching is further obscured by the biological complexity of the coral holobiont (a term used to describe the coral animal host, intracellular *Symbiodinium* spp., as well as associated bacterial and viral communities). For example, it is now well known that the genus *Symbiodinium* spp. is composed of several evolutionarily distinct clades and that these different clades have distinctive physiological tolerances and ecological roles [48, 49]. The patchy distribution and zonation of *Symbiodinium* spp. have been implicated as a possible explanation for patchy bleaching [50, 51]. Some evidence also points to the possibility that symbiont communities can be reshuffled after recovering from bleaching events to include more heat-tolerant clades [52, 53]. Other studies, however, report stable algal symbiont communities before and after bleaching episodes [54] or after transplant experiments [55]. Some evidence has pointed to *Symbiodinium* spp. clade D to be heat tolerant (reviewed in [48]), but as with our understanding of coral bleaching patterns, this conclusion is based on data following severe bleaching episodes. Uncovering finer-scale differences in the physiological roles and tolerances of the remaining *Symbiodinium* spp. clades may require a consideration of more finer temporal and spatial scale environmental differences. Nevertheless, what is clear is that there are other sources of small spatial scale or even individual-level variation on a reef. This study allows us to conclude that temperature variation can exist on the scale of meters and that this environmental heterogeneity is yet another source of individual-level variation that could explain why bleaching is patchy. Our finding that a significant amount of temperature variation was not explained by depth also is consistent with the fact that patchy bleaching is not generally described as a depth-associated phenomenon.

It is possible that temperature is acting as an organizing force at small spatial scales, influencing the distribution of individuals and species within a single reef. Thus, while climate change is a global-scale phenomenon, the appropriate spatial scale at which coral reefs should be managed to cope with this threat remains an open question and underscores the need for coral studies to proceed at multiple scales. As genetic or species diversity is thought to lend stability and resilience to communities [56], habitat heterogeneity may likewise structure reefs in ways that increase their ability to respond to climate change. In such a scenario, reefs that offer more intrareef microhabitat heterogeneity may also harbor heterogeneous communities acclimated to a range of environmental conditions and might therefore be prioritized as marine reserves. Microspatial scale environmental heterogeneity is information that probably should be incorporated into evolving coral reef management strategies. Our study demonstrates that while corals continue to be threatened on a global scale, integrating across multiple spatial scales is essential to understanding the ecological processes relevant to their survival.

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Review Article

"Coral Dominance": A Dangerous Ecosystem Misnomer?

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Over 100 years ago, before threats such as global climate change and ocean acidification were issues engrossing marine scientists, numerous tropical reef biologists began expressing concern that too much emphasis was being placed on coral dominance in reef systems. These researchers believed that the scientific community was beginning to lose sight of the overall mix of calcifying organisms necessary for the healthy function of reef ecosystems and demonstrated that some reefs were naturally coral dominated with corals being the main organisms responsible for reef accretion, yet other healthy reef ecosystems were found to rely almost entirely on calcified algae and foraminifera for calcium carbonate accumulation. Despite these historical cautionary messages, many agencies today have inherited a coral-centric approach to reef management, likely to the detriment of reef ecosystems worldwide. For example, recent research has shown that crustose coralline algae, a group of plants essential for building and cementing reef systems, are in greater danger of exhibiting decreased calcification rates and increased solubility than corals in warmer and more acidic ocean environments. A shift from coral-centric views to broader ecosystem views is imperative in order to protect endangered reef systems worldwide.

1. Introduction

Around the globe, tropical to subtropical reef ecosystems are at risk. Environmental threats in the form of pollution, overfishing, alien species, global warming, and ocean acidification have led to the documented decline of coral communities in numerous marine ecosystems [1–9] and allowed macroalgal overgrowth to result in potentially nonreversible phase shifts in many locations [5, 10–14]. Management efforts will hopefully help to preserve and protect the imperiled ecosystems in which corals live; however, scientific terminology may be thwarting responsible conservation efforts by creating false representations of tropical to subtropical reefs in the minds of the general public and governmental management agencies. Many reef systems contain areas composed primarily of coral, but these areas are interspersed among other types of ecologically necessary, hard-bottomed, carbonate-accreting, reef areas that contain little to no coral. Recognition of the essential role these noncoral-dominated reef areas play to the overall health status and accretion of reef ecosystems will help to ensure that effective reef management measures are accomplished.

2. What Constitutes a Healthy Reef?

Reef researchers from past decades described many healthy tropical to subtropical reef systems as containing a higher percentage of noncoral calcifying organisms than scleractinian corals [15–18]. As noted almost a century ago by scientists studying algal communities in tropical reef settings, the term "coral reef" itself fosters a false perception of many tropical to subtropical marine communities [17, 18]. This misnomer promotes one type of calcifying reef organism over numerous others that are also essential for healthy reef ecosystem function and growth. Researchers from the late 1800s and early 1900s tried to steer public and management agency views away from a coral-centric perception in order to force researchers to recognize that many reefs naturally exhibit low coral cover, and reef accretion occurs primarily from layers of calcified algal deposits and foraminifera [15–19]. More recently, some researchers have attempted to reinforce this historic concept by promoting terms such as "coralgal" or "tropical (or subtropical)" reef systems instead of "coral" reef systems [20–23]. Fortunately, these efforts have been successful among tropical marine scientists, who recognize the diversity of calcifying organisms necessary for healthy reef growth. An increasing number of management agencies and conservation programs are also broadening their scope and shifting from coral-centric research [24, 25] to ecosystem-based research that encompasses a varied mixture of calcifying organisms. In order for effective reef conservation efforts to progress in a meaningful way, continued recognition of the diversity of noncoral calcifying organisms that occur in healthy reef ecosystems, coupled with the recognition that many tropical marine ecosystems naturally contain vast areas of low coral cover, should be recognized.

Currently, no consensus exists among biologists on the best way to define a healthy tropical to subtropical, hard-bottomed, reef system. However, all researchers would likely agree that high biodiversity, high fish biomass, intact apex predator communities, low incidences of disease, and the ability to accrete calcium carbonate faster than erosion occurs are among key factors in defining health [23, 26–30]. During the past few decades, high coral cover (coral dominance) was also sometimes intrinsically equated with high reef health [30–33]; however, while high coral cover is a sign of high reef health in some cases, this paradigm does not hold true for many healthy reef ecosystems. As the title of this paper suggests, a danger exists in promoting healthy reefs as being those dominated by coral because other calcifying biological organisms, such as crustose coralline red algae, calcified macroalgae, and foraminifera, that are also critical for reef accretion and maintenance may get overlooked. Understanding the long-term effects of increased ocean acidity and temperature on noncoral calcifying organisms is just as important as understanding the long-term effects on coral for the survival of reef systems overall.

3. What Is Meant by Coral Dominance?

Why is there such a widespread belief (especially among nongovernmental organizations, the general public, and, subsequently, grass root conservation efforts) that: (1) high coral cover is necessary for reef accretion, (2) high coral cover indicates a healthy reef ecosystem, and (3) algae (particularly macroalgae) are detrimental to tropical reef environments? Some of these misconceptions may stem from the fact that early marine ecology programs historically were constituted with a diversity of botanists as well as zoologists [19, 34–36], but it is rare for current reef or marine ecology programs to include a diversity of (or even one) marine botanists. For example, despite the diversity of evolutionary groups represented by algae and foraminifera, as well as the concern over ecological impacts of algae to reef systems, only 3% of publications from the 11th International Coral Reef Symposium in 2008 focused on algae (40% dealt with coral, 12% with fish, and 7% with noncoral invertebrates) [37]. If coral biologists form the largest component of benthic monitoring programs, it is not surprising that an unintentional bias in sampling towards coral-dominated tropical ecosystems has occurred. Coral biologists usually do not visit hard-bottomed reef areas that do not contain coral. However, this has likely led to underrepresentation of hard-bottomed communities that naturally contain expansive stretches of algal-dominated environments in past scientific studies.

In order to create an understanding amongst scientists and reef managers, the scientific community must better define what is meant by "coral dominance" and how it relates to healthy reef ecosystems. How much coral exists in a "coral-dominated" environment [12]? Is coral dominance: (1) a state where corals cover more than 50% of the substrate, (2) a state where, out of the numerous organisms that occur in reef settings, corals occupy a greater percent of the substrate than any other type of organism (even though the actual percent cover of coral may be low), or finally (3) a state where corals occupy a greater amount of substrate than only a select group of organisms (e.g., macroalgae)? When hard-bottomed reef tracts are considered as a whole, very few of even the healthiest Pacific island reefs exhibit an average percent cover of corals over 50% (Figures 1 and 2) [22, 23]. Therefore, defining a coral-dominated reef system as one that naturally contains vast expanses where corals exceed 50% cover does not make sense for most Pacific island reef ecosystems. In fact, in the least impacted Pacific ecosystems monitored by the National Oceanic and Atmospheric Administration, Pacific Islands Fisheries Science Center's Coral Reef Ecosystem Division (CRED), the vast majority exhibit average island-wide percent cover of calcified red algae ranging from 1% to 42% and scleractinian corals ranging from 2% to 40% (Figure 2) [39]. Even when fleshy noncalcified macroalgae are considered, they often occupy a greater amount of substrate than hard corals at a majority of sites in some of the healthiest reef ecosystems in the Pacific (Figure 2) [22, 23, 40], and despite recent negative perceptions of the role of macroalgae in reef systems [5, 10–14], comparing ratios of these two functional groups often cannot be used to define the health status of the reef.

4. Why Should We Care about Algae on Reef Systems?

Clearly, constructional coral species have been important to the buildup of many reef systems for millennia on a global scale [41–47], and efforts to conserve extant areas of high coral cover are essential. However, the scientific community must create a better conduit to reef managers to promote the fact that not all reef systems are the same. While some healthy reefs are dominated by constructional coral species [41–45], others contain almost no coral (sometimes termed incipient reefs) [17, 19, 47, 48], and others rely on a mix of calcified algae, foraminifera, and coral [17, 20, 21]. As M. A. Howe states in a 1912 *Science* magazine article:

> "From what may be observed to-day in the tropics as to the relative dominance of calcareous marine plants and calcareous marine animals and from what has been determined by the study of cores obtained by boring into coral reefs, it would appear that sometimes the plants predominate and sometimes the animals."

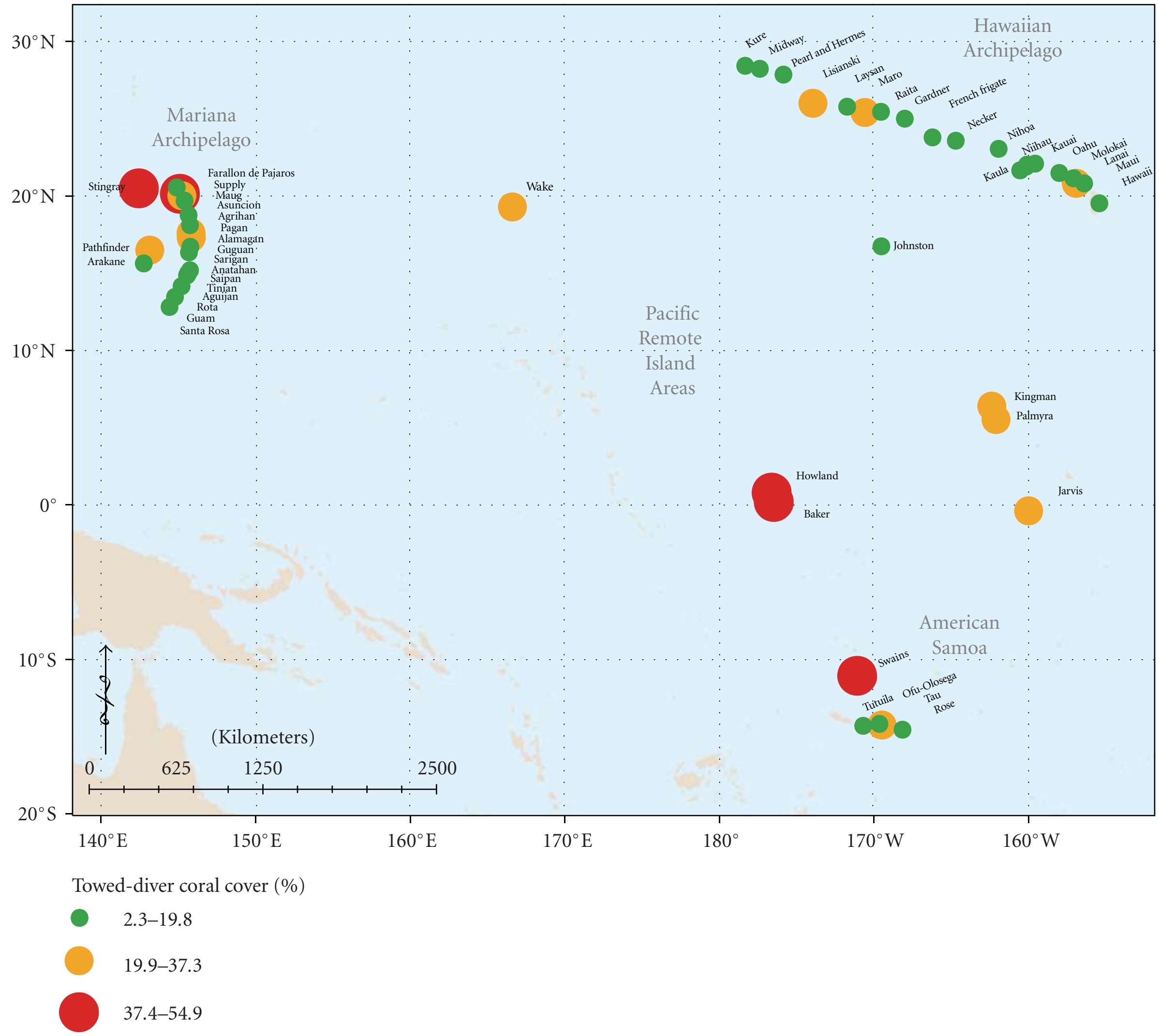
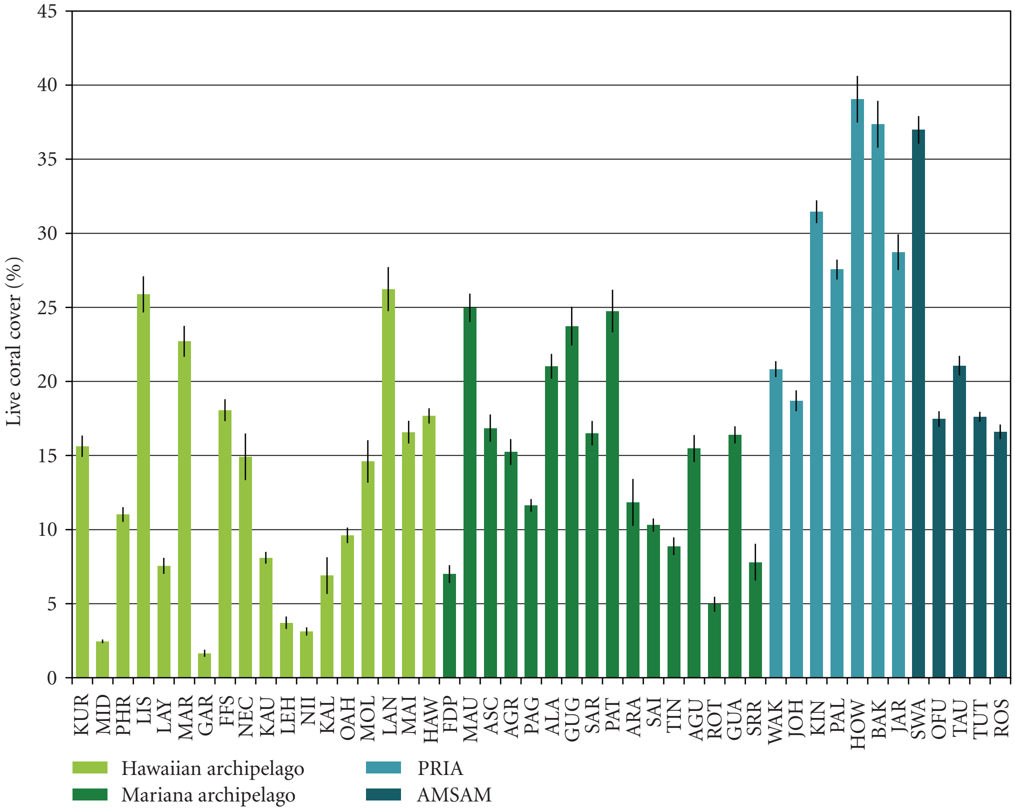


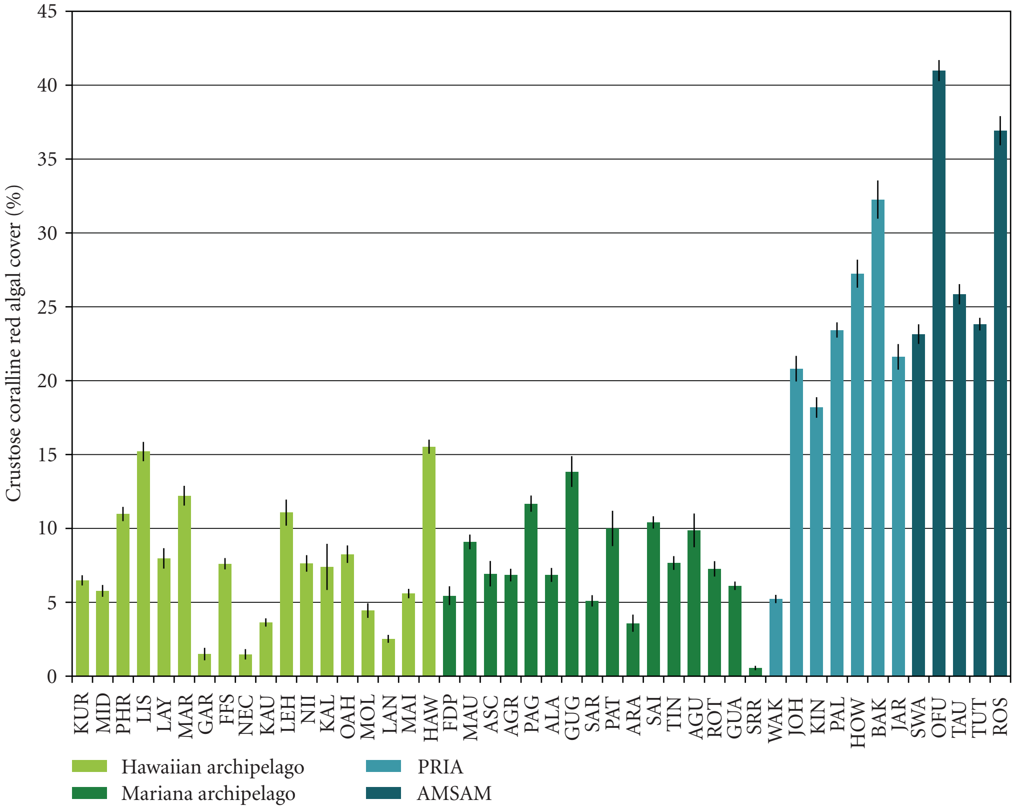
Figure 1: Average island-wide percent cover of scleractinian corals on islands under U.S. jurisdiction in the Pacific Ocean. Many of these reefs are considered to be among the least impacted tropical marine ecosystems in existence, yet average coral cover rarely exceeds 30% and is <18% at the majority of islands monitored. Percent cover data were collected via CRED towed-diver surveys [38] from 2000 through 2009 Reef Assessment and Monitoring Program research expeditions. Figure credit: Tomoko Acoba.

Calcareous algae include not only crustose coralline red genera, but also calcified macroalgae such as species of the segmented, green genus *Halimeda*, which are the main producers of carbonate sediments in many reef systems [16, 49–52]. A 1904 coring study that examined reefs to a depth of over 330 m at Funafuti Atoll (Tuvalu) revealed that the organisms responsible for reef accretion in order of importance were: (1) crustose coralline red algae, (2) *Halimeda*, (3) foraminifera, and lastly, coral [16]. Other classic and recent studies provide similar results, revealing portions of many fossil and existent reef systems from around the globe that are composed primarily of algal or foraminiferal deposits (e.g., Fiji [53], the Gilbert Islands [54], Indonesia [19], Bermuda [55, 56], Atol das Rocas (Brazil) [57], Ukraine [58], Hawaii [59], Australia [52], Spain [51], and Sardinia [60]. Despite these numerous studies, many (although not all) management agencies continue to remain fixated on coral as being the dominant organism responsible for reef growth [61] in all areas.

The adoption of randomly stratified sampling designs by current reef monitoring programs has greatly increased our understanding of the actual diversity and abundance of benthic communities that are typical of normal, healthy tropical to subtropical Pacific marine ecosystems, and reinforce historic reef concepts discussed by pioneer researchers more than a century ago [15–19, 53, 56]. Since 2000, CRED has been conducting interdisciplinary monitoring of ~50 islands scattered throughout the Pacific Ocean (Figure 1). Although every island monitored contains areas of dense coral cover, these coral rich areas are often limited in size, and the majority of hard-bottomed reef community consists of substrate dominated by algal functional groups [22, 23, 40, 62]. Thus, island-wide cover of live corals rarely exceeds more than 30%, and the majority of US-held islands in the tropical

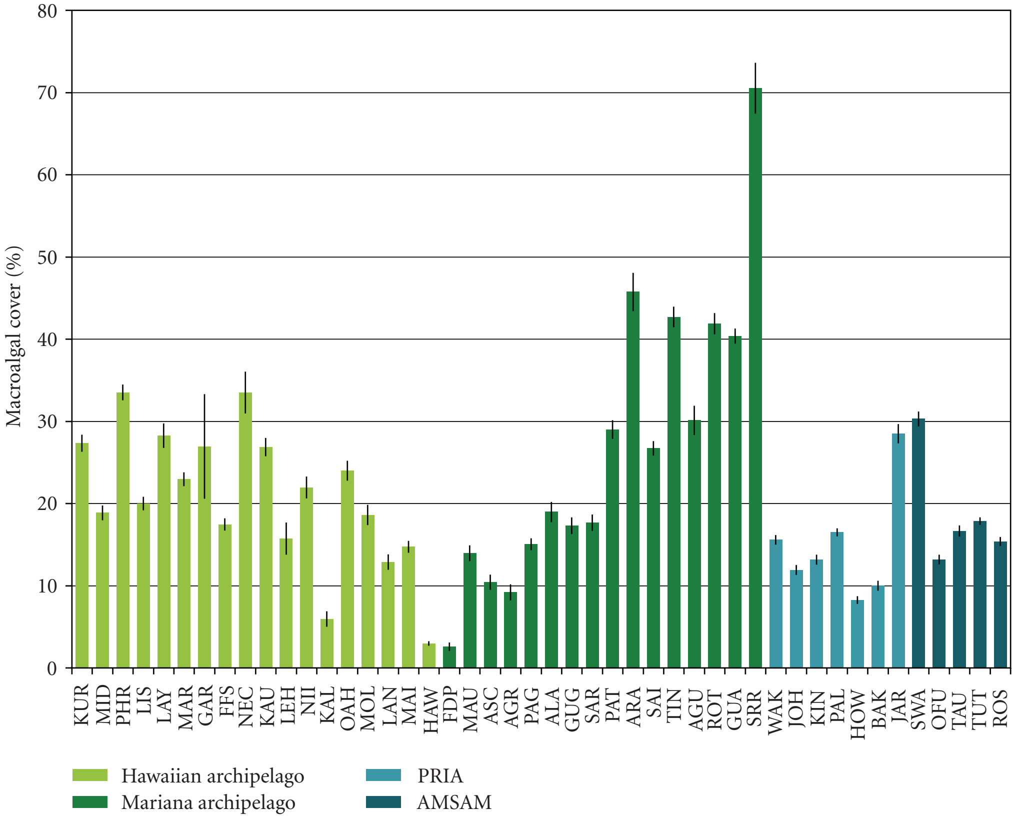


(a)



(b)

Figure 2: Continued.



(c)

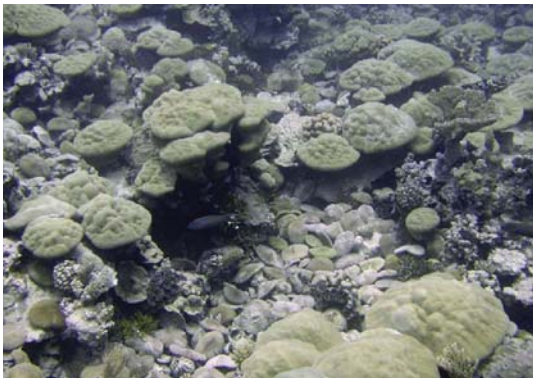
Figure 2: Average percent cover data of (a) live coral, (b) crustose coralline red algae, and (c) macroalgae (both calcified and noncalcified (fleshy) algae which often are attached on top of living CCA communities) collected via CRED towed-diver surveys [38] from 2000 through 2009 Reef Assessment and Monitoring Program research expeditions. Islands within each archipelagic system are arranged in geographic order from north to south (left to right), and archipelagic systems are also presented in geographic order from north to south (although latitudinal overlap between archipelagic systems is not represented; see Figure 1). Standard error bars are provided. Figure credit: Amanda Toperoff and Tomoko Acoba.

to subtropical Pacific contain island-wide percent cover of live coral <18% (Figures 1 and 2). CCA pavements and macroalgal communities (which often epiphytically grow on top of living CCA crusts, but rarely exceed 10–15 cm in height in tropical to subtropical reef systems) combined typically occupy a much greater percentage of substrate than live coral (Figures 2 and 3).

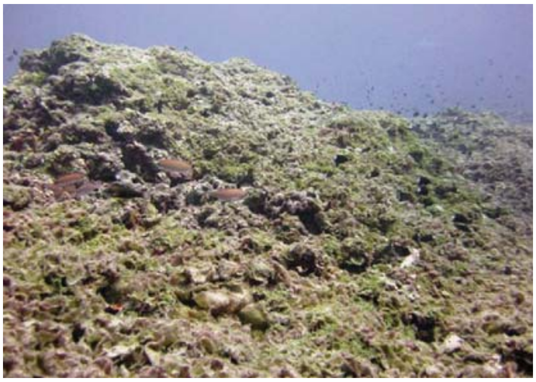
Considering that healthy reefs rely on significant populations of CCA (as well as other types of algal communities), I am concerned about reef management and funding agencies that are focused on monitoring health of just coral and fish communities. Reefs are integrated ecosystems, and our attempts to conserve coral communities will not be successful if efforts are not also made to conserve many of the noncharismatic organisms in reef systems. Recent research has documented that crustose coralline algal (CCA) communities are at greater risk to changes in sea surface temperature and ocean acidification than coral communities [63–67], yet rarely do we see the conservation of algal communities being promoted to the same degree as conservation of coral communities. Unlike coral skeletons that are composed primarily of aragonite and calcite, CCA skeletons contain magnesian calcite [63]. Magnesian calcite has a higher solubility than aragonite or calcite, and CCA growth is expected to be completely inhibited under less acidic conditions than would completely inhibit coral growth [63–65]. In other words, many calcified algae essential for reef accretion and reef cementation will be severely impacted by ocean acidification and warming before corals [66, 67]. Additionally, since CCA are one of the main settlement platforms for coral larvae, this will likely have a profound effect on coral survival [63].

5. Conclusions

The author's concerns over the misconceptions of "coral dominance" in reef systems are that: (1) reef management agencies are losing sight of ecosystem-based research and may potentially overlook many essential calcifying organisms (e.g., crustose coralline red algae, foraminifera, and *Halimeda*) that should be closely researched in order to better understand the effects of ocean acidification and warming, (2) unrealistic perceptions of what constitutes a healthy reef (e.g., that high coral cover is always necessary) may



(a)



(b)

Figure 3: Examples of two reef systems monitored by NOAA's Coral Reef Ecosystem Division. (a) Kingman Reef, US Line Islands. Kingman Reef contains areas exhibiting extremely dense and diverse scleractinian coral communities. Although this tropical marine ecosystem may approximate the idealized image of reef health held by the general public and some management agencies, this type of tropical reef community is one end of a spectrum that ranges from coral-dominated to algal-dominated environments in the healthy reef ecosystems monitored by NOAA on tropical to subtropical Pacific Islands. (b) Pearl and Hermes Atoll, Northwestern Hawaiian Islands. Containing ∼5% cover of scleractinian corals, this healthy reef system contains dense pavements of crustose coralline red algae overgrown by the foliose green macroalga, *Microdictyon*, which in turn is often covered with turf algal epiphytes. Such reef environments with relatively low coral cover are more representative of many types of reef communities monitored by NOAA on tropical to subtropical Pacific Islands than the coral-dominated environment picture in Figure 2(a). Photo credit: Cristi L. Braun (CRED).

permeate the public and reef management agencies and will be perpetuated indefinitely, and (3) reef management agencies might try to restore ecosystems to nonnatural states where essential elements of reef systems become lost because too much emphasis was placed on only a single type of organism (e.g., coral).

As reef scientists, we recognize the increasing number of threats that are causing reefs to decline worldwide. Coral rich areas are valuable reef resources, and need extra management protection, but not to the exclusion of noncoral dominated areas that also contain essential reef building organisms. In complex ecosystems, all organisms are interconnected. We know from current research that CCA communities will likely be adversely impacted by global climate change sooner than coral communities. Since many coral species rely on CCA as larval settlement platforms, efforts equal to understanding coral responses to global climate change should also be put towards understanding changes in algal communities. Fortunately, responsible reef management programs are increasingly recognizing the diverse suite of noncoral calcifying organisms present in reef settings that also deserve protection and study [61], but some programs do continue to overlook important calcifying organisms such as CCA, *Halimeda*, and foraminifera that are necessary for reef maintenance and accretion in many areas. As scientists, we should strive towards removing any remaining disconnects with management agencies and promote research and conservation of all calcifying, framework or sediment producing organisms that will be affected by global climate change. There is a common English idiom describing a person who cannot perceive the "big picture" because of concentrating too intently on minute details that states "one cannot see the forest for the trees." This is an apt saying that applies to reef research today. Please do not lose sight of the reefs because of the coral. Reefs are integrated ecosystems, and all components should to be studied and conserved for these endangered habitats to survive.

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Research Article

The Effect of a Sublethal Temperature Elevation on the Structure of Bacterial Communities Associated with the Coral *Porites compressa*

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Evidence points to a link between environmental stressors, coral-associated bacteria, and coral disease; however, few studies have examined the details of this relationship under tightly controlled experimental conditions. To address this gap, an array of closed-system, precision-controlled experimental aquaria were used to investigate the effects of an abrupt 1°C above summer ambient temperature increase on the bacterial community structure and photophysiology of *Porites compressa* corals. While the temperature treatment rapidly impacted the photophysiology of the coral host, it did not elicit a statistically significant shift in bacterial community structure from control, untreated corals as determined by terminal restriction fragment length polymorphism analysis of 16S rRNA genes. Two of three coral colonies harbored more closely related bacterial communities at the time of collection and, despite statistically significant shifts in bacterial community structure for both control and treatment corals during the 10-day acclimation period, maintained this relationship over the course of the experiment. The experimental design used in this study proved to be a robust, reproducible system for investigating coral microbiology in an aquarium setting.

1. Introduction

The worldwide degradation of coral reef ecosystems is due, in part, to the emergence of novel pathogenic diseases affecting scleractinian corals [1, 2], and it has been speculated that the widespread proliferation of coral diseases is linked to increasing sea surface temperatures (SSTs) [3, 4]. Many disease outbreaks correlate with temperature anomalies and seasonal warming [3, 5, 6], and increased SSTs have also been shown to affect the virulence of coral disease pathogens [7]. For example, infection of *Pocillopora damicornis* by the bacterial pathogen *Vibrio coralyticus* increases rapidly with increased temperatures [8], and disease outbreaks often follow or co-occur with temperature-induced coral bleaching [2, 6, 9]. Discriminating between bacteria acting as causative agents of coral bleaching [10, 11] versus postbleaching opportunists has been ambiguous [12, 13]. However, it remains undisputed that bacteria play important roles in both maintaining and destabilizing the health of the coral holobiont, which is composed of coral host polyps, symbiotic dinoflagellates known as zooxanthellae, and a diverse assemblage of associated algae, fungi, Bacteria, Archaea, and viruses associated with the skeleton, tissues, and mucus layer of adult coral colonies [14, 15].

Our limited understanding of the resident bacterial biota associated with corals during nondiseased states hinders our ability to understand many of the processes involved in coral disease. Corals harbor diverse bacterial communities that facilitate the transformation of organic carbon [15, 16], acquisition and transfer of macronutrients [17, 18], and resistance to pathogen invasion [19, 20]. The characterization of the diversity, function, and stability of these communities suggests a link between environmental stressors, coral-associated bacteria and coral disease. For example, increased temperatures, dissolved organic carbon loading, elevated nutrient concentrations, reduced pH, and point source coastal pollution have all been shown to drive shifts in the composition of bacterial community in corals [21–23]. A shift towards "disease associated" bacteria has been observed in some cases [23] and coral mortality in others [21]. Shifts in coral-associated bacteria have also been shown to occur in corals infected with a known coral pathogen [24], and changes in bacterial biota are often detectable prior to disease symptoms becoming visible. Coral associated bacterial communities are responsive to infection by disease agents and environmental stressors. As such, the structure of the coral-associated bacterial community could potentially serve as a biological indicator of coral health.

The goals of this study were to (1) examine the feasibility and potential effects of using a closed-system, precision-controlled experimental aquarium system to study the structure and dynamics of microbial communities associated with corals and (2) assess the effect of a sublethal, abrupt change in temperature on coral-associated microbial community structure in the context of the photophysiological health of the coral. Shifts in the bacterial communities associated with the Hawaiian reef building coral *Porites compressa* were assessed in coral fragments exposed to an abrupt 1°C increase in seawater temperature above ambient summer levels following a 10 d acclimation at ambient temperature. Terminal-restriction fragment length polymorphism (T-RFLP) analysis, a bacterial community fingerprinting technique based on the 16S rRNA gene, allowed for high-throughput examinations of seawater and coral-associated bacterial community structure throughout the course of the experiment. The finger coral *Porites compressa* was targeted because it is endemic to Hawaii and ecologically important in the region. The photophysiological response of *P. compressa* to the temperature increase was assessed using Pulse Amplitude Modulated (PAM) fluorometry [25–27], and experimental aquaria allowed for the precise control of environmental variables (such as temperature) and replication of treatments. The results show that the aquaria provided a robust platform for controlled and replicated alterations of environmental conditions that are of a relevant scale to fluctuations either experienced or anticipated to be experienced by corals in the near future, and that the thermal stress applied in this study rapidly impacted the photophysiology of the coral host. In contrast, no change in the structure of coral-associated bacterial communities was detected with the combination of temperature and duration of treatment used in this study.

2. Methods

2.1. Sample Collection and Experimental Design. On August 4, 2007, approximately 45 branch tips of *Porites compressa* (Dana 1846) 3 to 5 cm in length and 1 to 1.5 cm in diameter were removed from each of three coral colonies judged as nondiseased by gross visual assessment in central Kaneohe Bay off of the island of Oahu, Hawaii, in the Pacific Ocean. Source colonies were sampled at a depth of approximately 4 m and were located within 10 m of each other. Three fragments from each colony were immediately frozen in liquid nitrogen for analysis of bacterial community structure associated with the source colonies. The remaining fragments were immediately placed in containers with aerated seawater and transported back to the Hawaii Institute of Marine Biology (HIMB). In addition to the coral sampling, water samples were collected to characterize the bacterial communities in the planktonic environment surrounding the corals. Approximately 1 L of seawater was collected ~1.5 m above the reef, filtered through 25 mm diameter, 0.2 μm pore-sized polyethersulfone membrane filters (Supor-200; Pall Corp., East Hills, NY), and frozen for DNA analysis in 250 μL of DNA lysis buffer (20 mM Tris-HCl pH 8.0, 2 mM EDTA pH 8.0, 1.2% v/v Triton X100) [28].

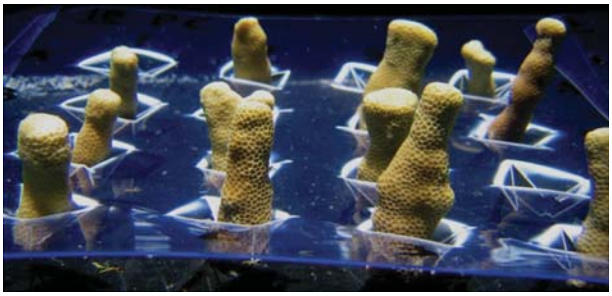


Figure 1: Photograph of *P. compressa* mounted in a vinyl sheet and held in a seawater holding tank prior to being placed into the experimental aquaria.

Upon return to the laboratory at the HIMB, coral fragments were rinsed with 1 μm-filtered seawater and placed in a holding tank of 1 μm-filtered seawater maintained at the ambient temperature of 27°C. Four fragments from each colony were mounted randomly in each of eight 0.76 mm thick clear vinyl sheets (Figure 1). A sheet was placed in each of eight independently controlled 60 L experimental aquaria. An additional 2–4 extra fragments per colony were also mounted in sheets as backups for fragment mortality. To minimize exposure to disturbance and handling upon removal from the reef, coral samples were collected between 0900 and 0945 and mounted in their final position in the aquaria by 1400 the same day.

All aquaria were filled with 1 μm-filtered, UV-treated seawater, which recirculated through the individual tanks for the duration of the experiment. Each tank was equipped with a full spectrum light (white and UV) on a 12:12 hr light:dark cycle, a protein skimmer, and a submersible pump flowing at 20 gal min^{-1}. The volume of seawater in each tank was monitored daily and salinities kept constant by the addition of sterile, milli-Q freshwater. Temperature and light levels in the tanks were monitored with Onset Computer HOBO temperature and light pendant loggers (UA-002-64 Onset Computer Corporation, Bourne, MA). The loggers were fixed horizontally (light meter facing up) to the vinyl sheets containing coral fragments with cable ties, and the sheets supporting the mounted corals were fixed to the bottom of the tank with suction cups. The seawater temperature was maintained at the ambient temperature of 27°C for 10 d to allow corals to acclimate.

After the acclimation period, four tanks were randomly assigned as controls (tanks 1, 8, 9, and 13) and four as treatment (tanks 3, 4, 15, and 16). At 1300 on that day, seawater and coral bacterial communities were sampled, and the seawater temperature in the treatment tanks abruptly increased to 28°C (+1°C over) in treatment tanks. Corals were subsequently sampled from the aquaria at the same time of day (i.e., initiated at 1300 and completed by 1430) after 2, 4, and 6 d of incubation and aquarium seawater after 2 and 7 d. Coral sampling consisted of removing one randomly selected coral fragment per colony per tank and freezing it in liquid nitrogen. Seawater (250 mL) was removed from each tank using acid-washed polycarbonate bottles and subsequently filtered through 25 mm diameter Supor-200 membranes (Pall Corp.). Filters were placed in 200 μL of DNA lysis buffer and stored at −80°C until further processed.

2.2. Pulse Amplitude-Modulated (PAM) Fluorometry. Pulse amplitude-modulated fluorometry was performed by taking one measurement per fragment on the fragment tip with a Walz Diving-B PAM Fluorometer (Heinz Walz GmbH, Germany) with an 8-mm fiber optic cable. The measurement tip of the PAM cable was sheathed in opaque tubing to prevent light pollution of the other fragments during measurements and to create a standard distance between the sample and the measuring tip. Sampling was performed in the evening after approximately 1 h of dark adaptation. The resulting Maximum Quantum Yield (MQY) data was analyzed with Minitab 15.0 statistical analysis software (Minitab Inc, State College, PA).

2.3. T-RFLP of Bacterial SSU rRNA Genes. Individual coral fragments were thawed, and a flame-sterilized stainless steel core borer was used to remove three random subsamples. Each subsample consisted of a 6-mm diameter, 6-mm deep core that included the coral tissue, overlying mucus layer, and underlying skeleton. The three subsamples were placed into one sterile bag containing 2 mL of 0.2 μm-filtered 10X Tris EDTA (100 mM Tris, 10 mM EDTA) buffer solution (pH 7.4) and airbrushed with an air gun and sterile pipette tip. The resultant slurry was centrifuged at 19,900 RCF for 30 min at 4°C. The supernatant was subsequently removed from the sample and the remaining sample pellet was frozen at −80°C until processed further.

After thawing, genomic DNA was extracted from the coral tissue pellets and seawater filters using the PowerSoil DNA Isolation Kit (MoBio Laboratories Inc., Carlsbad, CA) according to the manufacturer's protocol. Genomic DNA was eluted in sterile, 0.1 μm-filtered water and stored frozen at −20°C. Total genomic DNA yield was assessed on a SpectraMax M2 plate reader (Molecular Device Corp., Sunnyvale, CA, USA) using the Quant-iT PicoGreen dsDNA Assay Kit (Invitrogen Corp., Carlsbad, CA, USA), prepared according to manufacturer's protocol.

For terminal restriction fragment length polymorphism (T-RFLP) analysis [29], the general bacterial primers 27F-B-FAM (5′-FAM-AGRGTTYGATYMTGGCTCAG-3′) and 1492R (5′-GGYTACCTTGTTACGACTT-3′) were used for the amplification of small subunit ribosomal RNA (16S rRNA) genes from each sample via the polymerase chain reaction (PCR). The MasterTaq System (Eppendorf AG, Hamburg, Germany) was used for all PCR reactions, which were composed of the following (final concentrations): 1X MasterTaq reaction buffer, 2.25 mM Mg^{2+}, 0.5X TaqMaster reaction enhancer, 0.2 mM each of the forward and reverse primers, 0.2 mM of each dNTP (Promega, Madison, WI), approximately 160 to 280 ng of genomic DNA template, 2.5 units of MasterTaq DNA polymerase, and sterile water to a final reaction volume of 50 μl. A MyCycler thermal cycler (Bio-Rad Laboratories, Hercules, CA, USA) and touchdown protocol were used, which, after a 3 min incubation at 95°C, consisted of 30 cycles of 30 sec at 95°C, 1 min at 65°C (decreasing by 0.5°C per cycle), and 2 min at 72°C. This was followed by 10 cycles of 30 sec at 95°C, 1 min at 50°C, and 2 min at 72°C, and 1 cycle of 30 sec at 95°C, 1 min at 50°C, and 20 min at 72°C.

The fluorescently labeled amplicons were purified using the QIAquick PCR purification kit (Qiagen Inc.) following the manufacturer's instructions. Approximately 100 ng of each purified amplicon was subsequently digested in a 10 μL reaction containing 5 units of HaeIII restriction endonuclease (Promega, Madison, WI) at 37°C for 6 hours. After purification via gel filtration chromatography with Sephadex G-50 (Amersham Biosciences, Sweden), the restricted samples were adjusted to a final concentration of 35 ng μL^{-1} and separated via capillary electrophoresis on an automated ABI 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA). GeneMapper software (Applied Biosystems) was used to estimate the size and relative abundance of the resulting terminal restriction fragments (T-RFs), which were defined as fragments between 42 and 613 base pairs (bp) in length. Fragment lengths were rounded to the nearest integer value, aligned, and manually checked for possible errors in peak determination due to such factors as instrument variability, and so forth. The threshold below which peaks were excluded was determined via the variable percentage threshold method as described in Osborne et al. [30].

2.4. Statistical Analysis. After square root transformation of the T-RFLP data matrix, all subsequent statistical analyses were carried out in PRIMER 6 Version 6.1.13 and PERMANOVA + Version 1.0.3 (PRIMER-E Ltd., Plymouth, UK) [31–33].

A resemblance matrix was constructed based on Bray-Curtis similarity. Hierarchical clustering analysis (CLUSTER) of the resemblance matrix was used to construct similarity dendrograms, and a similarity profile permutation test (SIMPROF) was used to identify significant "natural groupings" of samples that were not structured *a priori*. CLUSTER analyses were based on the group average linking option and SIMPROF analyses were performed at a 5% significance level.

Table 1: PAM-derived maximum quantum yield regression values during acclimation and manipulation phases of *P. compressa*.

Group	Time	Slope	R^2	T statistic	P-value
Control	Acclimation	−0.00168	0.052	−3.61	.000
	Manipulation	−0.00392	0.070	−3.26	.001
Treatment	Acclimation	−0.00159	0.049	−3.54	.000
	Manipulation	−0.00875	0.273	−7.43	.000

Nonmetric multidimensional scaling (NMDS) ordination of the resemblance matrix was used to provide a 2-dimensional graphical representation of similarities in bacterial community structure (based on T-RFLP peak abundances) amongst samples [34, 35]. NMDS plots can be generally interpreted as follows: points that are closer together are very similar in community composition, and points that are further apart correspond to very different communities. NMDS was chosen because it makes no assumptions about the underlying distribution of data and is therefore appropriate for analyzing complex ecological communities. In some cases, data from CLUSTER analyses were used to overlay Bray-Curtis similarity boundaries onto NMDS plots to display percent similarity amongst samples.

An analysis of similarity (ANOSIM), performed on the resemblance matrix, was used to test for differences in bacterial community structure between predefined sample groups. The ANOSIM test is analogous to a standard univariate 1-way analysis of variance (ANOVA), and group specifications were made *a priori*. A "similarity percentages" routine (SIMPER) was used to identify the role of individual species in contributing to group differences as well as within group closeness. SIMPER dissects average Bray-Curtis dissimilarities between all pairs of samples into percentage contributions from each species and lists them in decreasing order of contribution [31]. An 80% cutoff was employed to focus on higher-contributing variables.

A permutational multiple analysis of variance (PERMANOVA) of the resemblance matrix was used to test for differences in bacterial community structure between temperature treatments, tanks, coral colonies, and time points. PERMANOVA tests the simultaneous response of one or more variables to one or more factors in an analysis of variance (ANOVA) experimental design on the basis of a resemblance measure, using permutation methods. The routine calculates an appropriate distance-based pseudo-F statistic for each term in the model based on the expectations of mean squares, and P-values are obtained using an appropriate permutation procedure for each term [32]. PERMANOVA tests were run with the following specifications: 999 permutations, permutation of residuals under a reduced model, Type III (partial) sum of squares, Monte Carlo tests, and fixed effects sum to zero.

3. Results

3.1. Photophysiology of P. compressa. Initially, both control and treatment fragments of *P. compressa* exhibited very high variability in MQY, presumably due to shock associated with their collection from the field, loading into sheets, and positioning within the aquaria (data not shown). By Day 3, however, the MQY had stabilized and remained nearly constant throughout the acclimation period (Figure 2). Statistical analyses revealed that the MQY of the control and treatment groups did not differ significantly during this acclimation phase (two sample t-test: $t = 0.74$, DF = 481, and $P = .459$), indicating there were no tank effects. In addition, the MQY of all colonies on the first and last days of the acclimation period were also not significantly different (two sample t-test: $t = 0.17$, DF = 239, $P = .867$), indicating that the MQY stabilized during acclimation. After the initiation of the temperature manipulation on Day 10 (+1°C), the MQY of both treatment and control samples decreased. However, linear regression of the control and treatment samples indicated a greater decline in the treatment samples over time (Table 1; Figure 2) with the slope of the control sample linear regression decreasing by a factor of 2.33 and the slope of the treatment by a factor of 5.50.

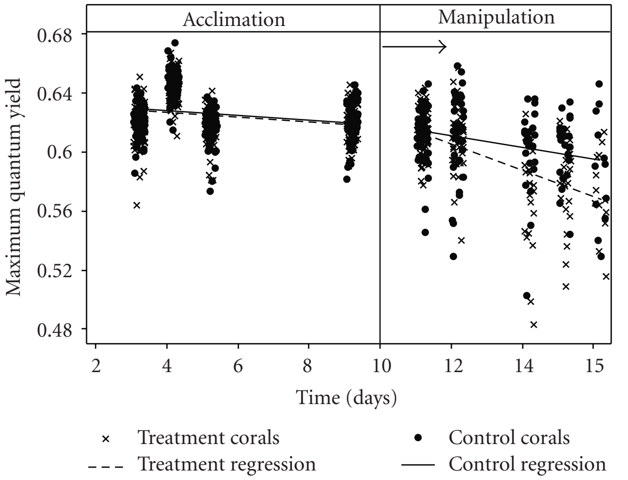


Figure 2: Maximum quantum yield of *P. compressa* during acclimation to experimental tanks (acclimation) and after a temperature increase of 1°C at Day 10 (treatment group tanks only; manipulation). Each point represents a single PAM measurement (points are shifted slightly in the ±x direction in order to reduce overlap). Lines are least-squares linear regressions. Control colonies: closed circles, solid regression; treatment colonies: x's, dashed regression. Note: the treatment and control regression lines overlap during the "acclimation" phase.

3.2. Planktonic Bacterial Community Analysis. CLUSTER and ANOSIM analyses of all coral-associated ($n = 99$) and seawater bacterial community ($n = 26$) samples collected

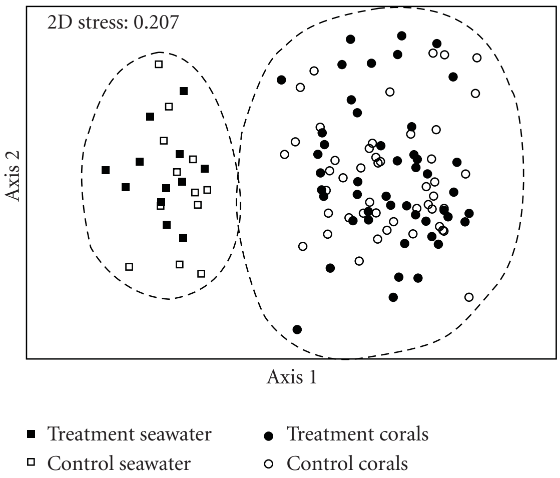


Figure 3: NMDS ordination of all coral ($n = 99$) and seawater ($n = 26$) bacterial communities sampled over the course of this study, based on a Bray-Curtis similarity matrix calculated from a square root transformation of the T-RFLP relative abundance data matrix. The dashed line indicates the 20% Bray-Curtis similarity threshold. Seawater samples are represented by squares and coral samples are represented by circles. Control and treatment samples are represented by open and closed symbols, respectively.

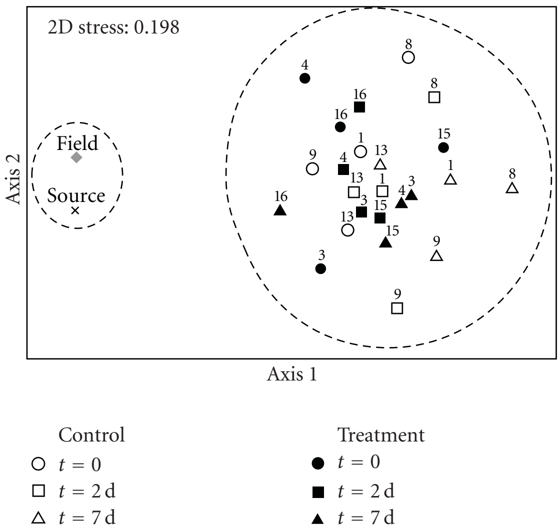


Figure 4: Comparison of seawater bacterial communities sampled over the course of this study ($n = 26$), based on a NMDS ordination of a Bray-Curtis similarity matrix calculated from a square root transformation of the T-RFLP relative abundance data matrix. The dashed line indicates the 20% Bray-Curtis similarity threshold. "Field" indicates the seawater bacterial community sampled from the field site in Kaneohe Bay, while "source" indicates the seawater system at HIMB used as a source for the aquaria. Control aquaria are represented by open symbols and are individually numbered 1, 8, 9, and 13, while treatment aquaria are represented by closed symbols and are individually numbered 3, 4, 15, and 16. Sampling times are indicated by circles ($t = 0$), squares ($t = 2$ d), and triangles ($t = 7$ d).

over the course of this study showed that the bacterial communities were significantly different between the two sample types (Global $R = 0.864$, $P = .001$). An initial NMDS ordination of all coral and seawater samples overlaid with a 20% Bray-Curtis similarity boundary resolved two distinct clusters clearly demonstrating this difference (Figure 3).

The microbial community in seawater from Kaneohe Bay taken near the corals sampled for this experiment ($n = 1$), from the source water produced by the HIMB seawater system ($n = 1$), and from the aquaria throughout the course of the experiment (0, 2, and 7 days; $n = 24$) were compared using CLUSTER and ANOSIM. These tests revealed a tight group of microbial communities from the seawater sample from Kaneohe Bay and from the HIMB seawater system, which was significantly different from the aquaria planktonic microbial communities, regardless of whether they originated from control or treatment tanks (Figure 4) (Global $R = 0.981$, $P = .003$). Thus, the planktonic bacterial community structure within the aquaria shifted over the 10 days between the time of collection and start of the experiment. A PERMANOVA test was used to investigate the differences in seawater bacterial communities amongst different aquaria throughout the experiment. This test revealed no difference between control or treatment tanks (Pseudo-F $= 0.619$, $P = .824$). However, the test did reveal differences in the bacterial communities in aquarium seawater over time (Pseudo-F $= 2.173$, $P = .003$) and between replicate tanks within control and treatment (Pseudo-F $= 2.119$, $P = .001$). An ANOSIM test confirmed differences in aquarium seawater bacterial communities over time (Global $R = 0.131$, $P = .019$), but only identified time points 0 d and 7 d as being significantly different from one another ($R = 0.33$, $P = .003$). Differences between tanks within control or treatments were also confirmed via ANOSIM (Global $R = 0.372$, $P = .001$), and pairwise comparisons revealed a range of similarities between tanks from both the control and treatment sets. For example, control tank 8 was highly distinct from the other three control tanks, with R values approaching 1 (8/9 $R = 0.704$; 8/1 $R = 0.852$; 8/13 $R = 0.889$) whereas control tank 4 and treatment tank 13 were highly similar ($R = 0$).

3.3. Coral-Associated Bacterial Community Analysis. Coral samples collected from source colonies in the field ($n = 3$) were compared to all experimental and control coral samples (0, 2, 4, and 6 d time points; $n = 96$) using CLUSTER and ANOSIM tests, which revealed a significant difference between source and aquaria maintained colonies (Global $R = 0.688$, $P = .001$). Thus, coral associated bacterial community structure appeared to shift between the time of collection and the start of the experiment 10 d later. A PERMANOVA test including all time points indicated that coral-associated bacterial communities did not differ between the control or treatment sets (Pseudo-F $= 0.791$, $P = .807$) or over time ($Pseudo - F = 1.257$, $P = .145$). Despite significant differences between tanks within control or experimental tank sets (Pseudo-F $= 1.532$, $P = .003$), significant intercolony differences in bacterial community structure were maintained over the course of the experiment across all tanks (Pseudo-F $= 8.338$, $P = .001$).

To further investigate intracolony differences, separate PERMANOVA tests were performed for each colony. This confirmed that bacteria associated with colonies 2 and 3 were not significantly affected by the treatment (Pseudo-F = 0.900, $P = .502$; Pseudo-F = 1.068, $P = .377$), time (Pseudo-F = 1.433, $P = .062$; Pseudo-F = 0.842, $P = .754$), or tank (Pseudo-F = 1.232, $P = .110$; Pseudo-F = 1.009, $P = .487$). While test results for colony 1 revealed that bacterial community structure was not significantly affected by treatment (Pseudo-F = 0.846, $P = .793$), it was significantly affected by tank (Pseudo-F = 1.305, $P = .036$) and time (Pseudo-F = 1.524, $P = .017$). An ANOSIM test of colony 1 data supported these observations (Global $R = 0.097$, $P = .028$), with significant differences between time points 0 and 4 d ($R = 0.218$, $P = .015$) and between 2 and 6 d ($R = 0.209$, $P = .043$), but not between 0 and 2 d ($R = 0.111$, $P = .136$), 2 and 4 d ($R = -0.049$, $P = .716$), 4 and 6 d ($R = 0.027$, $P = .352$), or 0 and 6 d ($R = 0.106$, $P = .095$). SIMPER analysis indicated that the terminal restriction fragment of 303 base pairs in length (T-RF 303) was the major contributor to observed differences between times, accounting for 4.85% of the average dissimilarity between time 0 and 4 d groups and 5.37% of average dissimilarity between 2 and 6 d groups. The relative abundance of T-RF 303 bp increased during the intermediate time points in control tanks 1, 8, and 13, and treatment tank 16, thus contributing to observed differences amongst tanks.

An NMDS ordination of the data set illustrated the shift in bacterial community structure between colonies sampled in the field and those sampled during the experimental time points (Figure 5(a)). The NMDS ordination also revealed that bacterial communities associated with source colonies 2 and 3 were more similar to one another than to colony 1. In spite of the overall shift in community structure between source and experimental coral-associated microbial communities observed for all three colonies, inter-colony differences were preserved over the course of the experiment: colonies 2 and 3 remained similar, while colony 1 remained distinct (Figure 5(a)). An ANOSIM test confirmed that the three colonies were significantly different from one another during the experiment (Global $R = 0.33$, $P = .001$), with pairwise comparisons highlighting that colonies 2 and 3 were more similar to one another than to colony 1 (2/3 $R = 0.164$; 2/1 $R = 0.427$; 3/1 $R = 0.437$; $P = .001$ for all tests).

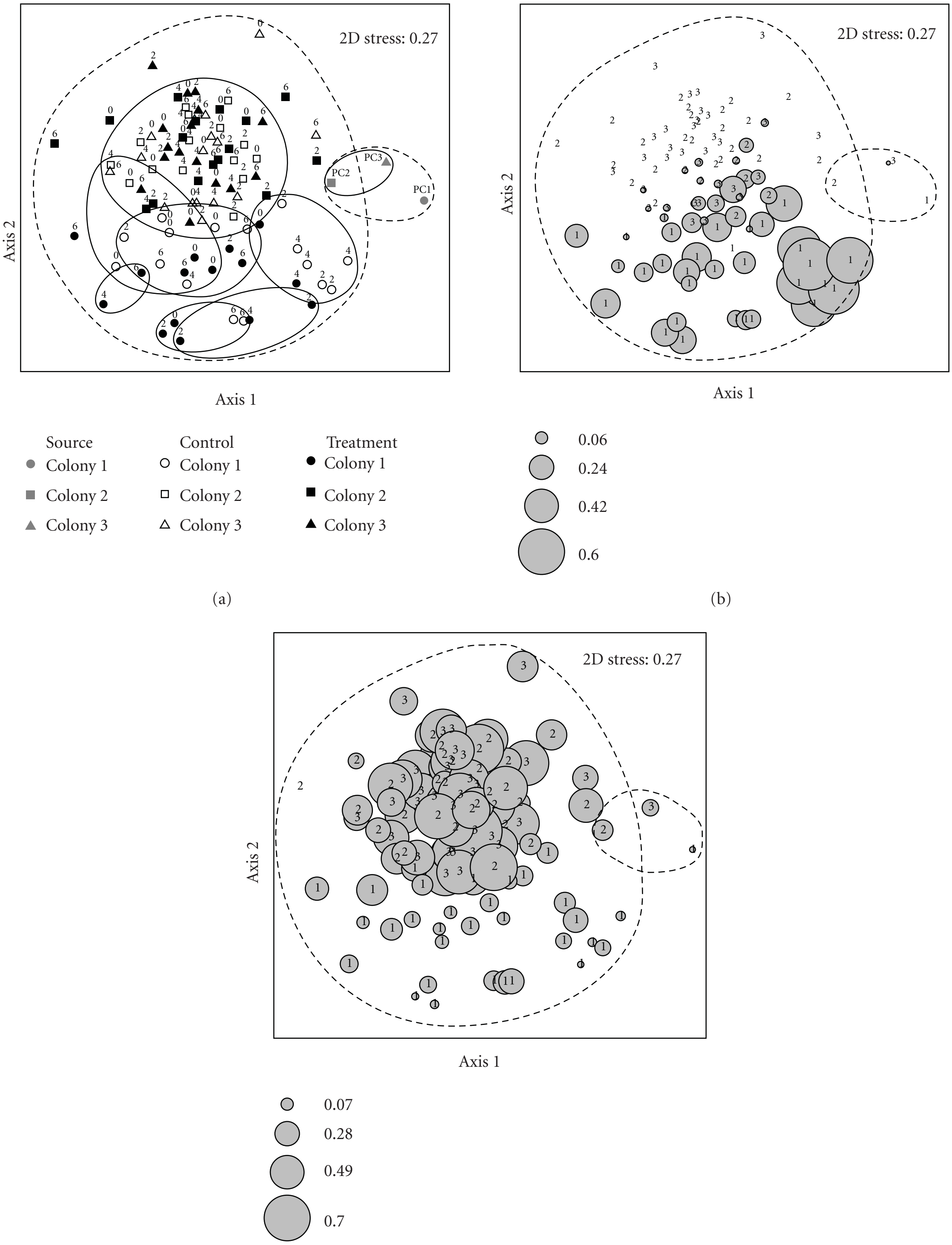
SIMPER was used to identify individual T-RFs that contributed most greatly to group differences and were defined within group similarities. Overall, T-RF 303 and T-RF 264 played large roles in discerning inter-colony differences (Figures 5(b) and 5(c)). T-RF 303 contributed to 6.61% of average dissimilarity between colonies 1 and 2 and 6.48% between colonies 1 and 3. T-RF 264 contributed to 4.78% of average dissimilarity between colonies 1 and 2, and 5.78% between colonies 1 and 3.

4. Discussion

As the integrity of coral reefs decline on a global scale, the development of effective means to monitor coral health has become critical. In particular, methods that detect the onset of physiological stress in corals prior to disease or death are essential for effective management. In addition to their utility in other areas of coral health and disease, we hypothesized that fluctuations in bacterial community structure associated with corals could be used as a sensitive indicator of physiological stress by the coral host. However, most studies to date that have related coral-associated bacterial community structure with coral health have focused on distant end-members (e.g. "healthy" versus "nonhealthy" or diseased) [24, 36, 37] and have not been able to tease apart the large gradient of health states in between these widely separated extremes. Experimental aquarium systems provide an opportunity to tightly control the environmental conditions experienced by the corals (and thus their associated microbiota) and consequently allow for the investigation of small, systematic, and ecologically relevant environmental disturbances.

In general, corals live within a relatively narrow temperature margin and will bleach in response to both high and low sea surface temperature anomalies [38, 39]. Bleaching due to elevated seawater temperatures occurs frequently, and even a small increase (e.g. 1-2°C) for several weeks during the summer season can induce bleaching [39, 40]. Using these observations as rationale, we exposed fragments of *P. compressa* to a one degree, sublethal temperature elevation over the ambient summer temperature at the time of sampling. This temperature increase elicited a rapid response by the coral host, resulting in a progressive decrease in MQY over the course of the six-day treatment, which we interpret to indicate a decrease in the photosynthetic efficiency of the coral. The control corals that were not subjected to the temperature increase also showed a progressive but far less dramatic decrease in MQY over time. Thus, while unidentified components of the experimental aquarium set up appeared to have a negative impact on the photosynthetic efficiency of the coral with time, the additive adverse effect of the minor increase in temperature was of significant enough magnitude to overshadow the tank effect. By contrast, after 6 d of experimental manipulation, no clear systematic segregation was detected between bacterial communities associated with control and treatment corals.

Our results do not imply that coral-associated bacterial communities were static: these communities changed significantly during the 10-day acclimation period when no treatment was applied, resulting in a distinct difference between the parent "source" colonies and the experimental coral fragments. Despite this divergence from source colony community structure during the acclimation period, for the most part, the coral-associated bacterial communities did not continue to systematically change during the treatment period. We interpret this to indicate that the coral-associated microbial community structure changed in response to acclimation to the experimental aquarium system, stabilized over the course of the initial 10-day period, and subsequently did not systematically respond to the temperature elevation treatment or experimental aquarium environment. The most plausible explanation for this observation is that the temperature increase was not significant enough in magnitude and/or duration to either directly impact the



(a)

(b)

(c)

Figure 5: NMDS ordination of coral-associated bacterial communities based on Bray-Curtis similarity. Points represent coral-associated bacterial communities sampled directly from the three source colonies in Kaneohe Bay (PC1, PC2, and PC3) and from experimental tanks. (a) Sampling times are listed adjacent to points, and colonies are represented by circles (colony 1), squares (colony 2), and triangles (colony 3). Control and treatment samples are represented by open and closed symbols, respectively. In (b) and (c), colony numbers are superimposed on the relative abundance bubbles, and the diameter of each bubble is correlated to the square root transformed relative abundance of (b) T-RF 303 or (c) T-RF 264 for each sample. The solid (a) and dashed (a)–(c) lines demarcate 40% and 25% Bray-Curtis similarity thresholds, respectively.

growth of the coral-associated bacterial biota or indirectly effect their growth by impacting the physiology of the coral to a degree that would impact the microbial community. In essence, PAM fluorometry appeared to be detecting changes in the photophysiology of the coral host that had no impact on the community structure of associated bacteria for the duration of our experiment. In future experiments, it will be valuable to extend the duration of the temperature treatment significantly (i.e., from days to weeks) to correlate bacterial community structure to a broader gradient of impact to the coral host, including the ultimate fate of the coral fragments subjected to sublethal increases in temperature.

It is interesting to note that the three *P. compressa* source colonies sampled for this experiment all possessed statistically different microbial communities. The structure of the bacterial communities of two of these colonies were much more closely related to each other than to the third, and, despite changes during the 10-day acclimation phase, this relationship was maintained throughout the duration of the experiment. The maintenance of this relationship throughout the acclimation and experimental periods suggests that the microbial communities either did not randomly diverge upon containment, but rather changed systematically, or that they diverged but the differences did not reach a significant enough magnitude for our methodology to detect. Extension of the duration of the experimental treatment would help to tease apart the interplay between these nonexclusive options.

Throughout the course of this study, several aspects of the experimental aquarium system were identified that had the potential to negatively impact this research by forcing environmental conditions to diverge from the natural environment, and thus would require additional attention in the future. In particular, technical limitations required that the seawater used to fill the experimental aquaria be recirculated within each individual tank. Thus, to limit microbial growth, the seawater initially supplied to the tanks was filtered to remove eukaryotic phytoplankton and treated with UV radiation to decrease the load of viable bacteria. As might be expected, the structure of planktonic bacterial communities within the experimental aquaria appeared to change in an unpredictable fashion over the course of this study, resulting in significant tank differences irrespective of whether they originated from treatment or control groups. While cellular abundance was not monitored, it is probable that the filtration and UV treatments initially decreased the cellular load, but the tank environment provided a hospitable environment for subsequent microbial growth. Ultimately, all tanks exhibited significant changes in planktonic bacterial community structure by the end of the experiment. The source coral colonies sampled in this study were subject to significant, variable flow, and thus experience a constantly refreshed microbial community. While the impact that aquarium-contained planktonic seawater bacterial communities may have on the corals in these aquaria (or their closely associated microbiota) cannot be predicted at the present time it is a potentially confounding factor that can be eliminated by employing a flow-through seawater system with natural seawater as source.

5. Conclusions

The primary goal of this study was to begin to explore the relationship between coral-associated bacterial community structure and coral health during an abrupt but sublethal temperature anomaly. More broadly, we sought to relate successional changes in bacterial community structure to gradients of physiological stress in the coral host, before the symptoms of the stress became visually apparent (e.g., bleaching and disease symptoms). While the thermal stress we applied rapidly impacted the photophysiology of the coral host, no changes in the bacterial community structure were detectable with the combination of temperature and duration of treatment used. Data from this study provide new information on the variability of coral-associated bacterial communities amongst colonies of the same species and serve as a guide to improve the design of future experiments aimed at elucidating the role that bacterial communities play in the responses of corals to climate change stressors such as elevated sea surface temperatures and ocean acidification.

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Research Article

Ecosystem-Scale Effects of Nutrients and Fishing on Coral Reefs

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Nutrient pollution and fishing are the primary local causes of coral reef decline but their ecosystem-scale effects are poorly understood. Results from small-scale manipulative experiments of herbivores and nutrients suggest prioritizing management of fishing over nutrient pollution because herbivores can control macroalgae and turf in the presence of nutrients. However, ecological theory suggests that the opposite occurs at large scales. Moreover, it is unclear whether fishing decreases herbivores because fishing of predators may result in an increase in herbivores. To investigate this paradox, data on the fish and benthic communities, fishing, and nutrients were collected on Kiritimati, Kiribati. Oceanographic conditions and a population resettlement program created a natural experiment to compare sites with different levels of fishing and nutrients. Contrary to theory, herbivores controlled macroalgae in the presence of nutrients at large spatial scales, and herbivores had greater effects on macroalgae when nutrients were higher. In addition, fishing did not increase herbivores. These results suggest that protecting herbivores may have greater relative benefits than reducing nutrient pollution, especially on polluted reefs. Reallocating fishing effort from herbivores to invertivores or planktivores may be one way to protect herbivores and indirectly maintain coral dominance on reefs impacted by fishing and nutrient pollution.

1. Introduction

Fishing [1–7] and nutrient pollution [8, 9] or both [10–14] are cited as the most important local causes of coral reef decline. It is difficult, however, to evaluate local fishing and nutrient effects independently because these factors are almost always confounded and large-scale experiments are infeasible. Results from theoretical and small-scale experimental studies (typically $<1\,\text{m}^2$, four from 50 to 250 m^2 [14]) suggest prioritizing management of herbivore populations because herbivores can control the effect of nutrients on macroalgal and turf abundance and nutrient enrichment alone is not sufficient to cause a phase shift from coral to macroalgal and/or turf algal dominance [11, 14, 15]. In order to apply these results and implement ecosystem-based management, information is needed on (1) how fishing and nutrients interactively affect the fish and benthic communities, (2) the mechanisms by which fishing (rather than cages that exclude fish) and nutrients are linked to shifts to macroalgal and turf algal dominance, and (3) whether herbivores can control macroalgae and turf algae when nutrient enrichment occurs at spatial scales of 10 s of kilometers, the spatial scale of local nutrient pollution.

Our understanding of how fishing and nutrients interactively affect fish and benthic communities is informed by a large number of factorial experiments that examine effects of herbivores and nutrients on benthic communities [14] and observational studies of the effects of marine reserves or fishing on the fish and benthic communities [1, 2, 4, 5, 7, 15–20]. A meta-analysis of factorial experiments that manipulated herbivores and nutrients suggests that low levels of herbivory are the primary factor increasing macroalgae on coral reefs but that nutrient enrichment can enhance this effect [14]. Nutrient enrichment, however, decreases turf algae in tropical systems when herbivores are present [14, 21]. In contrast, reef-builders (corals and crustose coralline algae (CCA)) are more abundant when herbivores are present [14, 21]. Nutrient enrichment affects corals and CCAs differently, just as it has different effects on macroalgae and turf algae. Corals are less abundant when nutrients are enriched [21], while CCA is more abundant when nutrients are enriched in the presence of herbivores [21]. Although there is a relatively good understanding of the effects of herbivores on algae, our understanding of the effects on corals is very limited because only one study to date is long enough to examine effects on coral recruitment [21].

No studies have factorialy manipulated fishing and nutrients and only limited inferences can be made from the results of experiments that use cages to reduce herbivory because it is unclear whether fishing also results in reduced herbivory. One hypothesis is that fishing removes top predators, indirectly increasing the abundance of herbivores and decreasing macroalgal and turf algal abundance through a trophic cascade [18–20]. There is limited evidence for trophic cascades on coral reefs probably because trophic linkages are diverse, some herbivores escape in size from predation, and some important herbivores, such as parrotfish, can be targets in mixed-gear coral reef fisheries [22]. Alternatively, fishing may first remove large, slow growing, late maturing fish and sequentially remove species with less vulnerable life histories [23]. In fisheries where these life history traits correspond well to specific trophic groups, this results in "fishing down the food chain" from top predators to carnivores to herbivores [24], which may increase macroalgal and turf algal abundance. Fisheries across a gradient of socioeconomic development show evidence of a transition from gillnets (nonselective) to spearguns (selective) to handlines (selective for predators/carnivores only) [25]. This suggests that more developed fisheries are more likely to cause a trophic cascade, while a fishery with a diversity of gear types may mask the effects of a trophic cascade by fishing simultaneously or sequentially down the food chain or size classes.

The relative importance of managing herbivore populations versus nutrient inputs depends on whether top-down control of macroalgae and turf algae, which has been shown in small-scale ($\sim 1\,\text{m}^2$) experiments, also occurs at large spatial scales. Using simple Lotka-Volterra models of nutrients, autotrophs, and consumers, Gruner et al. [26] predicted that top-down control should occur if herbivory increases proportionally with nutrient-induced increases in autotrophs. Therefore, top-down control could be an artifact of the small scale of an experiment if herbivores concentrate their grazing on small patches of nutrient enriched algae [14]. In contrast, empirical studies show that at larger spatial scales herbivores are less able to track resources because of increased resource heterogeneity or predation risk, suggesting that top down control will not be observed at large spatial scales [27–29]. Gruner et al. [26] found no association between the spatial scale of experiments and effect size of herbivores across 191 manipulative experiments; however, this may have been a result of comparing experiments across different ecosystems, over a small range of spatial scales (<1 to $\sim 400\,\text{m}^2$), or with few predators.

A population re-settlement program and island-wake upwelling (the vertical transport of nutrients from deeper waters caused by a current flowing around an island) on Kiritimati Atoll, Line Islands, Kiribati (Figures 1 and 2), created a unique large-scale natural experiment to test the ecosystem-scale effects of fishing and nutrients. Kiritimati was permanently settled less than 150 years ago but re-settlement of people from the capital, Tarawa (~3,000 km to the west), has caused rapid population growth (66% increase from 1985 to 2005) [30]. Despite the recent population growth, Kiritimati remains largely undeveloped with artisanal fishing being the primary economic activity. Spatial variation in fishing pressure is not expected to be caused by the variation in fish abundance because the spatial pattern of fishing is a consequence of the government program, an exogenous factor unrelated to fishing resources. Therefore, greater inference can be made about fishing as a factor in the observed ecosystem structure than in most studies along fishing gradients. Similar inferences can be made about the role of nutrients because island-wake upwelling is an exogenous factor that creates a zone of higher nutrients and primary production on the northwestern side of the island (Figure 2, see Figures S1, S2 in Supplementary Material available online at doi: 10.1155/2011/187248 for *in situ* data on currents, sea surface temperature, fluorescence, and phosphate). Importantly, fishing, and nutrients are not confounded because settlement has mostly occurred along the northern coastline and nutrient pollution from land is low because rainfall is low, there are no industrial activities, bird populations are lower near villages and, overall, the human population is relatively low [7, 31, 32].

Recent studies of the reefs in the upwelling zone on Kiritimati show that the water chemistry was more characteristic of nearshore reefs than oceanic reefs and had higher concentrations of microbes, which were associated with coral disease and fewer coral recruits [32]. These reefs also had fewer top predators and corals and more planktivores and macroalgae and turf algae compared to nearby unfished reefs (Palmyra Atoll and Kingman Reef) in less productive waters in the northern Line Islands [7]. However, the relative importance of fishing and nutrients is still uncertain because fishing was confounded with oceanographic conditions in previous studies of coral reefs in the northern Line Islands across a gradient of fishing pressure from unfished Palmyra and Kingman Atolls to fished Tabuaeran and Kiritimati (note that only sites in upwelling zone of Kiritimati were studied) [7, 32]. Here, I took advantage of the spatial variation in fishing and nutrients within Kiritimati to disentangle the effects of fishing and nutrients on coral reefs at the ecosystem scale.

In sum, I expected that reefs with higher nutrients should have a higher abundance of macroalgae, turf algae, herbivores, and planktivores, while fished reefs should have a lower abundance of top predators and carnivores (Table 1). I expected that fishing down the food chain and size classes should be the best supported mechanism for the pattern in fish abundance because Kiritimati has a fishery with a mix of gear types (Table 1). In addition, I expected that herbivores should not exhibit top down control of macroalgae and turf algae in the presence of nutrients because fishing and nutrients enrichment on Kiritimati occur at large spatial scales. I tested my expectations for the effects of nutrients and fishing on the abundance of fish and benthic community groups using a natural factorial experimental design (Figures 1 and 2). This natural experiment replicated small-scale manipulative experiments at a larger spatial scale and measured effects for a greater number of ecosystem

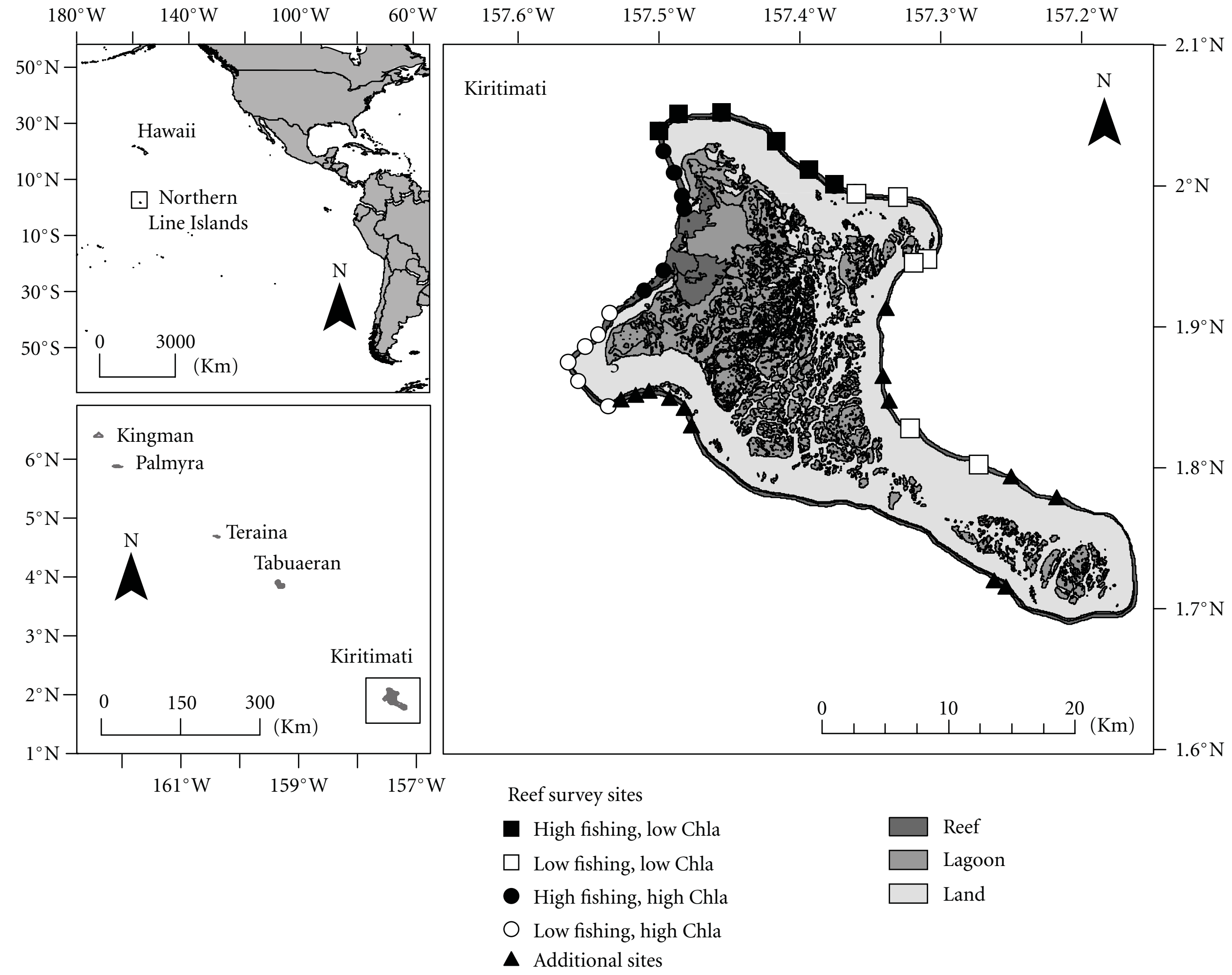


Figure 1: Location of ecological survey sites on Kiritimati, Line Islands, Republic of Kiribati. Twenty-four sites were chosen to create a balanced natural factorial experimental design to test the effect of nutrients (proxied by chlorophyll-*a*) and fishing on the fish and benthic communities. An additional 13 sites were chosen to capture the full fishing gradient and test mechanisms.

components. I then investigated the ecological mechanisms associated with fishing and top-down control of macroalgae and turf algae at large spatial scales using regression based-methods. These tests allowed for interpretation of the effects of fishing and nutrients on coral reef ecosystem structure in the context of ecosystem-based management [33].

2. Methods

2.1. Study Sites. I surveyed the benthic and fish communities at 37 sites in the fore-reef habitat (Figure 1) from July 20 to August 10, 2007. Of these, 24 were chosen using *a priori* knowledge of fishing and chlorophyll-*a* concentrations, based on the spatial distribution of upwelling and human settlements, to create a balanced factorial design with two factors (fishing and chlorophyll-*a*) and two levels of each factor (high and low). An additional 13 sites were chosen to capture the full fishing gradient and allow for tests of mechanisms using regression-based methods. These additional sites were not included in analyses of the natural factorial experiment because their inclusion would cause fishing and chlorophyll-*a* to be correlated; however, they could be used in the analysis of mechanisms linking changes in the fish community and chlorophyll-*a* to changes in the benthic community because chlorophyll-*a* was shown to not affect top predator or herbivore biomass (see results and Table S4 in Supplementary Material results of two-way ANOVA comparing effects of fishing and chlorophyll-*a* on fish biomass), and herbivore biomass and chlorophyll-*a* were not significantly correlated across the full range of sites (Spearman Correlation, rho $= -0.25$, $P = .14$). Sites were no less than 1 km apart (with one exception), and exact locations were chosen haphazardly. No sites were surveyed on the south central coast due to a lack of roads, the distance from the harbor, and large waves. Data on chlorophyll-*a* and fishing were estimated for each site using remote sensing and household survey data, respectively (Figure 2).

2.2. Data Collection

2.2.1. Benthic Cover. The percent cover of major benthic taxonomic groups [coral, CCA, turf algae, macroalgae, and

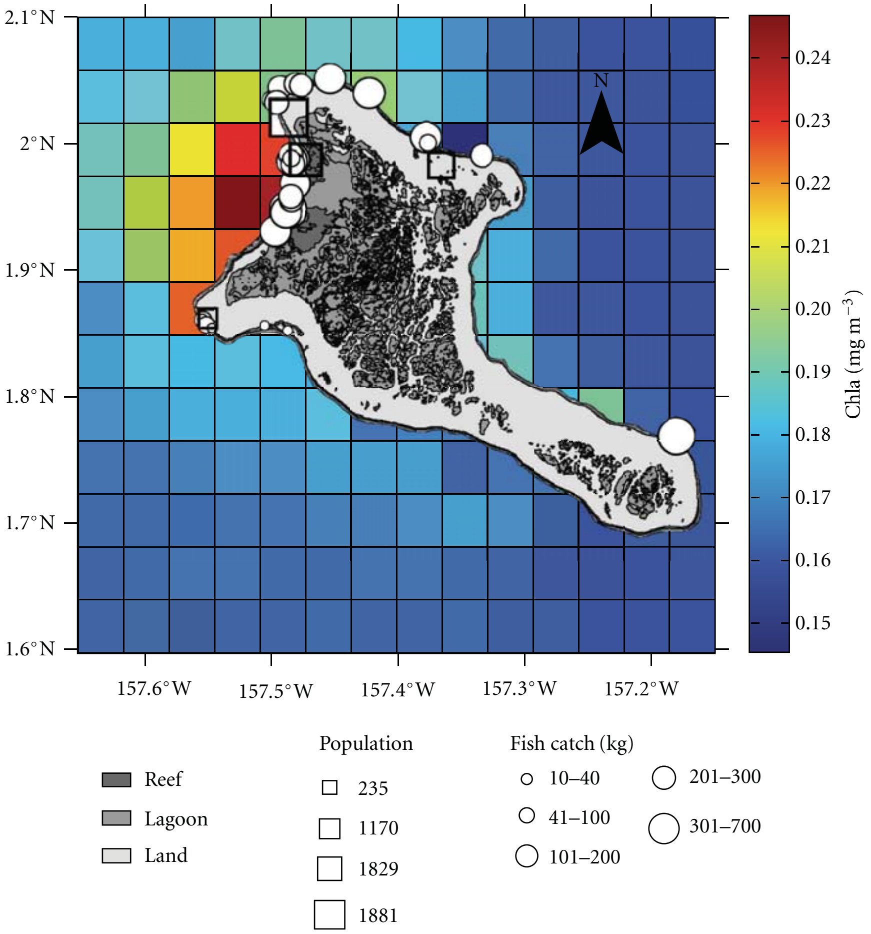


FIGURE 2: Chlorophyll-*a* (a proxy for nutrients) and fishing conditions. Island-wake upwelling in the northwest results in higher chlorophyll-*a* concentrations (September 16, 2002 to August 16, 2007 monthly average values). Fishing trips (represented as circles) cluster near the villages (represented as squares).

TABLE 1: Hypotheses for independent effects of nutrients and fishing*.

Dependent	Nutrients	Fishing					
		TC	SCC	FDFC		FDSC	
				Low	High	Low	High
Fish Community							
Top Predators	+	–	NA	–	–	–	–
Carnivores	+	–	NA	–	–	–/+	–
Planktivores	+	+	NA	NR	–	–/+	–
Herbivores	+	+	NA	NR	–	–/+	–
Large-bodied	+	NA	–	NA	NA	–	–
Small-bodied	+	NA	+	NA	NA	NR	–
Benthic Community							
Coral	–	+	–/+	NR	–	–/+	–
CCA	–	+	–/+	NR	–	–/+	–
Turf	+	–	–/+	NR	+	–/+	+
Macroalgae	+	–	–/+	NR	+	–/+	+

[*] This table shows the predicted response of fish trophic and benthic taxonomic groups to nutrients and fishing. Fishing may affect the fish and benthic community through four mechanisms: (1) trophic cascades (TC), (2) size class cascades (SCC), (3) fishing down the food chain (FDFC), and (4) fishing down the size classes (FDSC). Positive responses are indicated by +, negative responses by −, and ambiguous responses by −/+. No response is NR. Not applicable is NA. Predictions for responses to FDFC and FDSC are separated by low and high fishing pressure to distinguish between responses due to sequential fishing from high to low trophic levels or large-to small-bodied fishes.

other (see Table S1 in Supporting Information for assignments of benthic taxa to groups)] was measured using the photoquadrat method along two 25 m transects, separated by approximately 10 m at 10–12 m depth (for details see [7]). Five randomly chosen photographs from each transect were analyzed because additional photographs were determined to not significantly change the mean benthic cover of each functional group. In addition, a two-way ANOVA with site and photoquadrat as factors verified that the number of photoquadrats was sufficient to distinguish differences in percent cover of taxonomic groups between sites.

2.2.2. Reef Fish. Data on numerical abundance and length of reef fish species were collected by a pair of divers along three 25 m transects, separated by 10 m, on an isobath between 10–12 m depth at each site (for details see [7]). Counts were converted into biomass estimates using published length-weight parameters and summed by major trophic groups [top predators, carnivores, herbivores, and planktivores (see Table S2 in Supporting Information for assignments of fish species to trophic groups)]. As was done with the benthic data, a two-way ANOVA with site and transect as factors verified that the number of transects was sufficient to distinguish differences in biomass of trophic groups between sites.

2.2.3. Fishing. Surveys of fishing activity were conducted during July-August 2007 in the four villages of Kiritimati (Figure 2). The same percentage of surveys was conducted in each village (17%), except for the smallest village where a higher percentage (43%) was sampled to capture the expected variability in household fishing. Households were chosen haphazardly. The head of the household or other person sufficiently knowledgeable of the fishing activities of the household was interviewed after oral consent was obtained. The interviewee was asked to recall catch (kg) by family or species, effort, gear, location, and habitat for all fishing trips conducted over the previous seven days. Each trip was assigned a number, and the interviewee was asked to mark the location of each trip on a map. The fishing data were weighted by the reciprocal of the product of the number of households surveyed in a village and the probability that the household was chosen in order to make population-level estimates of fishing for each village.

2.2.4. Oceanographic Data. Chlorophyll-*a* was used as a proxy for nutrients because it is a more sensitive indicator of nutrient enrichment than nutrient concentrations themselves [34, 35]. Data on chlorophyll-*a* were obtained from MODIS on Aqua at a resolution of 0.04 degrees. Monthly chlorophyll-*a* data were collected from September 16, 2002 to August 16, 2007. Each site was assigned to the nearest cell, and the average value for the time series was used. When data were missing, the value of the cell was interpolated as the average of the adjacent cells. Chlorophyll-*a* data from the 24 sites, which were chosen to create the natural factorial design experiment, were tested for differences in chlorophyll-*a* concentrations inside and outside of the upwelling zone using a *t*-test. A categorical variable representing levels of chlorophyll-*a* (high and low) was then used in two-way fixed effects ANOVAs testing the effects of chlorophyll-*a* and fishing on benthic taxonomic and fish trophic groups at these 24 sites. Continuous site-specific chlorophyll-*a* data were used in regression based-analyses of the mechanisms structuring the fish and benthic communities.

Water samples were collected in July-August 2009 and analyzed for chlorophyll-*a* concentration to verify the patterns observed in the satellite data. A total of 21 surface water samples (500 mL) were collected in the upwelling zone, and 11 samples were collected outside of the upwelling zone while revisiting the 24 sites used to create the natural factorial design (Figure 1). Water was stored on ice, transported to shore, and filtered. Filters were stored in aluminum foil and frozen at −20°C. Upon returning to the lab, pigments were extracted from the filters with a 90% acetone solution. The extract was centrifuged, and the supernatant was analyzed for chlorophyll-*a* content using a Turner Designs Model 700 fluorometer. Since analyses could not be done immediately on island, chlorophyll-*a* concentrations were adjusted for degradation due to storage using the following formula: chl a concentration = $-17.31 * \log(\text{days stored at } -20^\circ\text{C}) + 95.88$ [36].

2.3. Data Analysis

2.3.1. Fishing Data. In total, 145 households were surveyed, which resulted in 248 fishing trips being characterized. The fore-reef habitat accounted for 23% of fishing trips ($n = 57$), and only these trips were analyzed. The remainder of the fishing trips were in the open ocean (28%), lagoon (44%), or in fish ponds (5%). Fish catch was binned by 2 km intervals along the coastline. The distance in either direction from each bin to each village was measured. An exponential function of this distance (x) was fit to the binned fish catch data (y) ($y = \beta_1 * \beta_2^x$) ($R^2 = 0.91$, $P < .001$). This function was weighted by the fraction of the fish catch in either direction from each village and then used to estimate fish catch at each ecological survey site using the distance from a village to the site. The total fish catch at a site was the sum of the fish catch from each of these village and direction-specific estimates. Fishing data from the 24 sites, which were chosen to create the natural factorial design experiment, were tested for differences in fish catch near and far from the population center using a *t*-test. As with chlorophyll-*a*, a categorical variable representing levels of fishing (high and low) was then used in two-way fixed effects ANOVAs testing the effects of chlorophyll-*a* and fishing on benthic taxonomic and fish trophic groups at these 24 sites. Continuous site-specific fish catch data were used in regression-based analyses of the mechanisms structuring the fish and benthic communities. Summary statistics on frequency of gear types and catch composition (percentage of top predator, carnivore, herbivore, and planktivore biomass) were calculated directly from the pooled catch data. Catch composition was compared across areas identified *a priori* as high and low fishing for the natural factorial experiment using MANOVA (Stata v9).

2.3.2. Ecosystem Structure. The differences in mean biomass of fish trophic groups (all log-transformed except for herbivore biomass) and percentage cover of each benthic taxonomic groups were tested using two-way ANOVA with chlorophyll-*a* and fishing as fixed effects (Stata v9). These data were tested for independence using Moran's I because sites within a given treatment were spatially clustered. There was no evidence of spatial autocorrelation for the nine response variables within any of the four treatments, except for herbivore biomass within the low chlorophyll-*a*/high fishing treatment (see Table S3 in Supporting Information for tests of independence for response variables within each treatment in the natural factorial experiment and across all sites). However, when herbivore biomass was estimated using ordinary least squares, the residuals were tested for spatial autocorrelation, and no evidence of spatial autocorrelation was found (Moran's $I = -0.04, P = .98$), validating the use of the two-way ANOVA. The percentage of variance explained by each fixed factor was calculated using omega squared ($\omega^2 = (\mathrm{SS}_{\mathrm{treated}} - \mathrm{df}_{\mathrm{treated}} * \mathrm{MS}_{\mathrm{error}})/(\mathrm{SS}_{\mathrm{total}} + \mathrm{MS}_{\mathrm{error}})$) [37, 38]. Negative values of ω^2 were set to zero because their effects were assumed to be negligible [37].

2.3.3. Mechanisms of Ecosystem Change. The full set of 37 sites was used to test mechanisms linking fishing to changes in the biomass of top predators, herbivores, large-bodied fishes (≥20 cm), and small-bodied (<20 cm) fishes. Two trophic-based fishing mechanisms (trophic cascades and fishing down the food chain) and two size-based fishing mechanisms (size class cascades and fishing down size classes) were tested. Size class cascades refer to patterns in which a low abundance of large fish, due to fishing, is associated with a high abundance of small fish, regardless of the trophic groups. For trophic-based models, I estimated the relationships between (1) fishing and top predators, (2) fishing and herbivores, and (3) top predators and herbivores. For size-class-based models, I estimated the relationship between (1) fishing and large-bodied fishes, (2) fishing and small-bodied fishes, and (3) large-bodied and small-bodied fishes. Linear and log-log models were estimated for the relationship between fishing and the biomass of fish groups. Linear, piecewise, and quadratic models were estimated for the relationship between the biomass of different fish groups. Piecewise models were estimated to test for evidence of fishing down mechanisms and identify points ("cut points") where fishing pressure switches from one fish group to another (see Supplementary Methods). Quadratic models were estimated to test for evidence of mixed control by cascading and fishing down mechanisms.

Prior to model estimation, top predator, herbivore, large-bodied fish and small-bodied fish biomass were tested for independence across all sites using Moran's I and failed (see Table S3). Models were then estimated using ordinary least squares. In the case of piecewise models with an unknown cut point, the cut point was first estimated using nonlinear least squares, and then the estimated cut point was used to estimate a piecewise function (see Supplementary Methods). After estimation of each model, the residuals were tested for spatial autocorrelation. If the residuals exhibited spatial autocorrelation, models were estimated using spatial simultaneous autoregressive linear models (R 2.7.0). Akaike's Information Criterion adjusted for sample size ($\mathrm{AIC_c}$) was used to assess the relative information content of each model. Normalized Akaike weights ($w_i = \exp(-(1/2)\Delta_i)/\sum_{n=1}^{N}\exp(-(1/2)\Delta_n)$) were presented to indicate the probability that the given model (i) was the best model out of the set of N models considered [39]. Monte Carlo permutation tests were used to test the robustness of the best models estimates because there were far fewer observations at sites experiencing high fish catch (R 2.7.0). P values were generated from comparisons of F-statistics associated with ordinary least squares estimates of a model using the observed data and 1,000 random permutations of the data.

The full set of 37 sites was also used to test for mechanisms linking fishing of herbivores and enrichment of nutrients to changes in benthic community structure. Six models representing all combinations of independent and interactive effects of herbivore biomass and chlorophyll-*a* were estimated for each benthic taxonomic group (coral, CCA, turf, macroalgae) (see Table S6). The four benthic taxonomic groups were tested for independence across all sites using Moran's I and failed (see Table S3). Following the same procedure as was used for models of fishing mechanisms, models were estimated using ordinary least squares, and the residuals were tested for spatial autocorrelation. When there was evidence of spatial autocorrelation, models were estimated using spatial simultaneous autoregressive linear models (R 2.7.0). The $\mathrm{AIC_c}$ and normalized Akaike weights were calculated for each model (see Table S6) to determine which models best explained the patterns of abundance in benthic taxonomic groups (for estimates of best candidate models, see Table S7).

3. Results

3.1. Fishing and Chlorophyll-a Conditions. The analysis of chlorophyll-*a* levels and fishing pressure for the subset of 24 sites validated the factorial experimental design. Fish catch was higher at sites that were *a priori* assigned to the high fishing "treatment" in the north near the two largest villages (141 $\mathrm{kg\,km^{-1}\,wk^{-1}}$), which are inside and outside of the upwelling zone, than away from the villages at sites that were assigned to the low fishing "treatment" (27 $\mathrm{kg\,km^{-1}\,wk^{-1}}$) ($t_{(22)} = -2.73, P < .01$; Figure 2), supporting the claim that patterns in fishing pressure have been determined exogenously by the population re-settlement program. However, fish catch was not significantly different across sites within the upwelling zone assigned to the high chlorophyll-*a* "treatment" and sites outside of the upwelling zone assigned to the low chlorophyll-*a* "treatment" ($t_{(22)} = 0.12, P = .90$).

Across all sites, fish catch ranged from 445 $\mathrm{kg\,km^{-1}\,wk^{-1}}$ to less than 1 $\mathrm{kg\,km^{-1}\,wk^{-1}}$. Half of fishing trips used hook

Table 2: Models of effects of fishing on fish trophic group and size-class biomass.

Dependent	Predictor	AIC_c	$\Delta\text{AIC}_\text{c}{}^\dagger$	w_i
	Trophic-based Models			
ln(Top Predators)	ln(Fish Catch)	93.67	0	99.8
	Fish Catch*	106.05	12.38	0.2
ln(Herbivores)	ln(Fish Catch)	113.73	130.52	$\ll$0.1
Herbivores	Fish Catch	−16.79	0	100.0
Herbivores	Top Predators*	−0.86	12.64	0.2
	Quadratic Top Predators	−6.75	6.75	3.3
	Piecewise Top Predators‡	−12.88	0	96.5
	Size-based Models			
ln(Large-bodied fishes)	ln(Fish Catch)	98.48	0	82.5
	Fish Catch	101.58	3.1	17.5
ln(Small-bodied fishes)	ln(Fish Catch)*	99.93	3.92	12.3
	Fish Catch	96.01	0	87.7
ln(Small-bodied fishes)	Large-bodied fishes*	98.35	12.28	0.2
	Quadratic Large-bodied fishes*	92.09	6.02	4.69
	Piecewise Large-bodied fishes‡	86.07	0	95.11

†Difference in AIC_c between a given model, i, and the model with the minimum AIC_c.

*All predictors are random variables, and models were estimated using ordinary least squares. However, if residuals exhibited spatial autocorrelation, relationships were estimated using spatial simultaneous autoregressive linear models.

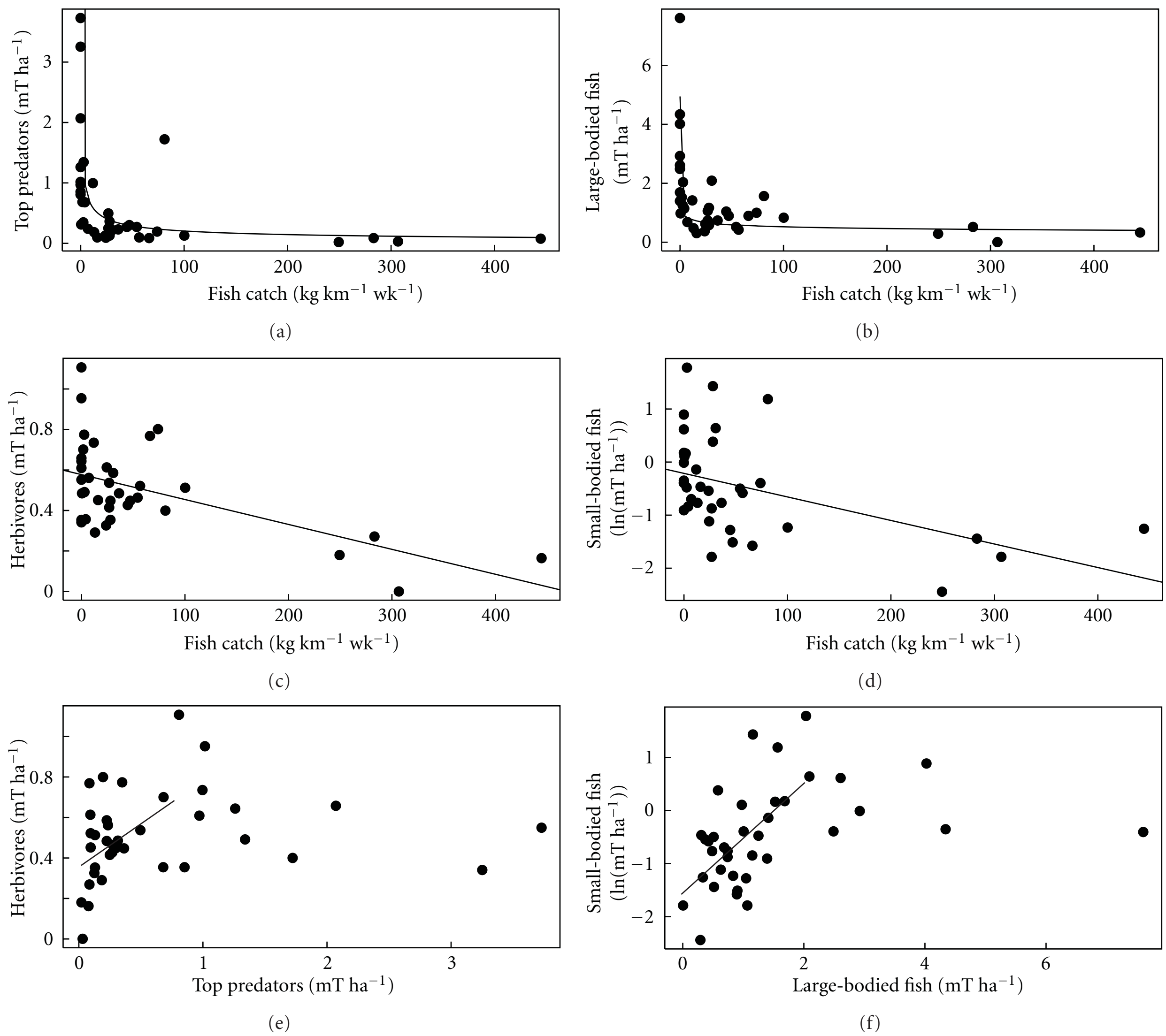
‡A piecewise regression model is of the form $y = a + b_1x + b_2x_c$, where a is the intercept, b_1 and b_2 are slopes, and $x_c = x - c$ (c is a cut point) if $x \geq c$ and $x_c = 0$ if $x < c$.

and line. Gillnets (26%) and spears (19%) were the next most common gear. A small percentage of fishermen (5%) used SCUBA and hand nets to collect fish for the aquarium trade. Top predators (37%) and herbivores (36%) comprised the largest percentage of the total catch by biomass. Carnivores (20%) were the next largest, and planktivores (7%) were a small percentage of the total catch. Catch composition (percentage of biomass by trophic group) was not different in areas with high and low fish catch ($F_{(4,76)} = 1.18$, $P = .32$).

The twelve sites along the northwestern coastline in the upwelling zone that were assigned to the high chlorophyll-*a* "treatment" had a 18.6% (95% CI: 17.7%–18.8%) higher mean chlorophyll-*a* concentration (0.221 mg m^{-3}), as observed monthly by MODIS on Aqua between 2002 and 2007 than the twelve sites along the northeastern coastline, which are outside of the upwelling zone and assigned to the low chlorophyll-*a* "treatment" (0.180 mg m^{-3}) ($t_{(22)} = -6.14$, $P < .0001$; Figure 2). *In situ* chlorophyll-*a* concentrations measured in 2009 also supported this pattern ($t_{(30)} = -2.16$, $P < .05$). When all sites were considered, a 41.2% (95% CI: 37.6%–44.4%) difference in chlorophyll-*a* concentration was observed from the highest to the lowest chlorophyll-*a* site. Satellite-derived chlorophyll-*a* levels were not, however, significantly different across areas within the high and low fishing "treatments" ($t_{(22)} = -1.35$, $P = .19$). Although the lagoon entrance and one of the two largest villages are in the upwelling zone, current and isotope data suggest that the nutrient patterns are determined exogenously by patterns of upwelling. Interpolation of surface currents from ACDP vector data shows an inflow of water to the lagoon (see Figure S1). Moreover, the lagoon waters are largely oligotrophic given the limited land runoff. In addition, Dinsdale et al. [32] found no evidence of human waste water in the nitrogen isotope signature of particulate organic matter in the upwelling zone.

3.2. Ecosystem Structure. Fishing had the largest effect on and explained most of the variance in the biomass of the upper trophic levels of the fish community (see Table S4 in Supporting Information). Top predator biomass was 75% higher at sites with low fish catch (0.78 mT ha^{-1}) as compared to sites with high fish catch (0.18 mT ha^{-1}) ($F_{(1,20)} = 8.37$,$P < .01$). Carnivore biomass was 63% lower at sites with high fish catch ($F_{(1,20)} = 7.80$, $P < .05$). In contrast, planktivore biomass was only 36% lower at these sites ($F_{(1,20)} = 4.54$, $P < .05$). Herbivore biomass showed no change over the range of fish catch captured in the factorial experimental design ($F_{(1,20)} = 1.22$, $P = .28$), although parrotfish biomass was marginally lower at sites with high fish catch ($F_{(1,20)} = 2.45$, $P = .13$).

Chlorophyll-*a* mainly affected the lower trophic levels of the benthic community (see Table S5 in Supporting Information for results of two-way ANOVA comparing effects of fishing and chlorophyll-*a* on benthic taxonomic group percent cover). Percent cover of both turf ($F_{(1,20)} = 10.24$, $P < .01$) and macroalgae ($F_{(1,20)} = 11.06$, $P < .01$) was higher at sites with high chlorophyll-*a*, whereas CCA cover was lower ($F_{(1,20)} = 17.56$, $P < .001$). Macroalgal cover was also higher at sites with high fish catch ($F_{(1,20)} = 4.86$, $P < .05$). Although macroalgal cover was affected by fishing and chlorophyll-*a*, coral cover was not affected by either fishing ($F_{(1,20)} = 0.00$, $P = .98$) or chlorophyll-*a* ($F_{(1,20)} = 1.75$, $P = .20$). The only fish group affected by chlorophyll-*a* was the planktivores ($F_{(1,20)} = 9.19$, $P < .01$). Planktivore biomass



(a)

(b)

(c)

(d)

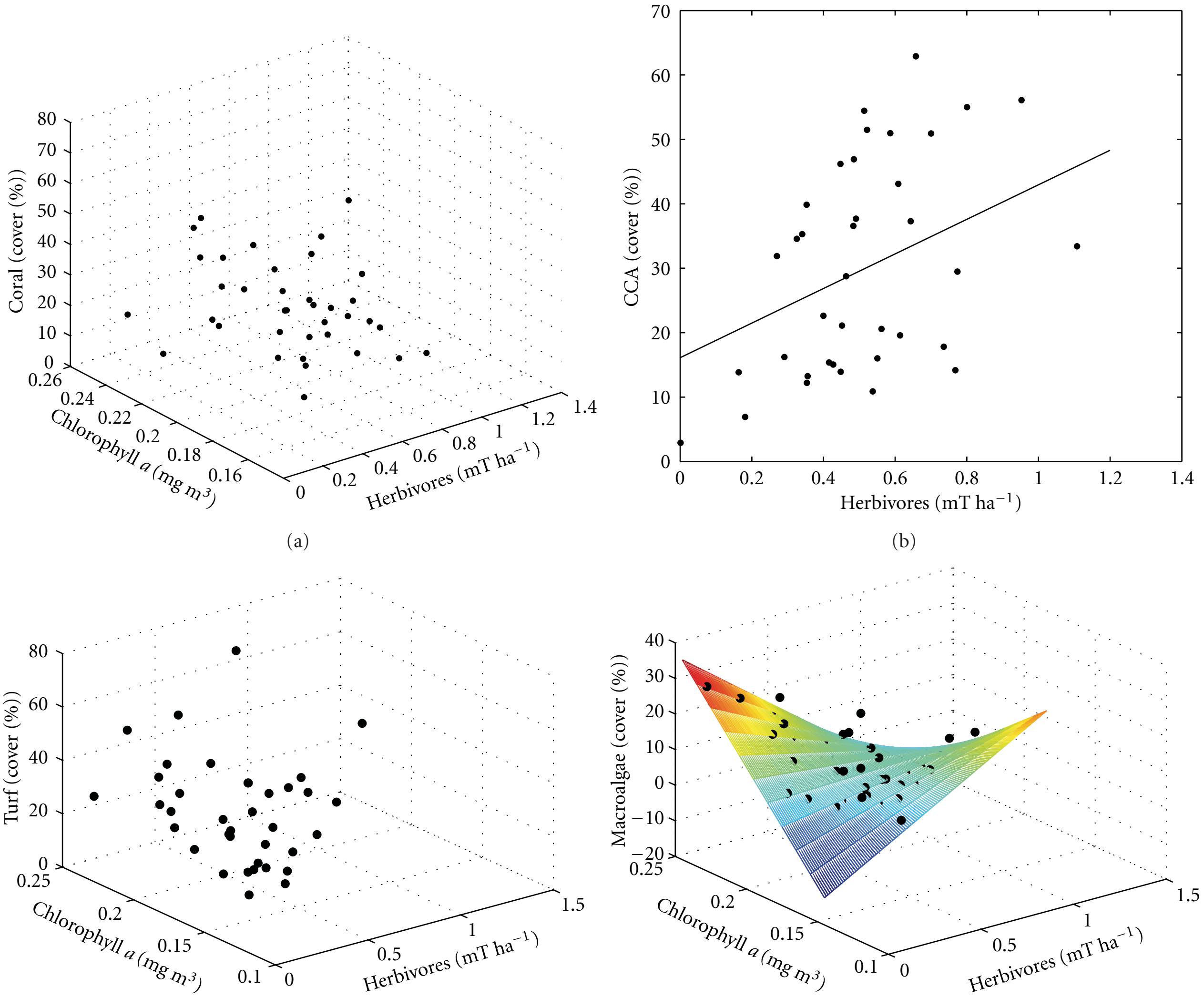
(e)

(f)

Figure 3: The effects of fishing on top predators, herbivores, large- and small-bodied fish biomass. Fishing resulted in exponential declines in top predator ((a) $R^2 = 0.58, P < .0001$; permutation test: $P < .0001$) and large-bodied fishes ((b) $R^2 = 0.43$, $P < .0001$, permutation test: $P < .0001$) biomass. Herbivores ((c) $R^2 = 0.30$, $P < .001$, permutation test: $P < .0001$) and small-bodied fishes ((d) $R^2 = 0.22$, $P < .01$, permutation test: $P < .01$) biomass declined linearly with fish catch. Herbivore biomass only declined when top predator biomass was less than 0.81 mT/ha (95% CI: 0.16, 1.44) ((e) $R^2 = 0.24$, $P < .01$, permutation test: $P < .05$). Small-bodied fish biomass only declined when large-bodied fish biomass was less than 2.04 mT/ha (95% CI: 1.16, 2.90) ((f) $R^2 = 0.41$, $P < .001$, permutation test: $P < .0001$).

was higher at low chlorophyll-*a* sites, outside of the upwelling zone. Planktivores outside of the upwelling zone were mostly large-bodied Fusiliers as compared to small-bodied *Anthias* and *Chromis* inside the upwelling zone.

3.3. Mechanisms of Ecosystem Change. The full set of 37 sites was used for tests of mechanisms linking (1) fishing to changes in top predators, herbivores, large-bodied fishes, and small-bodied fishes and (2) fishing of herbivores and enrichment of nutrients to changes in benthic community structure. Fishing resulted in an exponential decline of top predators from 3.73 mT ha^{-1} (73% of total biomass) at the least fished site to 0.02 mT/ha (6% of total biomass) at the most fished site (Table 2, Figure 3(a)). Large-bodied fishes showed a similar trend from 7.61 mT ha^{-1} (92% of total biomass) to <0.01 mT ha^{-1} (4% of total biomass) (Table 2, Figure 3(b)). Herbivore and small-bodied fishes declined less dramatically with fish catch (Table 2, Figures 3(c) and 3(d)); however, both were highly variable at sites with low fish catch. This pattern may be explained by the apparently bimodal relationships between trophic groups and between size classes. When top predator biomass is high (cut point: ≥0.81 mT/ha (95% CI: 0.16, 1.44)), corresponding to low fish catch, herbivore biomass was unrelated to top predator biomass but then declined when top predator biomass was low (<0.81 mT/ha), supporting the fishing down the food chain hypothesis (Table 2, Figure 3(e)). Small-bodied fishes biomass showed the same pattern, with biomass



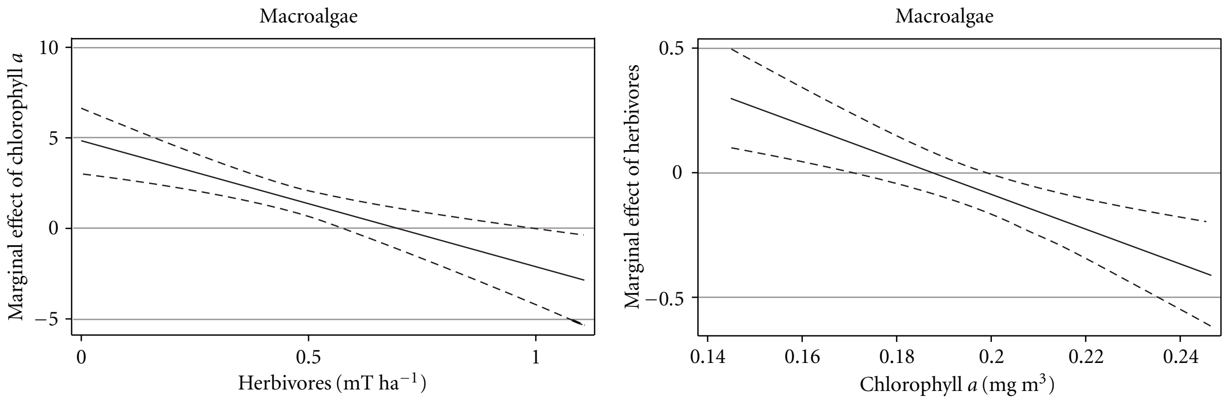
(a) (b)

(c) (d)

Figure 4: The effect of herbivores and chlorophyll-*a* on benthic functional groups. (a) Coral was not significantly affected by herbivores, chlorophyll-*a*, or their interaction, (b) CCA and fitted values (black line) as a function of herbivore biomass ($P < .01$) (pseudo $R^2 = 0.59$, $P < .05$), (c) turf was not significantly affected by herbivores, chlorophyll-*a*, or their interaction, and (d) macroalgae and fitted values (rainbow mesh) predicted by herbivores ($P < .01$), nutrients ($P < .001$), and an interactive term ($P < .01$) ($R^2 = 0.56$, $P < .0001$). See Tables S6 and S7 in Supporting Information for model selection and detailed statistics.

declining only when large-bodied fish biomass was low (cut point: <2.04 mT/ha (95% CI: 1.16, 2.90)), supporting the fishing down size classes hypothesis (Table 2, Figure 3(f)). Permutation tests verified the robustness of these model estimates to the low number of sites sampled under low fishing conditions.

No single model carried the majority of the weight (i.e., $w_i > 0.50$) in explaining the abundance of coral, CCA, and turf (see Table S6 in Supporting Information for results of selection of best models of the effect of herbivores and chlorophyll-*a* on the percent cover of benthic taxonomic groups). Coral cover was best explained ($w_i = 0.25$) by the additive effects of herbivore biomass and chlorophyll-*a* levels with all other models having weights equal or less than 0.20; however, these individual effects were not significant (Figure 4(a), Table S6, see Table S7 in Supporting Information for detailed statistics of model estimates of the effect of herbivores, chlorophyll-*a* and/or their interaction on benthic taxonomic groups from the best candidate models). Models with herbivore biomass alone ($w_i = 0.29$) and herbivore biomass and the interaction between herbivore biomass and chlorophyll-*a* ($w_i = 0.28$) were almost equally likely to provide the best estimates of CCA cover (see Tables S6 and S7). These models provide evidence that increases in herbivore biomass should be associated with increases in CCA cover but that the magnitude of this effect should decrease with increasing chlorophyll-*a* levels, although this interactive effect is only significant at a 90% confidence level (Figure 4(b), see Table S7). Models with herbivore biomass alone ($w_i = 0.24$) and herbivore biomass and the interaction between herbivore biomass and chlorophyll-*a* ($w_i = 0.26$) were also almost equally likely to provide the



(a)

(b)

Figure 5: The marginal effects of herbivores and chlorophyll-*a* on macroalgae. (a) The marginal effect of chlorophyll-*a* on macroalgae as a function of herbivore biomass and (b) the marginal effect of herbivores on macroalgae as a function of chlorophyll-*a*. Marginal effects were estimated from the best fit model of macroalgae to herbivores, chlorophyll-*a*, and their interaction (see Tables S6 and S7). Dotted lines are 95% confidence intervals.

best estimates of turf cover; however, the effects were not significant (Figure 4(c), see Tables S6 and S7).

A model of macroalgal cover including the predictor variables herbivores, chlorophyll-*a*, and their interaction, had a very high level of support ($w_i = 0.98$). Herbivores and chlorophyll-*a* had significant independent and interactive effects on macroalgal cover (Figure 4(d), see Tables S6 and S7). Increases in herbivore biomass were estimated to result in decreases in macroalgal cover, and this effect was enhanced with increasing chlorophyll-*a* (Figure 5(a)). Macroalgal cover was estimated to increase with increasing chlorophyll-*a*; however, increasing herbivore biomass reduced this effect (Figure 5(b)).

4. Discussion

The results of this large-scale natural experiment support those found at smaller scales, namely, that herbivores and nutrients control the balance between macroalgae and turf algae and reef-builders [14]. However, this study expands on previous research to show that (1) fishing primarily affects the fish community while nutrients primarily affect the benthic community, (2) fishing down the food chain or size classes are the best supported mechanisms by which fishing indirectly affects the benthos, and (3) herbivores and nutrients have unexpected interactive effects on macroalgal cover at large spatial scales. The first finding increases our understanding of the independent and interactive effects of nutrients and fishing on the benthic and fish community by including additional taxa and measuring fishing directly, while the other findings have important implications for management.

Fishing significantly decreased the biomass of all fish functional groups, when sites from the full fishing gradient were considered, and had the greatest effect on the upper trophic levels and large-bodied fishes. About half of fishing trips observed used hook and line, which selects for larger predators or carnivores. This was evidenced by the fact that almost 40% of the catch was comprised of top predators and 20% was carnivores. It is not surprising then that fishing had a strong effect on both top predator and large-bodied fish biomass. However, the exponentially lower level of these groups at sites with high fishing is probably due also to their extreme vulnerability to fishing since they tend to have slow growth and late maturation [23].

Herbivore and small-bodied fish biomass showed less dramatic differences between sites with different levels of fishing. Herbivore biomass was highly variable and not significantly affected by fishing when only the 24 sites included in the natural factorial design experiment, which do not include the mostly lightly fished sites, were evaluated. Gillnets, which are unselective and can capture herbivores and small fish, were used in about a quarter of all fishing trips. Spears, which are highly selective, were used in 14% of all fishing trips to catch larger herbivores, among other fish. Although almost 40% of the total catch was herbivores, the diversity of life histories of herbivores may ameliorate the effects on the entire functional group. In addition, there may have been insufficient statistical power to detect differences in herbivore biomass in the natural factorial experimental design, given the high variability of herbivore biomass at these sites. It is also possible that the variability in herbivore biomass at these sites reflects the higher variability in benthic community structure and is less related to fishing pressure.

There was no evidence that fishing top predators or large-bodied fishes was associated with higher levels of herbivores or small-bodied fishes, respectively. This is consistent with the general finding that trophic cascades are not widespread on coral reefs [22]. However, trophic cascades has been observed involving invertebrates, such as sea urchins and crown-of-thorns [40–43]. These invertebrates were virtually absent from reefs on Kiritimati; however, in more recent visits a high abundance of urchins have been observed at the most heavily fished sites. Evidence of an increase in the smallest size classes of fish have been observed on Fijian reefs [17]. However, this was not observed on Kiritimati possibly because the mixed gear fishery and flexibility of the local diet allow fishermen to switch to targeting herbivores and small-bodied fishes at sites where top predators and large-bodied fishes are not abundant. Together these findings help inform the debate over whether restoring top predator populations in marine reserves may have direct negative impacts on herbivore populations and indirect negative impacts on corals through reduced herbivory [18]. Marine reserves are unlikely to have negative indirect effects on corals if trophic cascades are uncommon on coral reef and spillover of predators from marine reserves may even help effectively protect herbivores outside the reserves if top predators are fished preferentially.

Herbivore biomass and nutrients (proxied by chlorophyll-*a*) were important predictors of benthic community structure. Coral, CCA, and turf algal cover exhibited mixed control, as evidenced by the fact that no single model of herbivore, nutrients, and their interaction had the majority of support (measured by AIC_c weights). In contrast, there was overwhelming support for a model including main and interactive effects of herbivores and nutrients as the best predictor of macroalgal cover. None of the predictors in the best supported models of coral and turf algal cover were significant at a 95% confidence level, while all predictors in the best candidate models for CCA and macroalgal cover were significant at this level. The intermediate response times of CCA and macroalgae in comparison to the very fast and very slow response times of turf algae and coral, respectively, may explain this difference in the significance of predictor variables. Turf may grow rapidly after being grazed making the effects of herbivores difficult to observe. Corals grow slowly and may maintain the same size over long time scales despite changes in nutrients and herbivores, making percent cover a less sensitive metric. Despite the lack of significant effects of herbivores and nutrients on corals, the observed decline in CCA and increase in macroalgae in response to fishing herbivores and nutrient enrichment suggest that future declines in corals may occur due to decreased survival of recruits [32]. These results also support the hypothesis that differences in the levels of reef-builder cover found for the leeward sides of the northern Line Islands must be due at least in part to differences in fishing pressure and cannot be attributed to oceanographic effects alone [7].

In contrast to theoretical predictions, a significant interactive effect of herbivores and nutrients on macroalgae was found at a large spatial scale (interactive effects were only significant at a 90% confidence level for turf algae) when all sites were analyzed using regression based methods. The natural factorial experiment results that were based on a subset of sites, however, did not find support for interactive effects of fishing and nutrients on macroalgae. This may be due to insufficient power, the insignificant effect of fishing on herbivores at these sites or that reductions in herbivores due to fishing, not fishing in general, affect macroalgae. Similar to small-scale manipulative experimental results, macroalgal cover was higher when nutrients were high and herbivores were low but nutrients had less of an effect on macroalgae when herbivores were high [14, 21]. This suggests that herbivores are able to track resources even at larger spatial scales and/or predators have a limited ability to control herbivores. In another large-scale natural experiment, Russ and McCook [44] found evidence that herbivores could control macroalgal growth following a cyclone that elevated nutrient inputs. However, a cyclone only results in a short pulse of nutrients while island-wake upwelling on Kiritimati results in persistently higher nutrients. In addition, the limited evidence for trophic cascades in this study and others supports the claim that predators do not control herbivore abundance. However, unlike small-scale experimental results, herbivores had less of an effect on macroalgae when nutrients were low. One possible explanation for this trend is that macroalgae are less susceptible to herbivory at lower nutrient levels due to plasticity within a species or changes in community composition [26]. In fact, *Peyssonnelia* spp. and *Lobophora* sp., which have been shown to be highly resistant to herbivory, were more abundant at sites with lower chlorophyll-*a* concentrations [45, 46]. This result may not be commonly reported because the time scale of manipulative experiments may be too short to observe shifts in species composition or algal defenses [26]. To resolve these issues, experimental designs that extend the spatial *and* temporal scale of these impacts are needed [21, 26].

This study provides insight into how the results of small-scale experiments apply to ecosystem-based management because it was conducted at a large scale and measured effects on the fish and benthic communities. It also improves upon studies that have used natural gradients in nutrients [13, 47] or fishing [4, 5, 7] by taking advantage of orthogonal gradients in both factors, measuring fishing directly through the use of household surveys rather than using human population as a proxy, and using spatial simultaneous autoregressive linear models to address issues of spatial autocorrelation, when necessary.

This study, however, is still limited because it examined a relatively small number of reefs on a single island in a single season, it did not experimentally manipulate the factors, and nutrient enrichment was natural and relatively low compared to polluted reefs (reefs polluted by sewage in Kaneohe, Hawaii had chlorophyll-*a* levels up to $0.68\,\text{mg}\,\text{m}^{-3}$ [48]). Ideally the study would have examined multiple sites with all combinations of high and low fishing and nutrient pollution or manipulated these factors over 10s of kilometers. However, I am unaware of sites with these conditions, and large-scale manipulations may be impractical or unethical. Despite the small number of sites surveyed, especially in low fishing conditions, permutation tests verified the robustness of these results. In addition, fishermen noted during household surveys that fisheries on Kiritimati have limited seasonality, suggesting that a survey in a single season may be a good representation of fishing activities. By taking advantage of a unique situation in which fishing and nutrients can be argued to be determined exogenously by oceanography and government policy, some inference can be made about the causal role of fishing and nutrients in ecosystem patterns at large spatial scales. However, other factors, such as wave exposure, light, and temperature, could not be controlled across “treatments.” Data on mean wave direction from the Christmas Island Buoy shows that the island is exposed to both north and south swells with similar frequency, therefore, it cannot be concluded that there are consistent differences in wave exposure at sites with different levels of fishing or nutrients [49] (Figure S3). Given that nutrient concentrations vary due to upwelling, light and temperature would be expected to be confounded with nutrients. Although the role of light and temperature cannot be rejected with the data presented here, a study of upwelling, caused by internal tidal bores, on Florida coral reefs showed increased N and δ^{15}N and decreased C : N ratio in benthic macroalgae across a gradient of increased exposure to upwelling, which provides evidence for a mechanistic linkage between nutrients and algal growth despite evident differences in temperature and light [47].

Natural and manipulative experiments have their limitations, but results from both are needed especially for the development and evaluation of ecosystem-based management strategies [50]. Future research should develop a set of ecosystem-based management scenarios by conducting manipulative experiments at reef sites that represent the range of nutrient and fishing conditions and then use economic valuation methods to estimate the costs and benefits of reducing fishing and/or nutrients under different background conditions.

The common coincidence of fishing and nutrient enrichment, either due to better weather conditions for fishing in the lee of islands where island-wake upwelling occurs or the proximity of fishing grounds to sources of pollution, suggests that coral reefs in preferred fishing areas may be more sensitive to overfishing. Two management strategies are suggested by this study, which warrant further investigation. In the case of island-wake upwelling, reserves or spatial fish catch limits could be used to shift fishing pressure away from areas of high nutrients in order to reduce the risk of losing reef-builders. Similar policies could be used in the case of nutrient pollution; however, the costs of fisheries regulations should be weighed against the benefits of reducing other economic activities, which cause nutrient pollution. Fishing regulations should specifically aim to shift fishing effort away from herbivores and toward invertivores or planktivores, which may not have negative indirect effects on corals. Although managing both fishing and nutrients is important, protecting herbivore populations may result in greater relative benefits since herbivores can control macroalgae in the presence of nutrient enrichment, are even more effective grazers of macroalgae at high nutrient levels, and independently promote higher CCA cover.

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Review Article

The Ecology of Coral Reef Top Predators in the Papahānaumokuākea Marine National Monument

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Coral reef habitats in the Papahānaumokuākea Marine National Monument (PMNM) are characterized by abundant top-level predators such as sharks and jacks. The predator assemblage is dominated both numerically and in biomass by giant trevally (*Caranx ignobilis*) and Galapagos sharks (*Carcharhinus galapagensis*). A lower diversity of predatory teleosts, particularly groupers and snappers, distinguishes the PMNM from other remote, unfished atolls in the Pacific. Most coral reef top predators are site attached to a "home" atoll, but move extensively within these atolls. Abundances of the most common sharks and jacks are highest in atoll fore reef habitats. Top predators within the PMNM forage on a diverse range of prey and exert top-down control over shallow-water reef fish assemblages. Ecological models suggest ecosystem processes may be most impacted by top predators through indirect effects of predation. Knowledge gaps are identified to guide future studies of top predators in the PMNM.

1. Introduction

Large predators are becoming scarce on many coral reefs, with fishing thought to be a major factor in declines [1–7]. Coral reef top predators often command high market prices, providing strong economic incentives for commercial harvesting [8, 9]. Major contributors to commercial overharvesting of coral reef predators include the shark fin fishery [8, 10–12] and the live reef food fish trade [9, 13]. Consequently, intensive commercial exploitation has resulted in dramatic declines in reef predators in many locations [4, 13], and recent studies suggest even subsistence fishing can deplete reef predators [2, 5, 6]. Although less clear cut than in terrestrial systems (e.g., [14, 15]), there is growing evidence that removal of top predators from marine ecosystems may trigger trophic cascades resulting in phase shifts [2, 6, 16–19]. In coral reef ecosystems, these shifts appear to favor algal-dominated reefs populated by small planktivorous fishes and echinoderms, at the expense of reef-building scleractinian corals [2, 6, 16, 19]. Collectively these studies indicate that effective conservation of top level predators is important for coral reef ecosystem health.

Science-based management and effective conservation of coral reef top predators requires a broad understanding of their ecology. We need to know which species are present, their abundance, spatial dynamics and habitat requirements, rates of growth, reproduction and mortality, diet, and ecological interactions with other species. Unfortunately, the natural ecology of top predators has already been substantially altered in heavily impacted ecosystems. For example, overfishing has resulted in extirpation of spawning aggregations of coral reef top predators such as grouper and snapper in many areas [3]. Social learning, or tradition, may play a key role in the development and repeated formation of individual spawning aggregations [20], and this knowledge may be lost when the aggregations are overharvested [3]. Empirical data from areas in which predator ecology is minimally impacted by humans would be useful for determining how we have altered predator ecology in heavily impacted areas and for setting management goals to help restore predator populations and ecosystem function. One such minimally impacted area is the Papahānaumokuākea Marine National Monument (PMNM) in the Northwestern Hawaiian Islands. The PMNM consists of a series of rocky

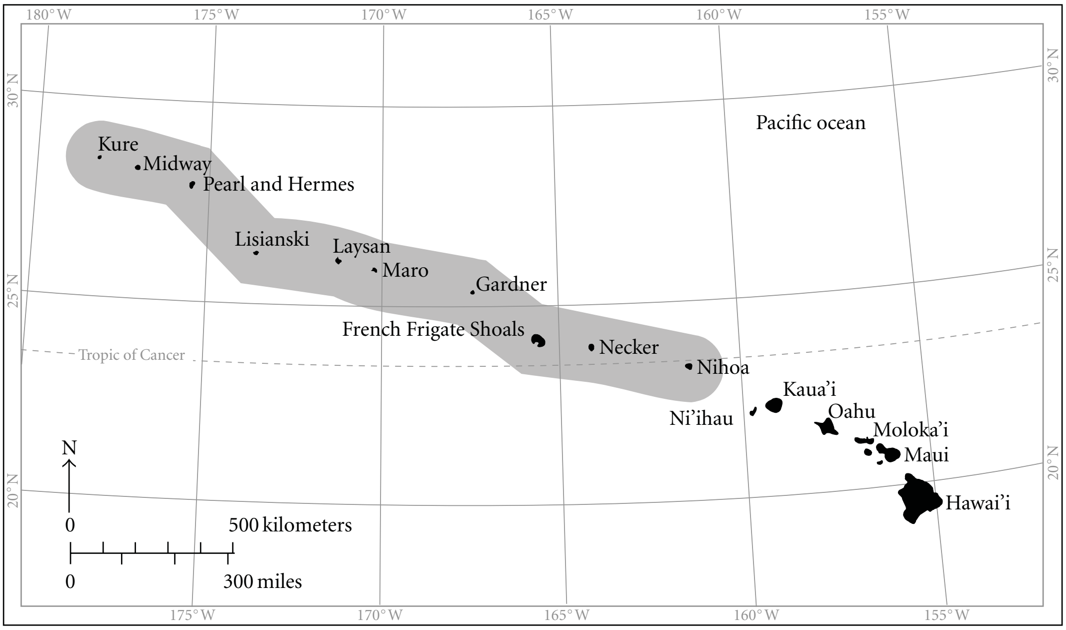


Figure 1: Map of the Hawaiian Archipelago showing major islands, reefs, and atolls. Shaded zone represents boundaries of the Papahānaumokuākea Marine National Monument.

pinnacles, atolls, reefs and submerged banks extending 1,930 km from Nihoa Rock to Kure Atoll and encompassing an area of 341,360 km^2 (Figure 1). These sites are closed to fishing and are characterized by predator-dominated fish assemblages [1]. Here, we review what is currently known about top predator ecology in the PMNM and identify important knowledge gaps that limit our understanding of this ecosystem.

2. Species Composition and Abundance

Our knowledge of the species composition and abundance of coral reef-associated predators in the PMNM comes from studies utilizing a variety of fishing and visual census sampling methods, which collectively suggest reef habitats in this region are dominated, both numerically and in biomass, by a small number of predator species, especially the giant trevally (*Caranx ignobilis*) and the Galapagos shark (*Carcharhinus galapagensis*) (Figure 2). Giant trevally account for 55% of all top predators counted by divers in the PMNM (Figure 2) and comprise 71% of apex predator biomass (equivalent to about 39% of total fish biomass) in this region [1, 21]. Galapagos sharks are the most abundant elasmobranch, accounting for 9.3% of all top predators counted during towed-diver surveys and comprising 36 to 53% of all sharks sampled by towed-diver surveys or longline fishing methods (Figure 2) (see [21, 22], J. Dale, unpublished data). Other relatively abundant top predators on PMNM reefs include tiger sharks (*Galeocerdo cuvier*), grey reef sharks (*Carcharhinus amblyrhinchos*), whitetip reef sharks (*Triaenodon obesus*), green jobfish (*Aprion virescens*), bluefin trevally (*Caranx melampygus*), amberjack (*Seriola spp.*), and the endemic Hawaiian grouper (*Epinephelus quernus*) (see [1, 21–23], J. Dale, unpublished data) (Figure 2). Less abundant predators documented from PMNM coral reefs include several other carcharhinid sharks, hammerhead sharks, and large jacks (see [21, 22], J. Dale, unpublished data) (Figure 2).

Overall species composition of reef-associated predator assemblages is broadly similar throughout the Hawaiian chain, but there are marked differences in abundance between the PMNM and Main Hawaiian Islands (MHI) [1]. The most notable difference is a general lack of sharks and large teleosts, such as giant trevally, on shallow MHI coral reefs possibly as a result of overfishing [1]. However, recent studies conducted around Hawaii Island indicate giant trevally are still relatively abundant in deeper (>80 m) MHI habitats, suggesting these deeper areas may provide a partial refuge from fishing mortality (C. Meyer, unpublished data). Reef-associated sharks are not targeted by fisheries in the MHI, yet are rarely seen during diver surveys in this region [1]. Although direct population assessments are lacking, several historical, recent, and ongoing studies suggest that MHI coastal shark populations remain robust (e.g., [22, 34–37], J. Dale, unpublished data). Specifically, these studies show similar shark catch rates and sizes in the MHI compared with the NWHI whereas fished populations characteristically yield lower catch rates and catches composed of smaller individuals. In addition, coastal sharks are not sold in local Hawai‘i fish auctions or markets indicating an absence of any directed shark fishery. Low shark abundance on diver surveys may simply indicate avoidance behavior or a deeper depth distribution of sharks in this area [22, 37]. There are also several notable biogeographic patterns of predator distribution within the Hawaiian chain which may result from different habitat preferences, competitive interactions, or thermal tolerances. For example, grey reef sharks are

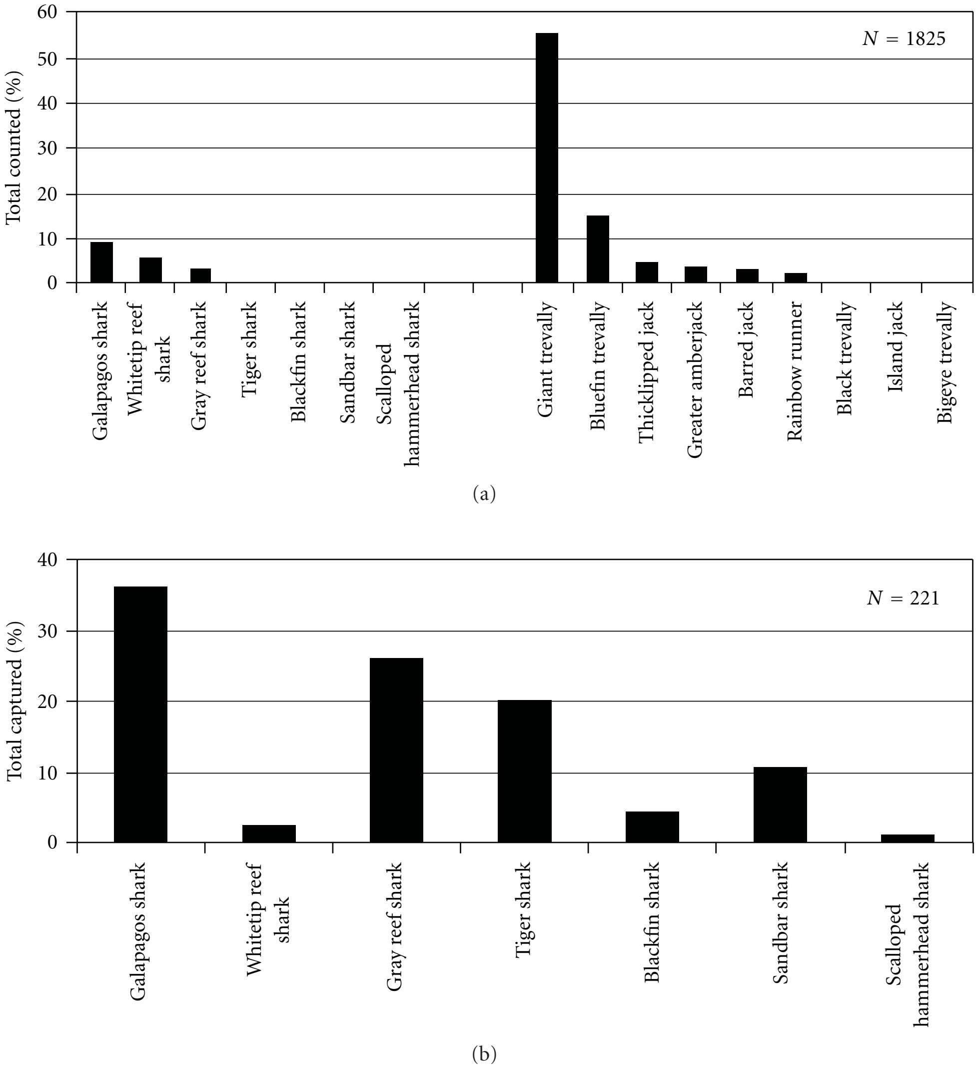


Figure 2: Species composition of the Papahānaumokuākea Marine National Monument top predator assemblage obtained by towboarding (underwater visual census) ($N = 1825$) and shark longline fishing surveys. Adapted from Holzwarth et al. [21] and J. Dale (unpublished data).

abundant in the PMNM and rare in the MHI whereas the reverse may be true for sandbar sharks [22, 32]. However, sandbar sharks accounted for 10% of all sharks captured on longlines set at French Frigate Shoals atoll (J. Dale, unpublished data), and we do not yet know how abundant they are at other locations within the PMNM because comparable fishing surveys have not yet been undertaken at these other sites. Grey reef sharks are generally more abundant at atolls than high islands throughout their geographic range, suggesting they are better adapted to, or prefer, atoll habitats [32]. Sandbar and grey reef sharks also have high dietary overlap in locations where they co-occur, suggesting competitive exclusion may play a role in their distributions [22]. Tropical submergence [38] clearly influences the depth distributions of other species including Hawaiian grouper, a heavily-targeted endemic species, along the Hawaiian chain [39]. This species is common in shallow (<30 m) reef habitats at Kure and Midway Atolls (C. Meyer, pers. obs.) but occurs at deeper depths throughout the rest of the archipelago [40], including atolls as far northwest as Pearl and Hermes Reef (adjacent to Midway Atoll in the Hawaiian chain). Coral reef habitats in the PMNM have remained largely unfished in recent decades, suggesting Hawaiian grouper depth distribution is not simply an artifact of fishing pressure. The whitetip reef shark is rare at the two northern-most atolls but common throughout the rest of the chain [21]. A lack of targeted fisheries for this species in Hawaii suggests their distribution may be influenced by low winter sea temperatures at the northern end of the archipelago.

The PMNM predator assemblage mirrors the high predator abundances seen at other remote, unfished atolls in the Pacific (e.g., [6]), but has a different species composition probably due to broad regional differences in fauna. The diversity of shark species in the PMNM is similar to that of other isolated atolls in the Indo-Pacific where a

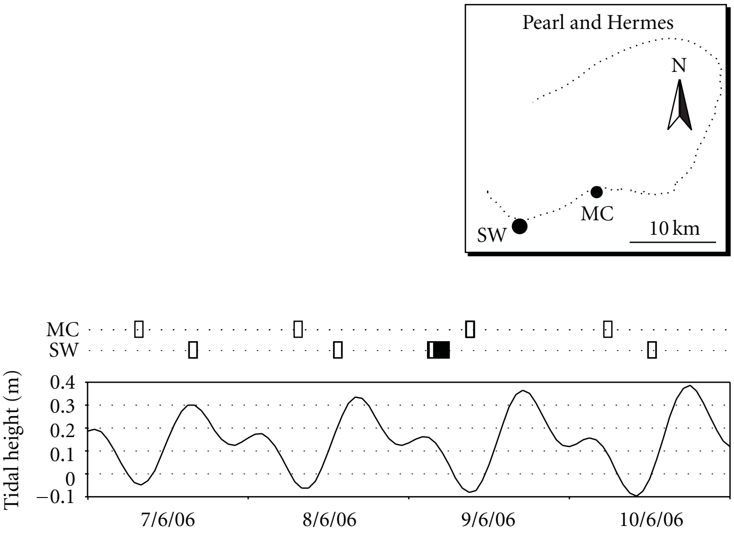


FIGURE 3: Tidal rhythmicity in green jobfish movements at Pearl and Hermes Reef (PHR). Top panel: receiver locations (solid circles) on the south side of PHR. Middle panel: detections of a single green jobfish (open rectangles) at PHR over 4 d in June 2006. Bottom panel: tidal curves for the 4 d period. The green jobfish was detected in the vicinity of the main channel (MC) around low tide and moved toward the south west tip of Pearl and Hermes Reef (SW) on the flooding tide. Return migrations from the SW tip to the main channel occurred on the ebbing tide. From Meyer et al. [51].

few species numerically dominate the shark assemblage [5, 41–46]. A lack of blacktip reef sharks (*Carcharhinus melanopterus*) distinguishes the PMNM shark assemblage from those at many other Indo-Pacific atolls, where this species is abundant [41, 47, 48]. The teleost component of the PMNM predator assemblage is distinguished from those at other remote Indo-Pacific atolls by lower diversity and a general lack of groupers and snappers, especially the twinspot snapper (*Lutjanus bohar*) which is a numerically dominant teleost predator at many other central Pacific locations (e.g., [5]).

Previous studies of PMNM top predators have quantified relative abundance and/or density (number/biomass per unit area), but there have been few attempts to determine actual population sizes. Very different methods (e.g., diver transect, towed-diver, and fishing surveys) yield broadly similar estimates of top predator relative abundance, but there are clear examples of sampling bias influencing results for some species. For example, tiger sharks are very rarely sighted during visual census surveys but account for up to 20% of all sharks captured on longlines set in PMNM habitats (see [1, 21, 22], J. Dale, unpublished data) (Figure 2). In contrast, 30% of all sharks sighted during towboard surveys are whitetip reef sharks, yet this species accounts for <3% of sharks captured on longlines in the PMNM (see [21, 22], J. Dale, unpublished data) (Figure 2). Predator behavior may also have considerable impacts on density estimates derived from visual census surveys. For example, giant trevally are highly attracted to divers in the PMNM but typically flee humans in the MHI (C. Meyer, pers. obs.), potentially leading to divergent, skewed estimates of abundance between the two regions. Giant trevally are also known to form seasonal, lunar spawning aggregations which result in fish from across entire atolls concentrating at a few sites during summer full moons [49]. Such phenomena may bias population density estimates and/or inflate variances of the estimates if visual surveys are carried out during aggregation times. Mark-recapture techniques provide an alternative method for calculating top predator population sizes, but to date, there have been few attempts to apply these methods in the PMNM due to the considerable effort required to obtain sufficient sample sizes for robust estimates of population size. A recent study used mark-recapture to calculate a population size of 668 (95% CI 289–1720) Galapagos sharks at FFS (J. Dale, unpublished data). This calculation was based on only 4 (5.4%) recaptures of 73 tagged sharks captured during 3 months of intensive shark fishing at this location. However, recent work (see section on movements below) indicates most top predators are site attached to their “home” atolls, and hence they are theoretically suitable candidates for mark-recapture estimates derived from closed population models. Top predator population size estimates are a key knowledge gap in our understanding of PMNM ecology. Although logistically challenging to obtain, such empirical estimates would be extremely valuable for validating density estimates produced from visual census surveys and parameterizing ecosystem models (e.g., [50]).

3. Movement Patterns and Habitat Preferences

A series of recent electronic tagging studies at PMNM sites suggest individuals of the most abundant species of coral reef top predators are generally site-attached to their “home” island or atoll, but many move extensively within atolls during diel, tidal, lunar, and seasonal migrations [36, 49, 51–53] (Figure 3). For example, giant trevally spend most of the year in relatively small (maximum linear dimension = 5 km) home ranges, where they exhibit clear diel habitat

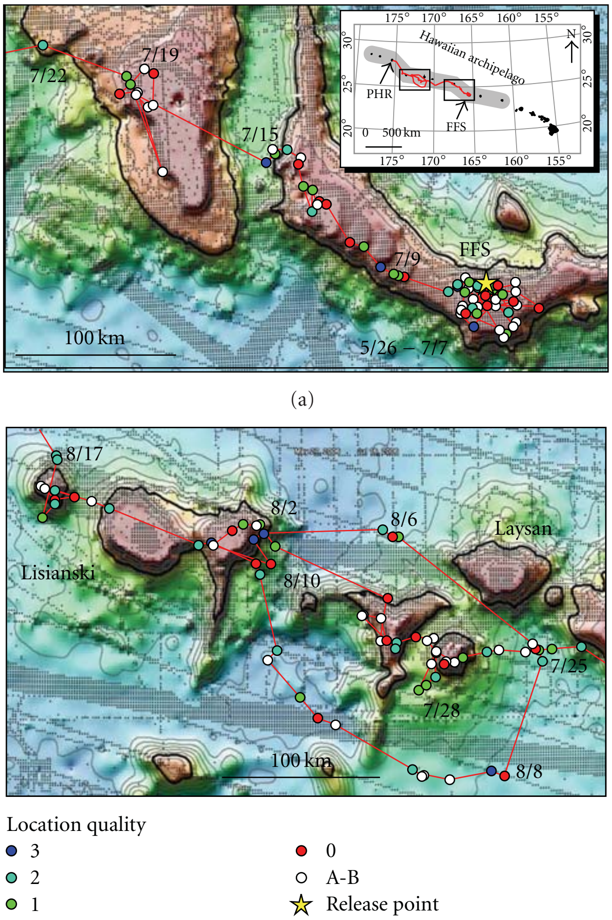
(a) (b)

Figure 4: (a) Color dimorphism in giant trevally from school at Rapture Reef. (b) Giant trevally school at Rapture Reef (FFS Atoll), May 23 2006. Photographs reproduced by permission of Jill Zamzow. From Meyer et al. [49].

shifts (see [49], C. Meyer, unpublished data), but migrate up to 40 km to spawning aggregation sites during summer full moons (see [49], C. Meyer, unpublished data) (Figure 4). Green jobfish are also seasonally site attached to core activity areas of up to 12 km in length, and range up to 19 km across atolls [51]. Within their core areas, green jobfish exhibit diel and tidal habitat shifts (Figure 3), with the latter resulting in round trips of up to 24 km in 24 h [51]. Galapagos sharks also appear to be primarily resident at "home" atolls, with adults moving extensively throughout atolls and juveniles exhibiting diel migrations between fore reef and reef flat habitats [52, 53]. Tiger sharks are the notable exception to the atoll-residency pattern. Although some individuals are detected at their home atoll year round, others routinely swim hundreds or thousands of km along the Hawaiian chain or out into open ocean [49, 53–55] (Figure 5).

Data from diver transect and towed-diver visual surveys and fishing and tagging studies show that the most common top predators occur throughout all major atoll and bank habitats, but some species exhibit preferences for particular habitat types or locations (see [21, 23, 49, 51–53], J. Dale, unpublished data). Indeed, electronic tagging studies show individual predators often utilize multiple different habitats at PMNM atolls, but are detected most frequently in just a few [49, 51–53]. Collectively, these studies suggest large predators in the PMNM, as elsewhere in the central Pacific [56], are generally most abundant in atoll fore reef habitats and least abundant in shallow (<3 m) lagoon and back reef habitats (see [21], J. Dale, unpublished data). However, electronic tagging data also indicate many tiger sharks and some Galapagos sharks actively seek out shallow habitats around small sandy islets, presumably because of abundant, large prey (birds, turtles, and seals) in these locations (see [52, 53]—see also diet section below), and core home ranges of some giant trevally individuals are located in these shallow areas [49]. Top predators also select specific habitats for biologically important activities such as spawning. For example, during summer full moons, giant trevally from across FFS congregate in fore reef habitat on the south side of the atoll [49] (Figure 4). Few data are available on vertical movements of top predators in the PMNM but limited satellite tagging in this region has shown both Galapagos and tiger sharks primarily use the mixed layer (<100 m depth) and make occasional deeper dives through the thermocline down to 680 m [53] (Figure 6).

In many cases, movement data from teleost predators tagged in the PMNM are among the first available for those species, precluding comparisons with other areas. Overall, PMNM teleost predators exhibit rhythmic patterns of movement that are broadly similar to, but wider-ranging than, other coral reef fishes (e.g., [57]), which has important implications for Marine Protected Area (MPA) design (e.g., [49, 51]). Recent studies suggest giant trevally movement patterns in the MHI closely resemble those documented in the PMNM (C. Meyer, unpublished data), and this species is known to form lunar spawning aggregations at predictable locations in other areas of the Pacific [58–62]. Little is known about Galapagos shark movements in any part of their geographic range, but the few data available suggest broadly similar patterns of site fidelity and vertical movement to those observed in the PMNM. A Galapagos shark tagged off Bermuda was recaptured 2,859 km away off the coast of Suriname, but most recaptures (12 of 14) were within 100 km of the original capture sites [63]. In the MHI, Galapagos shark abundance at cage diving ecotourism sites has clear, annual cycles, indicating seasonal movements to and from this location [51]. Galapagos sharks in Hawaii have been captured at depths of 0 to 286 m although most were caught between 30 and 50 m [30]. Tiger shark movements within the PMNM are also similar to those documented elsewhere, showing these sharks occupy large home ranges within which they employ specific localized patterns of movement and habitat use [25, 36, 54, 63] (Figure 5). Seasonal movements may occur at the latitudinal extremes of their distribution [64, 65]. Active tracking of tiger sharks equipped with acoustic transmitters off Oahu, Hawai'i revealed orientation



(a)

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Figure 5: Inset: Overview of a tiger shark (TS5) SPOT track (red line) from French Frigate Shoals (FFS) to Pearl and Hermes Reef (PHR) within the Papahānaumokuākea Marine National Monument (shaded area). Boxes indicate regions of track shown in detail in top and bottom panels. Top panel: concentration of SPOT detections at FFS between 5/26/06 and 7/7/06, and route taken after departure from FFS on 7/8/06. Bottom panel: detail of SPOT detections associated with submerged banks and seamounts surrounding Lisianski and Laysan islands. From Meyer et al. [53].

to the bottom in depths <300 m and to the mixed layer (0–80 m) in deeper waters with occasional brief dives as deep as 335 m [54].

Many sharks and teleosts use well-defined nursery habitats (e.g., [66, 67]), but relatively little is known about juvenile top predator habitat use in the PMNM. Among teleosts, young-of-the-year Hawaiian grouper inhabit turf algae-dominated deep-bank terraces whereas giant and bluefin trevally recruit to the shoreline edge of protected sandy areas adjacent to reefs [68]. Specific nursery habitats have not yet been identified for any shark species in the PMNM, but fishing surveys capture immature Galapagos, tiger and grey reef sharks (see [22, 30, 32], J. Dale, unpublished data), and aggregations of immature Galapagos sharks can be seen predictably at several locations within the PMNM (Figure 7).

Although recent studies have provided important insights into long-term movement and habitat-use patterns of coral reef predators in the PMNM, significant knowledge gaps remain. We still lack any empirical movement data for several relatively abundant predator species in this region, including amberjack and whitetip reef sharks, and we have no fine-scale habitat use or depth data for most species. The importance of juvenile recruitment to adult stocks underlies the need to identify key nursery areas for both sharks and large teleosts. Future fishing surveys could utilize gear configurations specifically targeting juveniles to address this knowledge gap. More fundamentally, we understand few of the specific drivers of the observed predator movements and habitat use. Presumably, predators visit specific locations to engage in biologically significant behaviors of foraging and reproduction, and site selection is driven by biological and physical characteristics of those sites. The few cases in which we can tie movement patterns directly to specific biological activities (tiger shark foraging on fledging sea birds, Galapagos shark predation on Hawaiian monk seal pups, giant trevally spawning aggregations) all involve visual confirmation of the behavior (Figure 8). However, in most cases, ecologically important behaviors occur completely unseen by humans. Fortunately, a new generation of "ecology tags" promises to provide important new insight into the ecology of marine animals. These devices include accelerometer dataloggers which provide high-resolution spatial tracks and biomechanical data on swimming activity, stomach tags which measure changes in stomach pH to identify feeding events, and hydrophone tags which record biologically significant sounds and interanimal interactions (e.g., [69–72]). Future studies could shed light on the frequency and locations of feeding and mating by combining instruments which tell us about spatial behavior and physical oceanography with this new generation of "ecology tags".

4. Trophic Ecology

Top predators in the PMNM consume a wide variety of prey including invertebrates, fishes, marine mammals, turtles, and sea birds. Giant trevally are the most abundant predator in the PMNM, and diet studies suggest their foraging activities significantly impact lower trophic levels [24]. Their diet is dominated by reef fishes and invertebrates, including octopus and adult lobsters, but also includes pelagic species such as squid and mackerel scad (*Decapterus macarellus*). Overall diet indicates giant trevally forage primarily in shallow-water reef habitats but also feed in open water [24, 73]. Their diet contains a large amount of nocturnally active prey indicating a significant amount of nighttime feeding by this species [24]. Dietary overlap between giant and bluefin trevally (another abundant reef-associated jack) is moderate, with shallow-water reef fishes and small crustaceans, respectively, making larger and smaller contributions to bluefin trevally diet [24]. A low incidence of nocturnally active prey items and the absence of pelagic species suggest bluefin trevally are primarily diurnal foragers in shallow-water reef habitats. Differences in foraging strategies and the ability of large adult giant trevally to feed on larger prey (e.g., adult lobsters) may

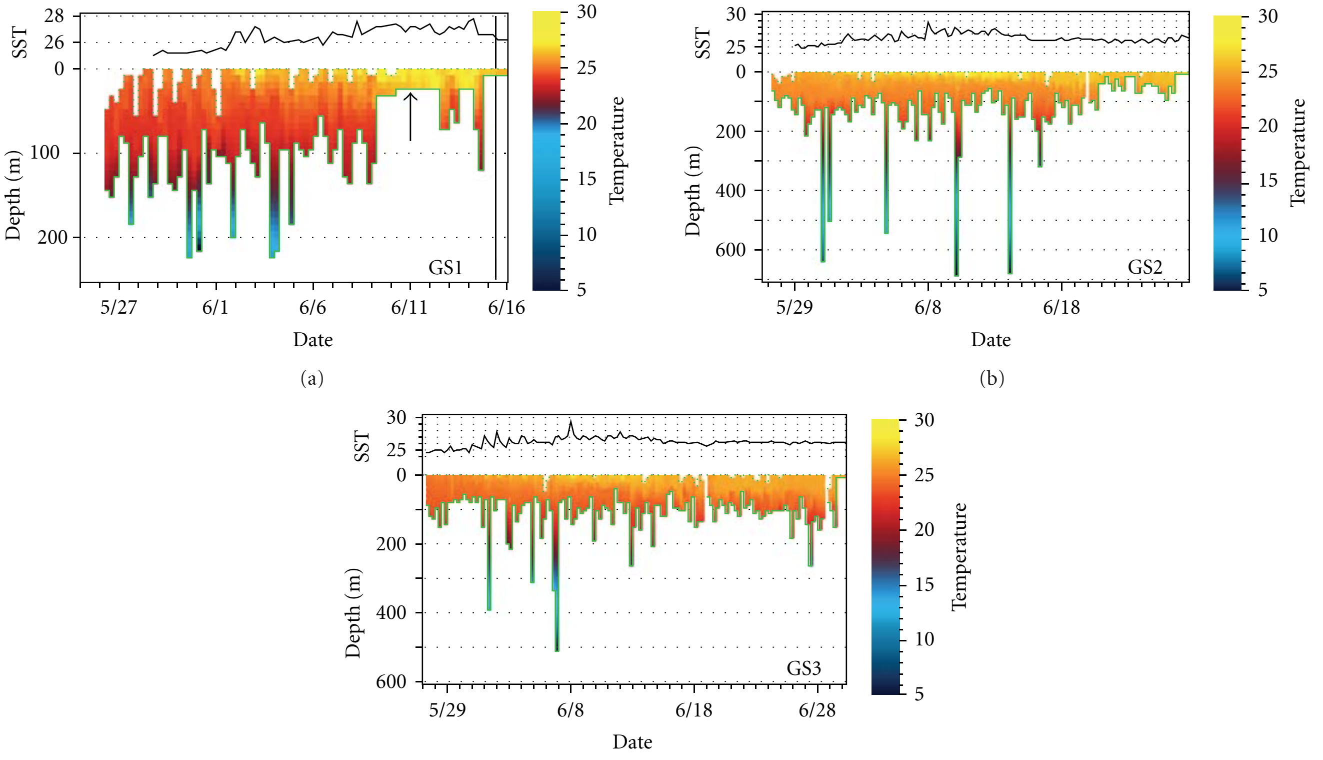

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Figure 6: Popup Satellite Archival Tag (PAT) depth-temperature histograms (6 h bins) and Sea Surface Temperature (SST) plots for three Galapagos sharks captured at French Frigate Shoals (FFS) in May 2006. Note 3 day period spent swimming shallower than 30 m depth by GS1 (Arrow). From Meyer et al. [53].

Figure 7: Aggregation of juvenile Galapagos sharks at Midway Atoll. Photograph reproduced by permission of Kevin Flanagan.

Figure 8: Tiger shark foraging on fledging blackfoot albatross at East Island, French Frigate Shoals. Photo A. Rivera.

reduce niche overlap between these two sympatric species [24, 73].

Other abundant teleost predators in the PMNM include green jobfish, Hawaiian grouper, and amberjack. Although these commonly occur in shallow-water (0–40 m) areas, existing diet data are garnered from individuals captured in deep-water PMNM habitats (55–250 m) [74–78]. All three species are primarily piscivorous although crustaceans contribute significantly to the diet of Hawaiian grouper. Hawaiian grouper and amberjack are primarily benthic carnivores, but larger amberjacks consume significant amounts of mid-water prey. Consumption of larval and mid-water prey also suggests pelagic foraging by green jobfish. Green jobfish are diurnal predators whereas Hawaiian grouper appear to feed nocturnally or during crepuscular hours, and the timing of amberjack feeding is unknown.

Our knowledge of shark diets in both the MHI and PMNM comes from a series of historical fishing surveys [28, 30, 32, 34, 79], which collectively suggest sharks have broadly similar foraging habits throughout the Hawaiian archipelago.

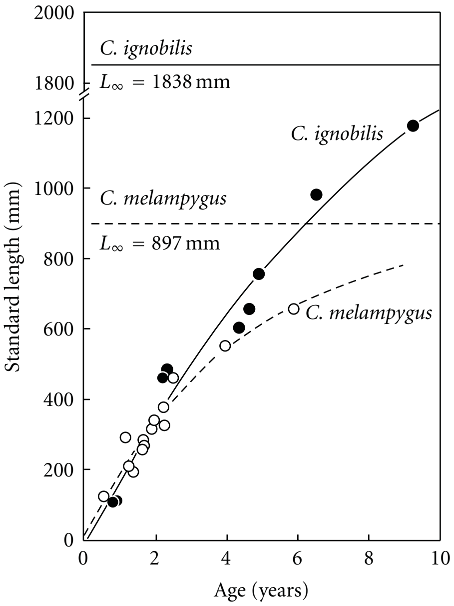

Figure 9: Growth data and von Bertalanffy growth curves derived for *Caranx melampygus* and *Caranx ignobilis*. Age was estimated by counting daily growth increments of otoliths. From Sudekum et al. [24].

Overall, shark diets are dominated by teleosts, but also include significant amounts of cephalopods and crustaceans. Clear ontogenetic shifts in diet are evident, with decreases in the contribution of teleosts accompanied by increases in prey diversity with increasing shark size. Dietary overlap between shark species is generally low whereas intraspecific overlap along the Hawaiian chain is high. Notable exceptions to these general trends include high dietary overlap between sandbar sharks and grey reef sharks (species which show opposite patterns of geographic abundance along the Hawaiian chain [22, 32]), and between large Galapagos and tiger sharks [22], both of which consume large prey such as elasmobranchs, sea birds, turtles, and marine mammals. Tiger sharks diets also contain more of these large prey in the PMNM than in the MHI [79], presumably reflecting differences in prey availability between these two regions. The PMNM contains important breeding grounds for sea birds, turtles, and the critically endangered Hawaiian monk seal (*Monachus schauinslandi*), creating high densities of potential shark prey, particularly during the summer months. Tiger sharks can be seen foraging seasonally on fledging albatross (primarily blackfoot albatross, *Phoebastria nigripes* [52]) (Figure 8) and are also known to prey on monk seals [28]. Galapagos sharks are occasionally witnessed preying on monk seal pups and are suspected of additional, unseen predation at pupping beaches [80].

Several key knowledge gaps remain in our understanding of trophic ecology of top predators in the PMNM. For example, we lack basic diet data from shallow-water coral reef habitats for several abundant predators such as green jobfish, Hawaiian grouper, and amberjack. Although we know what many sharks and fishes eat, we still know little about when they feed or how much they consume each day. Bioenergetic models have been used to estimate prey consumption by sharks and trevally [24, 28] at French Frigate Shoals, but have lacked robust empirical data for key input parameters such as population size and metabolic rates [82], greatly increasing uncertainty of the results. For example, model estimates suggest giant and bluefin trevally consume more than 30,000 mt of prey per year at FFS, exceeding the estimated combined consumption of tiger, Galapagos, and grey reef sharks at the same atoll by a factor of 40. We need to understand the transfer of energy between trophic levels in order to comprehend how these ecosystems function, hence additional empirical data on consumption rates are required. Emergent technologies such as pH and acceleration tags [70, 83] show promise for providing these data. In blacktip reef sharks, prey consumption rapidly increases stomach pH and the amount of prey consumed is linearly related to the magnitude of pH changes, providing the potential for direct estimates of the timing and frequency of feeding as well as the daily ration. In captive scalloped hammerhead sharks (*Sphyrna lewini*), body acceleration was linearly related to metabolic rates, providing the potential to quantify these rates for free-swimming sharks [83]. These methods offer promising tools for validating existing estimates of prey consumption in the field.

5. Age, Growth, and Reproduction

The PMNM top predator assemblage is characterized by large-bodied, long-lived sharks, and jacks. Maximum size reached by adult predators ranges among species from <1 to >4 m, and growth rates also vary interspecifically [24, 28]. Maximum observed age estimates range from 6 years for bluefin trevally [24] to 22 years for tiger sharks [28], with reproductive size reached in 2 to 10 years [24, 28]. Predatory teleosts reproduce at an earlier age and reach smaller maximum sizes than sharks in the PMNM. The timing of spawning/birthing for top predators is highly seasonal, generally occurring in the spring and summer months [24, 30, 32].

Giant trevally grow slightly faster and reach a larger maximum size than the closely related bluefin trevally (Figure 8), but the latter reproduce at an earlier age and smaller size [24] (Table 1). Based on the von Bertalanffy growth coefficient (K), giant and bluefin trevally attain 95% of their theoretical maximum sizes at 31 and 15 years, respectively, but these are likely only minimum estimates as maximum observed ages were 9 and 6 years (Table 1, Figure 9). Bluefin trevally are highly fecund (>4 million mature ova in the ovary of a 6.5 kg female), with an exponential increase in the number of eggs produced with size [24]. Spawning activity peaks for both giant and bluefin trevally between May and August [24]. Age, growth, and reproductive data are not available for other common teleost predators in the PMNM, but green jobfish in the MHI reach sexual maturity between 0.45–0.5 m Fork Length (FL) (Table 1) and have a protracted spawning season between May and October [26]. Green jobfish on the Great Barrier Reef (GBR) reach maximum ages of 16 years and a theoretical maximum size of 0.7 m FL [27] (Table 1).

Table 1: Summary of life history studies conducted on top predators in the Hawaiian archipelago. SL: Standard Length, FL: Fork Length, and TL: Total Length.

Species	Max size	Max growth rate	Max age	Size at maturity	Age at maturity	Litter size	Source
Bluefin trevally	0.9 m SL	18 cm/yr	15	0.35 m SL	2 y	—	[24]
Giant trevally	1.8 m SL	19 cm/yr	31	0.6 m SL	3.5 y	—	[25]
Green jobfish	0.7 m FL	—	16	0.3–0.5 m FL	—	—	[26, 27]
Tiger shark	4.4 m TL	40 kg/yr	28	290–345 cm TL	10 y	32.6	[28, 29]
Galapagos shark	2.9 m TL	14 kg/yr	24	205–245 cm TL	10 y	8.7	[28, 30, 31]
Grey reef shark	2.2 m TL	5 kg/yr	18	120–140 cm TL	6 y	4.1	[28, 32, 33]

Size of sexual maturity for green jobfish on the GBR was not determined, but all sampled fishes were mature at 0.3 m FL.

Among PMNM sharks, tiger sharks are the largest and fastest growing followed by Galapagos and grey reef sharks (see [28, 33, 81], C. Meyer, unpublished data) (Table 1, Figure 10). Tiger sharks also reproduce at a larger minimum size and have a higher maximum age than these other species [28–33, 81] (Table 1). Age at first reproduction for female gray reef sharks is 6 years, and 10 years for both Galapagos and tiger sharks [28]. Tiger sharks have larger mean litter sizes than both Galapagos and grey reef sharks [29, 30, 32] (Table 1). Mating occurs in the winter and spring with parturition in the spring and summer following 12 (Galapagos and grey reef) or 16 (tiger) month gestation periods [29, 30, 32]. Reproduction is thought to occur every 2-3 years for these species [29, 30, 32]. We lack age, growth, and reproductive data for other common sharks in the PMNM.

Several important caveats limit our understanding of top predator age, growth and reproduction in the PMNM. For example, the few studies available are mostly based on relatively small sample sizes. For age and growth, the periodicity of band formation in otoliths (teleosts) or vertebrae (sharks) has only been partially validated in two teleost species (giant and bluefin trevally [24]), and longevity estimates for these predators have never been confirmed. Daily growth increment validation was conducted on fishes smaller than the maximum observed sizes, and increment formation in the otoliths of larger individuals may be slower [85], leading to underestimates of age and overestimates of growth rate. Reproductive traits such as gestation length and reproductive periodicity are only preliminary estimates, and additional data are required to confirm them. Additional, similar studies could provide age, growth, and reproductive data for other common species but would require several hundred individuals to be sacrificed. Mark recapture studies provide an alternative, nonlethal method for calculating growth, and could also provide much needed population size estimates, but require considerable effort to obtain adequate sample sizes. Sexual segregation is prominent for sharks in the PMNM, and in other locations, this phenomenon has been linked to reproductive behavior [86, 87], yet little is known of the specific environmental and behavioral factors driving sexual segregation in the PMNM. Identification of spawning and mating sites could provide insight into the habitat requirements for such behaviors, essential information for

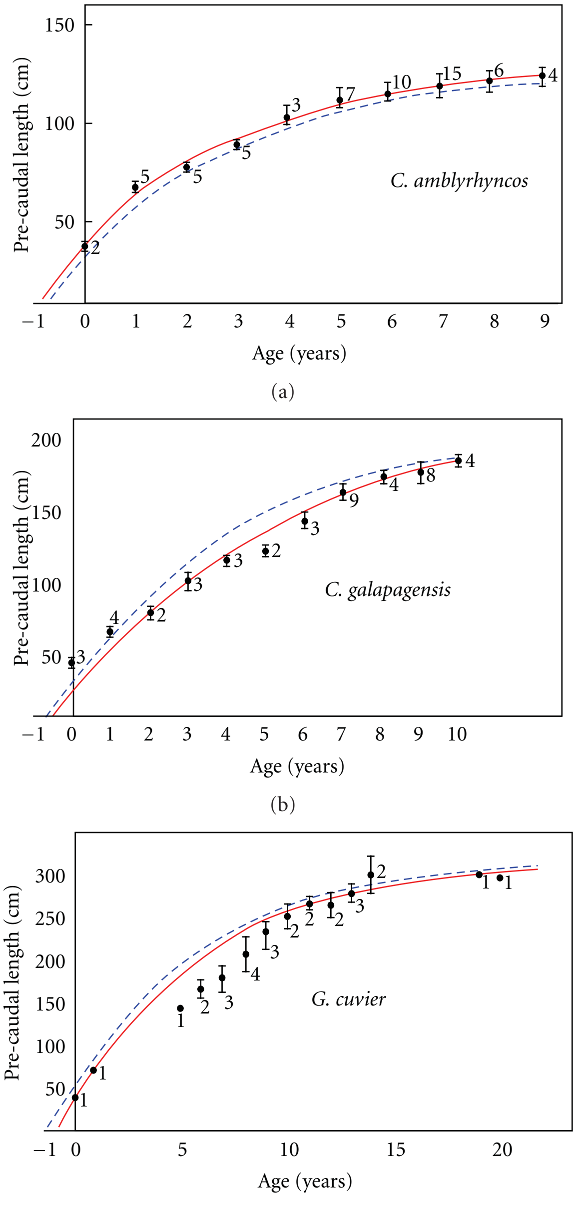

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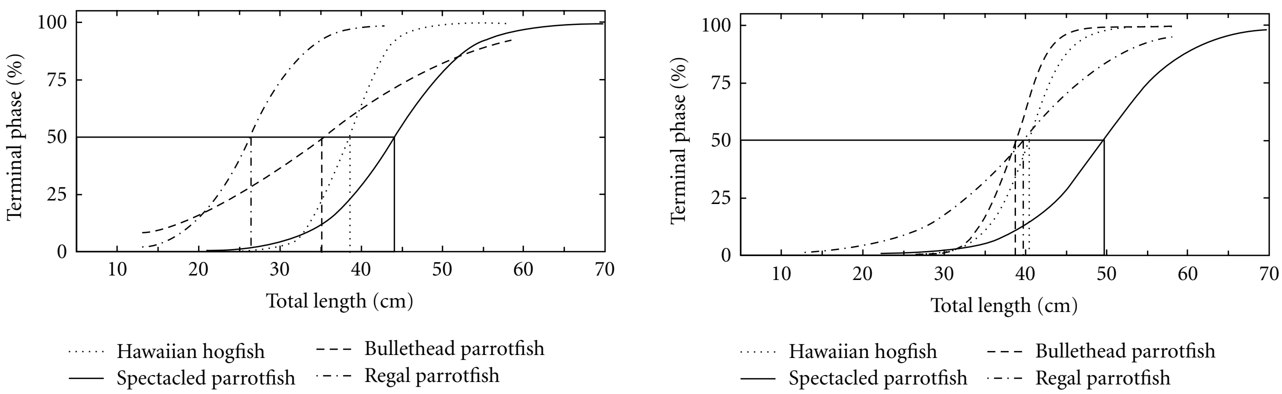
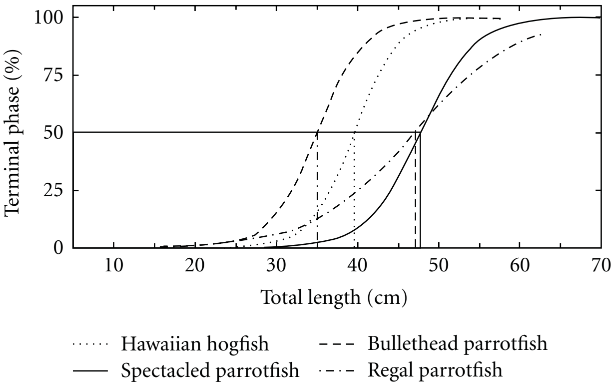
Figure 10: Von Bertalanffy growth curves calculated from the vertebral age determination data (solid line)—with mean length of age class indicated by dots, the range by bars, and the sample size by numbers—and from a length-frequency analysis of data from Tester [81] (dashed line). From DeCrosta et al. [28].



(a) Pearl and Hermes (b) Kure



(c) Midway

Figure 11: Scatterplots and logistic spline curves (predicted fits) of percentage terminal phase (for all individuals observed, both initial and terminal phases) by 5 cm total length class, for each of 4 major species of labroids (1 labrid plus 3 scarids), at Pearl and Hermes, Kure, and Midway atolls in the NW Hawaiian Islands during September to October 2000 and 2002. Vertical lines indicate estimated body length at which 50% of individuals are terminal phase. From DeMartini et al. [84].

the design of MPAs implemented to protect highly vulnerable seasonal aggregations [3].

6. Ecological Interactions

The predator-dominated coral reefs of the PMNM [1] provide a rare opportunity to investigate the impacts of top predators on ecosystem dynamics, and recent empirical studies suggest predation pressure influences size composition, life-history characteristics, distribution, and abundance of prey species [84, 88, 89]. For example, size at sex change and mean body size of protogynous labroids are inversely related to giant trevally densities at PMNM atolls [84] (Figure 11). Intra-atoll distribution and abundance of prey fishes may also be influenced by predation pressure. An inverse relationship between abundances of top predators and small carnivores in barrier and patch reef habitats may result from small-bodied prey utilizing patch reefs (which have higher densities of shelter holes) as refuge sites from predation (see [21, 68, 88, 89], J. Dale, unpublished data). Similarly, top predators on low-relief, submerged banks in the PMNM may restrict movements of prey fishes away from sheltering sites, possibly reducing prey foraging and growth rates [23]. Theoretical modeling also suggests significant impacts of top predators on PMNM ecosystem dynamics. For example, models of the French Frigate Shoals ecosystem predict removal of tiger sharks would cause system-wide changes in abundance of a variety of taxa, including those not preyed upon by tiger sharks [90]. Such results highlight the potential importance of indirect effects of top predators on ecosystem function.

Although the effects of predation on lower trophic levels are fairly well documented [23, 84, 88, 89], the effects of inter-specific interactions between top predators are less well understood. We do know predatory fishes and sharks may be an important source of interference competition for critically endangered Hawaiian monk seals in the PMNM. Seal-borne video cameras show giant trevally, bluefin trevally, amberjacks, green jobfish, and reef sharks swimming in close association with monk seals, and competing for prey items flushed from cover by the foraging seals [91]. However, seals still have their greatest foraging success in the presence of these competitors, suggesting benefits of feeding in prey-rich patches may outweigh costs of interference competition [91]. New technologies such as hydrophone tags, which record biologically significant sounds and inter-animal interactions [72], could further clarify the nature and importance of inter-specific competition between top predators.

Relatively little is known about the ecological impacts of top predators in the MHI and most other Indo-Pacific locations, due to the generally low abundance of top predators on shallow coral reefs in areas impacted by humans [1]. The few data available suggest top predators exert similar ecological impacts on shallow-water coral reef ecosystems across a wide geographic area. For example, mean size at sex change for parrotfishes (Scaridae) increases with decreasing densities of top predators in the Northern Line Islands, where the abundance and trophic structure of fishes parallel those of the PMNM (i.e., both have predator-dominated fish faunas) [5, 84]. In the MHI, distributions of smaller sharks may be driven partly by predation and behaviorally mediated interactions [22, 37]. For example, young-of-the-year scalloped hammerhead sharks aggregate in turbid bays and estuaries, presumably to avoid predation pressure from larger sharks [92]. MHI sandbar shark abundance is inversely related to abundances of larger tiger and Galapagos sharks which prey on sandbar sharks and may also exclude them through competitive dominance [22, 37]. In Australia, tiger sharks exclude bottlenose dolphins (*Tursiops aduncus*) from productive seagrass foraging habitats, potentially decreasing dolphin fitness [93].

To date, our understanding of the ecological role of top predators in coral reef ecosystems is based largely on correlative studies (e.g., giant trevally density versus size at sex change of labroids [5, 84]), but manipulative experiments are required to definitively demonstrate causation. The PMNM provides ideal environments for conducting manipulative experiments without the confounding effects of anthropogenic influences. Such experiments would greatly increase our understanding of the specific biological and physical factors driving observed relationships.

7. Conclusions

Limitations inherent in single species management plans have generated burgeoning interest in ecosystem-based management [94]. This approach requires a thorough understanding of ecosystem processes including species composition, abundance, distribution, spatial utilization, and life-history characteristics, as well as trophic relationships among constituent organisms. As one of the few remaining near-pristine coral reef ecosystems [1, 95], the PMNM provides a rare opportunity to study ecosystem function and processes free from human disturbance. Top predator studies to date indicate strong top-down control on coral reef fish assemblages in the PMNM. These effects are most clearly evident for giant trevally which structure prey size, distribution, and habitat use, as well as influence reproductive and growth characteristics of prey on shallow-water coral reefs. Large sharks are a significant source of predation on endangered species such as the Hawaiian monk seal, blackfoot albatross, and green sea turtle (*Chelonia mydas*). Removal of top predators would theoretically lead to large-scale trophic cascades suggesting ecosystem processes may be most impacted by predators through indirect effects of predation [19, 90].

The wide-ranging behavior of most top predators has important implications for management of these species. Large MPAs (i.e., entire atolls, islands, or banks) would be required for complete protection of giant trevally, green jobfish, and most shark populations. MPAs of this scale would be effective when preservation of entire coral reef ecosystems is the management objective, but unrealistic in populated areas due to resistance from stakeholders [96–98]. In fished areas such as the MHI, alternative strategies need to be evaluated for the management of top predator populations. Protecting sites of spawning activity is of particular importance, as large spawning aggregations are highly susceptible to rapid depletion [3]. The use of conventional fishing restrictions (e.g., slot and bag limits and seasonal closures) in conjunction with small MPA's aimed specifically at protecting known spawning and nursery habitats may provide an effective alternative to large MPA's in fished areas.

Although a substantial amount of information is available concerning the ecology of top predators, significant knowledge gaps still remain. Little is known about the life-history and population sizes of most top predators in the PMNM, and the majority of existing studies are based on small sample sizes. These parameters are required for calculations of growth rate, mortality rate, and productivity, making them among the most important variables for understanding population dynamics [99]. An understanding of feeding periodicity, daily ration, inter-specific interactions, and the specific drivers of observed movement and distribution patterns will provide critical empirical data for parameterization of ecological models. These knowledge gaps could be filled by using a combination of classical techniques (e.g., mark recapture estimates of growth and abundance) and novel methods such as newly developed "ecology tags".

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Review Article

Tempering Expectations of Recovery for Previously Exploited Populations in a Fully Protected Marine Reserve

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Centuries of resource extraction have impacted coral reef ecosystems worldwide. In response, area and fishery closures are often enacted to restore previously exploited populations and reestablish diminished ecosystem function. During the 19th and 20th centuries, monk seals, pearl oysters, and two lobster species were overharvested in the Northwestern Hawaiian Islands, now managed as the Papahānaumokuākea Marine National Monument, one of the largest conservation areas in the world. Despite years of protection, these taxa have failed to recover. Here, we review each case, discussing possible factors that limit population growth, including: Allee effects, interspecific interactions, and time lags. Additionally, large-scale climate changes may have altered the overall productivity of the system. We conclude that overfishing of coral reef fauna may have broad and lasting results; once lost, valuable resources and services do not quickly rebound to pre-exploitation levels. In such instances, management options may be limited to difficult choices: waiting hundreds of years for recovery, actively restoring populations, or accepting the new, often less desirable, alternate state.

1. Introduction

For centuries, coral reef ecosystems have been viewed as renewable resources, from which countless organisms have been harvested to serve dependent human communities [1, 2]. There is an underlying assumption that marine species are highly resilient to large population reductions and that abundance may be quickly restored by area or fishery closures [3–5]. The capacity for self-repair, however, is dependent upon the extent of human impact and system resilience [6, 7]. Excessive and prolonged anthropogenic exploitation may reduce resilience, that is, the capacity of a system to persist while maintaining key relationships and absorbing disturbances [8]. For example, 15 years after fishery closures, there has been little recovery of several marine fish stocks that were previously reduced 45%–99% [9, 10]. Thrush and Dayton [11] review several examples of marine ecosystem ratchets, in which recovery to pre-exploitation levels is no longer possible [12]. In such instances, managers are forced to accept the new, often less desirable, alternate ecosystem state.

The Northwestern Hawaiian Islands (NWHI) span the center of the Hawaiian-Emperor seamount chain, the world's most geographically isolated archipelago (Figure 1) [13]. As of 2006, these small islands, atolls, reefs, and surrounding areas comprise the Papahānaumokuākea Marine National Monument, one of the largest marine protected areas in the world. Fishing is not permitted, and the human population is small (i.e., managers, researchers, and a small crew to staff an emergency runway at Midway Atoll). Thus, the NWHI coral reef ecosystem is widely regarded to be "nearly pristine," hosting predator-dominated communities, large fish populations, numerous coral species, and a healthy algal assemblage [14]. It has not, however, escaped human impact

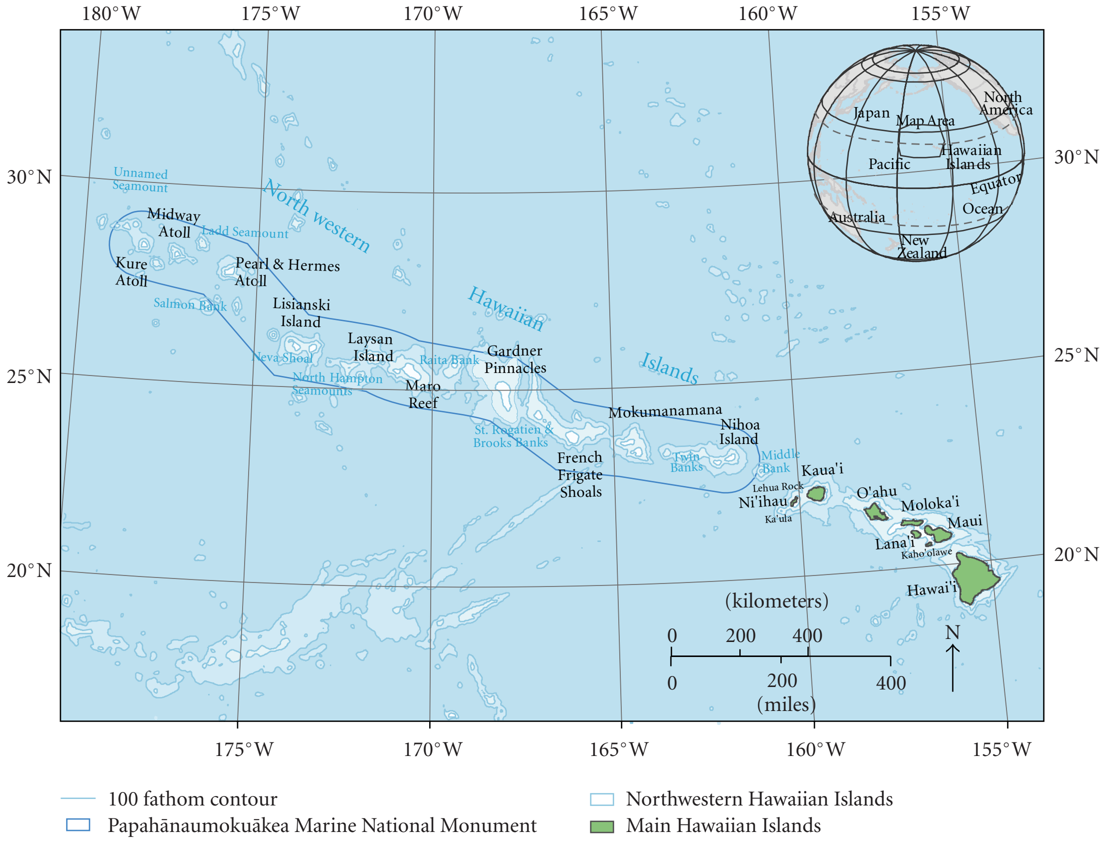


Figure 1: The Northwestern Hawaiian Islands, protected as the Papahānaumokuākea Marine National Monument since 2006 (NOAA map).

[15], and modern species assemblages may only *appear* to be intact because baseline levels of abundance prior to exploitation are unknown (i.e., shifting baseline theory) [16].

2. Objectives

Here, we review anthropogenic impacts on the NWHI coral reef ecosystem, focusing on four of the best-studied species: Hawaiian monk seal (*Monachus schauinslandi*), black-lipped pearl oyster (*Pinctada margaritifera*), Hawaiian spiny lobster (*Panulirus marginatus*), and scaly slipper lobster (*Scyllarides squammosus*). The lack of recovery demonstrated by these taxa may be a result of Allee effects, inter-specific competition, and time lags. In addition, large-scale climate processes may have altered the carrying capacity of the entire system. We consider the implications of these losses and provide recommendations for ecosystem-based management in the NWHI, now protected as the Papahānaumokuākea Marine National Monument.

3. A Brief History of Anthropogenic Impacts in the NWHI Coral Reef Ecosystem

The NWHI ecosystem has been significantly altered by humans, beginning with early Native Hawaiian settlers (1000–1700 AD) and Western explorers of the late 18th century [17]. Habitat disturbances include: guano mining at Laysan; modification of essential beach habitat by military actions at Midway Island, French Frigate Shoals, and Kure Atoll; creation of channels at Midway and FFS; marine debris accumulation; and pollution [18–20]. In addition, a myriad of species occupying several trophic levels were harvested for subsistence, food markets, bait, feathers, and shells (Table 1).

Between 1842 and 1915, a minimum of 1.3 million seabirds was harvested at Laysan, Lisianski, and Midway Islands [18, 21, 22]. Hunted for human consumption and to be used as shark bait, Hawaiian monk seals (*Monachus schauinsalndi*) and green sea turtles (*Chelonia mydas*) were nearly extirpated by the 20th century [19, 23]. Sharks were heavily fished during the late 19th century [24–26] and as recently as 2000, when 990 individuals were taken in a single 21-day exploratory shark-fishing trip [27]. Bottomfish stocks have been fished since the 1930s [28]. Harvest of pelagic and nearshore fish species, including scrombrids and trevally, began after World War II and continued until the early 1990s. Approximately 150,000 black-lipped pearl oysters (*Pinctada margaritifera*) were harvested at Pearl and Hermes Reef between 1928 and 1930, severely depleting the population [29]. Precious coral beds (*Corallium* spp.) have been exploited since 1965 [30]. In the mid-1970s, a commercial lobster fishery targeting Hawaiian spiny lobsters (*Panulirus marginatus*) and scaly slipper lobsters (*Scyllarides squammosus*) became the state's most valuable demersal

Table 1: A brief history of extraction in the NWHI: Kure Atoll (Kur), Midway Island (Mid), Pearl and Hermes Reef (PHR), Lisianski Island (Lis), Laysan Island (Lay), and French Frigate Shoals (FFS). This list is not exhaustive and does not represent all extraction occurring in the NWHI.

Year(s)	Site	Taxa	Notes
1842–1915	Lay Lis Mid	Seabirds: Sooty tern (*Onychoprion fuscatus*) Laysan albatross (*Phoebastria immutabilis*) Black-footed albatross (*P. nigripes*) Grey-backed tern (*Sterna lunata*) White tern (*Gygis alba*) Masked booby (*Sula dactylatra*) Lesser frigate bird (*Fregata ariel*) Great frigate bird (*F. minor*) Red-tailed tropicbird (*Phaethon rubricauda*)	1.3 million taken (recorded legal and illegal harvests); this does not include: records of implied harvest at additional locations and in additional years, consumption by shipwrecked sailors, egg harvest, nesting habitat loss from guano harvest (450,000 tons at Laysan Island), introduced species, and chick mortality due to removal of parents [18–116].
19th century	NWHI	Hawaiian monk seal (*Monachus schauinslandi)*	Hunted to near-extinction for meat, skins, and bait for shark fishery [23, 35]. For details, see Table 2.
18th–19th centuries	NWHI	Green sea turtle (*Chelonia mydas*)	Extensively hunted for meat and eggs. Also used as bait in shark fishery. Exploited for subsistence and market in the 1940s and 1950s by commercial fishermen on FFS [117, 118].
1859–1900; 2000	NWHI	Sharks: Tiger (*Galeocerdo cuvier*) Galapagos (*Carcharhinus galapagensis*) Sandbar (*C. plumbeus*) Grey reef (*C. amblyrhynchos*) Blacktip (*C. limbatus*)	From 1859 to 1900, several vessels took part in a fishery for shark fins and oil, removed a large but unknown number of sharks [25]. In 2000, 990 sharks removed in a single 21-day shark fishing trip to Nihoa Island, Necker Island, Gardner Pinnacles, St. Rogatien Bank, and FFS [27].
1913–2002	NWHI	Fish: Trevally (*Pseudocaranx spp.*) Amberjacks (*Seriola spp.*) Big-eyed scad (*Selar crumenopthalmus*) Yellowfin tuna (*Thunnus albacares*) Bigeye (*T. obesus*) Skipjack tuna (*Katsuwonus pelamis*) Pink snapper (*Pristipomoides filamentosus*) Oblique-banded snapper (*P. zonatus*) Lavender snapper (*P. seiboldii*) Longtail snapper (*Etelis coruscans*) Squirrelfish snapper (*Etelis carbunculus*) Hawaiian grouper (*Epinephelus quernus*) Grey jobfish (*Aprion virescens*)	In 1913, Honolulu-based sampans began fishing for trevally and amberjacks. A bottomfish fishery operated from 1930 to 2010. Following World War II, vessels from Honolulu participated in a NWHI mixed-species fishery for bottomfish, lobsters, reef fish, inshore species, and turtles. In 1946, fishing companies began using FFS as a base of operations with planes exporting, among other species, big-eyed scad [119]. Foreign and domestic longline fleets exploited yellowfin and bigeye tuna while pole-and-line fleets targeted skipjack tuna and baitfish as early as the 1950s. The foreign longline fishery ended in 1980, the domestic longline fishery lasted until 1991. A recreational fishery for a variety of species operated at Midway Island from 1996 to 2002, breaking several International Game Fish Association line class world records.
1882	Lay Lis PHR FFS	Sea cucumber (Holothuria)	755 sea cucumbers (bêche-de-mer) were harvested at Lay, Lis, and PHR; an unknown amount were taken from FFS by the vessel Ada [18, 21, 27].
1928–1930	PHR	Black-lipped pearl oyster (*Pinctada margaritifera*)	~150,000 harvested [29].
1965–1980s	NWHI Gardner Lay	Pink coral (*Corallium spp.*)	Since 1965, foreign vessels used tangle nets to harvest precious coral; Taiwanese vessels illegally poached 100 tons near Gardner Pinnacles and Lay [30].
1970–1999	NWHI	Hawaiian spiny lobster (*Panulirus marginatus*) Scaly slipper lobster (*Scyllarides squammosus*)	11 million individuals landed [32].

fishery, worth \$6 million per year and landing ∼11 million individuals between 1983 and 1999 [31, 32].

Among the most heavily exploited species were seabirds, sea turtles, monk seals, pearl oysters, and lobsters. Dramatic population declines precipitated taxon-specific legislation to protect and promote growth within each of these species. The earliest protection of NWHI fauna was awarded to seabirds in 1909 via establishment of the Hawaiian Islands Reservation. Overharvesting of black-lipped pearl oysters at Pearl and Hermes Reef resulted in a 1930 moratorium on harvest that was never lifted. The Hawaiian monk seal became protected under the US Marine Mammal Protection Act (1972) and the US Endangered Species Act (ESA 1976). The green sea turtle was listed under the ESA in 1978. The NWHI lobster fishery was closed indefinitely in 2000. Such legislative acts were accompanied by requirements for stock assessments. As a result, these taxa have become the best-monitored species in the NWHI, and the only ones for which long-term time-series data are available (i.e., the population status of sharks, bony fishes, and precious corals are uncertain due to infrequent, outdated and spatially limited fishery and survey data). In addition, broad habitat protections were awarded to the NWHI when it was named a Coral Reef Ecosystem Reserve under NOAA's Office of National Marine Sanctuaries in 2000 and a Marine National Monument in 2006. These two executive acts have essentially protected coral reef habitats and eliminated all recreational and commercial exploitation within the NWHI.

Dedicated research surveys have since documented large populations of seabirds and sea turtles in the NWHI; however, four species have not rebounded to pre-exploitation levels: the Hawaiian monk seal, black-lipped pearl oyster, Hawaiian spiny lobster, and scaly slipper lobster. The lack of population growth in these taxa may be a result of species-specific factors, including Allee effects (mechanisms that lead to inverse density dependence at small population sizes [33]), redefined inter-specific interactions, or simply an inadequate amount of recovery time. Alternatively, large-scale climate processes may have altered productivity and trophic function of the entire ecosystem. Here, we explore how various factors may have prevented the recovery of seals, oysters, and lobsters in the NWHI and discuss implications for management of the Papahānaumokuākea Marine National Monument.

4. Hawaiian Monk Seal

In 1805, Russian explorer Yuri Lisianski provided the first written account of the Hawaiian monk seal [34]. Early on, population abundance was described in historical documents as "numerous," "many," and "considerable" [35]. In the next 80 years, hundreds to thousands of seals were killed for their meat, skins, and oil by sealers and shipwrecked sailors [23]. By the turn of the century, few seals were observed over 1–14 months, as reported by several vessels traveling throughout the NWHI (Table 2) [35]. Commercial hunting ceased due to a lack of profitability, and the species was thought to be extinct.

Observations of monk seals in the early 20th century indicated that at least 23 individuals must have survived at the nadir of the bottleneck [36]. By 1958, 916 nonpup seals (i.e., seals over the age of one) were counted in the first systematic beach survey [37, 38]. From this count, total population size was estimated to be 1350–2962 individuals [38, 39]. The species was thought to be on the path to recovery, similar to other previously exploited pinniped populations.

By 1978, however, low juvenile survival had resulted in a 50% population decline (Table 2). Despite active protection and management, overall species abundance continues to decline at ∼4.1% per year as a result of low reproductive rates and high juvenile mortality, attributed to emaciation, shark predation, and entanglement in marine debris [40, 41]. The most recent estimate of total population size is 1,146 individuals [41]. The International Union for Conservation of Nature (IUCN) has listed the species as Critically Endangered, reflecting its high risk of extinction in the wild [42].

The stunted recovery and subsequent decline of the Hawaiian monk seal may be attributed to Allee effects. Video footage reveals that female seals defend their preweaned pups against predation by Galapagos sharks. A larger number of nursing females would provide increased vigilance (e.g., observance and barking) and aggression (e.g., biting). Inbreeding depression (i.e., diminished fitness of inbred individuals) is a common Allee effect that often results in high juvenile mortality rates and low reproductive rates, both of which are exhibited by the species. Further research is required to determine the impact of inbreeding depression on the population [36]. Genetic diversity has been virtually lost throughout the genome, likely as a result of long-term population reduction [36, 43–46]. Though genetic diversity is essential for population persistence and to mount an effective immune response [47], its contribution to the current decline of the species remains unknown.

Another explanation for the current decline in monk seals is inter-specific competition and reduced prey abundance. Emaciation and poor survival of juvenile seals in the NWHI suggests food limitation and stress in the forage base [48]. Dietary overlap has been documented between seals and large predatory fish in the region [49–53], and overall prey scarcity intensifies competition among these top-level predators. Cameras mounted on the backs of seals show jacks, snappers, and sharks attempting to steal prey that seals have flushed from cover; these predatory fish also bully the seal for prey in its mouth [53]. Juvenile seals appear to be most vulnerable to the impacts of competition. Furthermore, pre-weaned pups are increasingly preyed upon by sharks in the NWHI [40]. In contrast, there is high pup and juvenile survivorship in the main Hawaiian Islands [54], where the biomass of large predatory fish is an order of magnitude lower [55]. Without time-series data on shark, jack, and prey populations in the NWHI, we cannot determine whether predatory fish have assumed the niche once held by seals, nor whether there is increased competition due to diminished prey abundance.

Compared to other apex predators, seals are unique in their ability to forage across a wide depth range and to

Table 2: Historical counts of Hawaiian monk seals in the NWHI, at: Kure Atoll (Kur), Midway Island (Mid), Pearl and Hermes Reef (PHR), Lisianski Island (Lis), Laysan Island (Lay), and French Frigate Shoals (FFS). These do not represent overall population estimates. Numbers in bold represent seals killed; numbers in italics represent seals observed. Annotated from Ragen [5] and Hiruki and Ragen [6].

Year	Site	Seals **taken** or *observed*	Notes
1805	Lis	**4**	Exploratory tour of NWHI [34]
1842	Kur	∼ **60**	Food for shipwrecked crew [120]
1850	Lis	**?**	Food for shipwrecked crew [121]
1850	PHR	**10–12**	Food for visiting crew [122]
1859	NWHI	**1500?**	Returned with “1500 seal and shark skins” [123]
1870	Mid, Kur	>**60**	Food for shipwrecked sailors [124]
1886	Lay	**?**	Bait for shark fishing [125]
1888	Mid	*0*	Shipwrecked crew observed no seals in 14 months [125, 126]
1891	NWHI	*1*	Sealing mission; only one seal observed [127]
1891	Lay	*0*	No seals observed in six weeks [128]
1896	Lay	*0*	No seals observed in three months [129]
1905	Lay	*0*	No seals observed [130]
1911	Lay	*0*	No seals observed in six weeks [131]
1912	FFS	*0*	No seals observed [126]
1912	Lay	*1*	One seal observed in three months [126]
1912	Lis	*2*	Two seals observed [126]
1913	Mid	*5-6*	[132]
1923	Lay	*4*	[132]
1923	Lis	**10**	10 seals taken [126]
1923	PHR	*125*	[119]
1923	Kur	*40–50*	Seals observed [133]
1934	Kur	*50–60*	Seen in water or land [21]
1941	Mid	*6*	Observed over 6 month period [134]
1949	Lay	*20–30*	Partial count [126]
1949	PHR	*100*	More than 100 seals [126]
1950	Lis	*100*	At least 100 seals observed [135]
1958	NWHI	*916*	Beach count of nonpups [37, 38]
1968	NWHI	*456*	Incomplete beach count (J. Baker, pers. comm.) [136]
1978	NWHI	*468*	Incomplete beach count (J. Baker, pers. comm.) [136]
1988	NWHI	*486*	Beach count of nonpups (J. Baker, pers. comm.) [40]
1998	NWHI	*391*	Beach count of nonpups (J. Baker, pers. comm.) [40]
2008	NWHI	*293*	Beach count of nonpups [41]

access cryptic prey found under rocks and buried in the sand. As central-place foragers, they undertake extensive movements to feed at neighboring banks, across habitat types and down to subphotic depths [56]. They are generalists and exert top-down pressure that can structure their diverse prey community, including demersal and benthic species [49, 52]. Patterns of prey depletion persist in the slow-growing fish communities at subphotic depths close to the seal colonies [57]. Therefore, changes in monk seal abundance could have major impacts at lower trophic levels.

5. Black-Lipped Pearl Oyster

The black-lipped pearl oyster is harvested and cultivated throughout its range in the Indian and Pacific Oceans for pearls and the nacre of the shell, or “mother of pearl.” Though the species is uncommon throughout the NWHI, there was once a large population at Pearl and Hermes Reef [58]. Between 1928 and 1930, approximately 150,000 pearl oysters were taken, eliciting a ban on harvest by the Hawai‘i Territorial government with the expectation that the fishery would reopen in five years [59]. In 1930, Galtsoff [29] conducted a six-week abundance survey of the Pearl and Hermes Reef stock; he found 480 individuals and concluded that the population was too depleted to sustain further harvesting. A 1993 study indicated that pearl oyster densities had not increased after 60 years of protection [60]. Additional surveys in 2000 and 2002 found few oysters [61]. In 2003, Keenan et al. [59] conducted an in-depth survey of pearl oyster abundance and found a lower average density than that of similar areas in 1930 (Table 3). Additional surveys (2004–2006) confirmed that the Pearl and Hermes Reef population remains in its depleted state after 80 years of protection [58].

Table 3: Harvested numbers and survey counts of black-lipped pearl oysters at Pearl and Hermes Reef.

	1928–1930 (harvest)	1930 (post harvest)	2003(recent survey)
No. of pearl oysters observed	~150,000	480	1047
Density (ind./km^2)	Unknown	209–349	177
Average shell length (cm)	Unknown	20.2	20.2
Depth range (m)	Unknown	2.5–15	0.3–6.0
Depth most abundant (m)	1.0–3.0	4.4–8.3	0.5–2.2
Source	[29]	[29]	[59]

As described by Keenan et al. [59], Allee effects may have prevented recovery of the black-lipped pearl oyster at Pearl and Hermes Reef. Depletion of the adult population likely resulted in reduced reproductive potential of these broadcast spawners, as a result of an overall decrease in the abundance of gametes and a reduced chance of fertilization [62]. Additionally, pearl oysters are protandrous hermaphrodites, starting life as males with a proportion of the population becoming female when larger. The removal of the largest adults would have removed a high percentage of the females, thereby skewing the sex ratio and decreasing the overall fecundity of the population [62]. Because the planktonic larvae settle gregariously on the shells of adult oysters, the loss of settlement cues would also diminish recruitment [59]. The importance of these processes is highlighted by the fact that the Pearl and Hermes Reef pearl oyster population has not increased for nearly 80 years after the cessation of harvest.

Though the last harvest of NWHI pearl oysters occurred in 1930, population recovery may require additional time. Unlike the monk seal, pearl oysters are not endemic to Hawaiʻi, and their recovery may be aided by external recruitment. Pearl oysters are sessile as adults, and the pelagic larvae settle 20–23 days after fertilization [63]. Given the extreme isolation of the Hawaiian Archipelago and the rarity of the species throughout Hawaiʻi, external recruitment is likely uncommon, but the chance of such an occurrence increases with time. Also, it is possible that environmental conditions are rarely favorable to produce or support large populations in the NWHI, accounting for their scarcity throughout the archipelago. Therefore, recovery may require evolutionary time scales (i.e., hundreds of years or more) rather than management time scales (i.e., years or decades).

As filter feeders, pearl oyster populations have the potential to greatly affect levels of phytoplankton in the surrounding water column [62]. The black-lipped pearl oyster has a large gill size and a high pumping rate, which makes it viable even in nutrient poor waters [64]. It can graze plankton down to extremely low levels [65]. For this reason, oysters are a mechanism for strong benthic-pelagic coupling, transferring planktonic energy to the benthic environment [66]. The organics and minerals from the water column make up the shell and soft body tissue of the oyster, and the unassimilated portion of the filtered plankton (discarded as feces) enriches the seafloor [65]. These filter-feeders also influence the ecosystem by decreasing the particle load in the water column, which allows light penetration to depths and improves conditions for photosynthesis. Therefore, the depletion of the large population at Pearl and Hermes Reef likely had a strong impact on ecosystem function, as a result of the loss of the benthic/pelagic coupling and filtering capacity.

6. Hawaiian Spiny Lobster and Scaly Slipper Lobster

In 1975, the National Marine Fisheries Service, the U.S. Fish and Wildlife Service, and the Hawaiʻi Division of Fish and Game conducted a five-year survey and assessment of the marine resources of the NWHI. Populations of the endemic Hawaiian spiny lobster were found throughout the NWHI, with particularly high concentrations at Necker Island and Maro Reef [67]. Survey catch rates “showed excellent potential for development” [68] and were followed by industrialized commercial exploitation. Fishing efforts remained relatively low (<10 vessels, 400 traps hauled/vessel day) until 1984 when the introduction of new traps resulted in a fourfold increase in effort in just two years (16 vessels, 1000 traps hauled/vessel day). In addition, the new traps had a smaller mesh size that increased catch of the scaly slipper lobster, also found throughout the NWHI (Figure 2) [69, 70].

The NWHI lobster fishery was unregulated and unmonitored until 1983. Despite several management measures, the fishery suffered severe declines in catch per unit effort (CPUE) as determined in near-annual stock assessments from 1985 to 2000 (Figure 3). Archipelago-wide spiny lobster trap CPUE, considered an adequate proxy for density [71, 72], fell from 3.41 in 1983 to 1.0 in 1986. In particular, the historically high density Necker Island population CPUE fell from 4.0 in 1983 to 1.2 in 1987. Archipelago-wide slipper lobster CPUE also declined quickly from a high of 1.21 in 1985 to 0.17 in 1991. The declining CPUE of both species resulted in a complete fishery closure in 1993, a shortened (8 week) fishery in 1994, and a one vessel exploratory fishery in 1995. The fishery was indefinitely closed in 2000 because of increasing uncertainty in the population models used to assess stock status [73]. An extensive tagging program, designed to examine lobster dynamics, demonstrated that NWHI lobster abundances have not increased appreciably from 1999 levels. Spiny lobster CPUE in 2008 was 0.80, 0.29, and 0.77 at Necker Island, Gardner Pinnacles, and Maro Reef, respectively [74]. Slipper lobster CPUE was 0.26, 0.23, and 0.75 at Necker Island, Gardner Pinnacles, and Maro Reef, respectively.

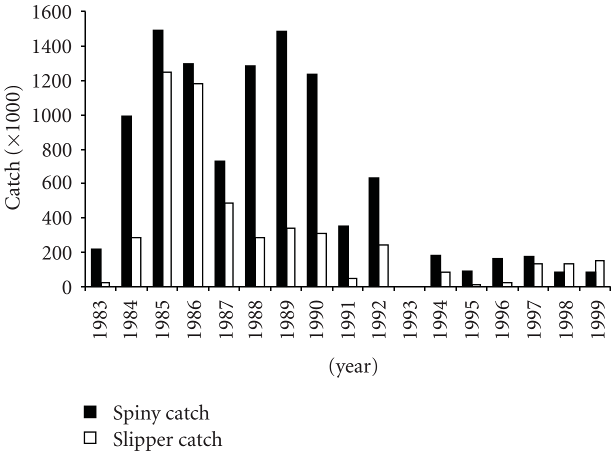


Figure 2: Commercial catch (×1000) of Hawaiian spiny lobster (*Panulirus marginatus*) and scaly slipper lobster (*Scyllarides squammosus*) in the NWHI from 1983 to 1999. The fishery was closed in 1993, and management measures impacted catch in 1994 and 1995.

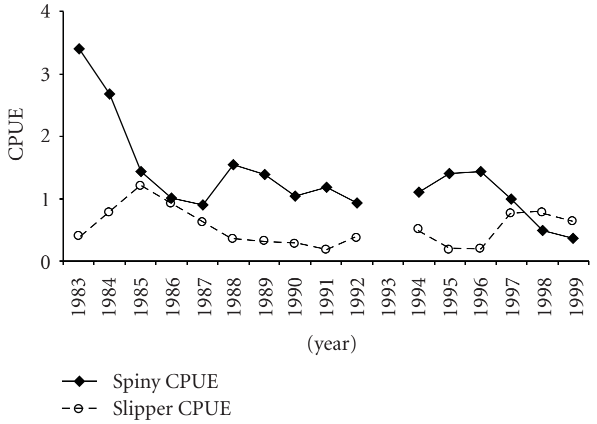


Figure 3: Commercial catch per-unit effort (CPUE; number of lobsters captured per trap haul) for Hawaiian spiny lobsters (*Panulirus marginatus*) and scaly slipper lobster (*Scyllarides squammosus*) in the NWHI from 1983 to 1999. The fishery was closed in 1993.

Allee effects could be delaying the recovery of lobsters in the NWHI. Spiny and slipper lobster egg production was significantly reduced by the removal of females in past decades. The loss of larger females was particularly damaging, because they produce a disproportionately greater number of eggs [75, 76]. As lobster densities decreased due to fishing, Necker Island spiny lobster size-specific fecundity increased, a negative density-dependent, or compensatory, response [76, 77]. Although the long pelagic duration stage typically decouples recruitment success from fecundity [78], the lack of recovery indicates that the compensatory response may not have been enough to counter survival component Allee effects, such as the "dilution effect" (as prey groups get smaller or prey populations sparser, individual prey vulnerability increases [79]), during the pelagic or early benthic stage. The gregarious nature of palinurids and scyllarids also leaves them vulnerable to Allee effects. While it is unclear exactly which cues pelagic-phase NWHI lobsters (phyllosoma, puerulus, and nisto) utilize to orient towards their benthic settlement habitat, laboratory and field research of *P. argus* suggest that conspecific cues play an important role [80]. The gregarious behavior is also generally thought to be a defense mechanism via group vigilance, aggression, and the dilution effect [81, 82]. At minimum, the "guide" effect reduces individual exposure to predation by allowing conspecifics to locate nearby, high-quality shelter [83, 84].

The recovery of lobster populations may be only a matter of time. At the time of the fishery closure, it was assumed that lobster populations would rebound quickly and commercial fishing would commence in a few years. Palinurids are resilient to high fishing mortality and have the potential to recover quickly from low abundances. Pollock [85] attributes this to density-dependent factors, such as labile size-at-maturity, juvenile growth, and survival rates, which increase egg production at lower population densities. Several highly exploited species rebounded in less than a decade, including New Zealand and Australian rock lobsters (*Jasus edwardsii* and *P. cygnus*), the ornate spiny lobster (*P. ornatus*) of the Torres Strait and Papua New Guinea, and six species of *Palinurus* in Japan [86–89]. Therefore, it is somewhat surprising that NWHI lobster populations have not recovered in the past decade, especially since fishing has ceased, egg production should be increasing, and oceanographic conditions favorable to lobster recruitment occurred in 1988–2002 and 2007–2009 (http://jisao.washington.edu/pdo/PDO.latest).

Severe declines in lobster populations likely impacted ecosystem function. Lobsters and other macroheterotrophs feed on the detrital and planktonic energy that is stored in the benthos as infauna (micro molluscs, annalids, etc.). Field evaluations of lobsters have found that their nutritional condition can vary over space and time, presumably in relation to prey availability [90]. Gleaning energy from the benthos, populations of macro-heterotrophs comprise a pathway to higher trophic levels, serving as prey items for sharks, jacks, and seals [49, 51, 91, 92]. A sizable reduction in macro-hetereotrophs has the potential for reducing the flux of energy through the benthos and up the food web. Therefore, the loss of lobster populations could result in a benthic energy sink, constraining the flow of energy to upper trophic levels.

7. Oceanographic Processes

Large-scale oceanographic processes have the potential to alter trophic interactions throughout a food web. Such regime shifts result in profoundly different ecosystem structure. There is some evidence for large-scale ecosystem changes in the NWHI, linked to productivity. Of the six taxa for which long-term, in-depth population data is available, only two have recovered to significant abundance: seabirds and sea turtles. These species differ from seals, oysters, and lobsters in that they utilize the NWHI for reproductive purposes only and not to forage. Turtles and seabirds receive little energy input from the NWHI and are not trophically dependent upon this coral reef ecosystem.

Alternatively, species dependent on the NWHI for nutrient uptake have not rebounded to pre-exploitation levels. The Hawaiian monk seal, black-lipped pearl oyster, Hawaiian spiny lobster, and scaly slipper lobster represent various trophic levels in a coral reef ecosystem. The monk seal is a high trophic level species that exerts top-down predation pressure in shallow and deep-water reefs. Lobsters are low trophic level heterotrophic benthos carnivores that transfer benthic productivity up the food chain. Pearl oysters harvest planktonic productivity from surrounding waters, such that these nutrients become incorporated into coral reef food webs. Though these taxa have different life histories, population dynamics, and ecological niches, all have failed to recover from exploitation. What mechanisms could account for diminished productivity across such varied trophic levels? Marine ecosystems in the Hawaiian Archipelago may be impacted by three large-scale climate processes operating on different time scales: the inter-annual El Niño Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and long-term, global climate change. At any time, all three of these climate signals may be impacting Hawaiʻi with varying intensities.

The best evidence of a link between climate and an ecosystem response in the NWHI occurs at the northern atolls. In some winters, often during El Niño years, the vertically mixed high-surface chlorophyll transition zone, termed the Transition Zone Chlorophyll Front (TZCF), shifts sufficiently far south that the three northern atolls (i.e., Kure Atoll, Midway Island, and Pearl and Hermes Reef) lie within its productive waters (Figure 4) [93]. The temporal dynamics of monk seal populations at these northern atolls is characterized by large interannual variation in pup survival, rather than the long-term declining trend observed for the largest population at French Frigate Shoals [94]. Further, monk seal pup survival increases two years after the TZCF shifts southward. The two-year lag between the position of the TZCF and monk seal pup survival is thought to represent a temporal lag between changes at the base of the food web and monk seal prey items several trophic steps removed [94]. This hypothesis is supported by an ocean-plankton model indicating a strong physical, chemical, and biological gradient that impacts lower trophic level productivity [95]. The relationship appears only to impact the northern atolls, so it does not account for overall monk seal dynamics or the trends observed in lobster species at the southern atolls. It may, however, have a profound impact on pearl oysters in the NWHI, which have only ever occurred in large numbers at Pearl and Hermes Reef.

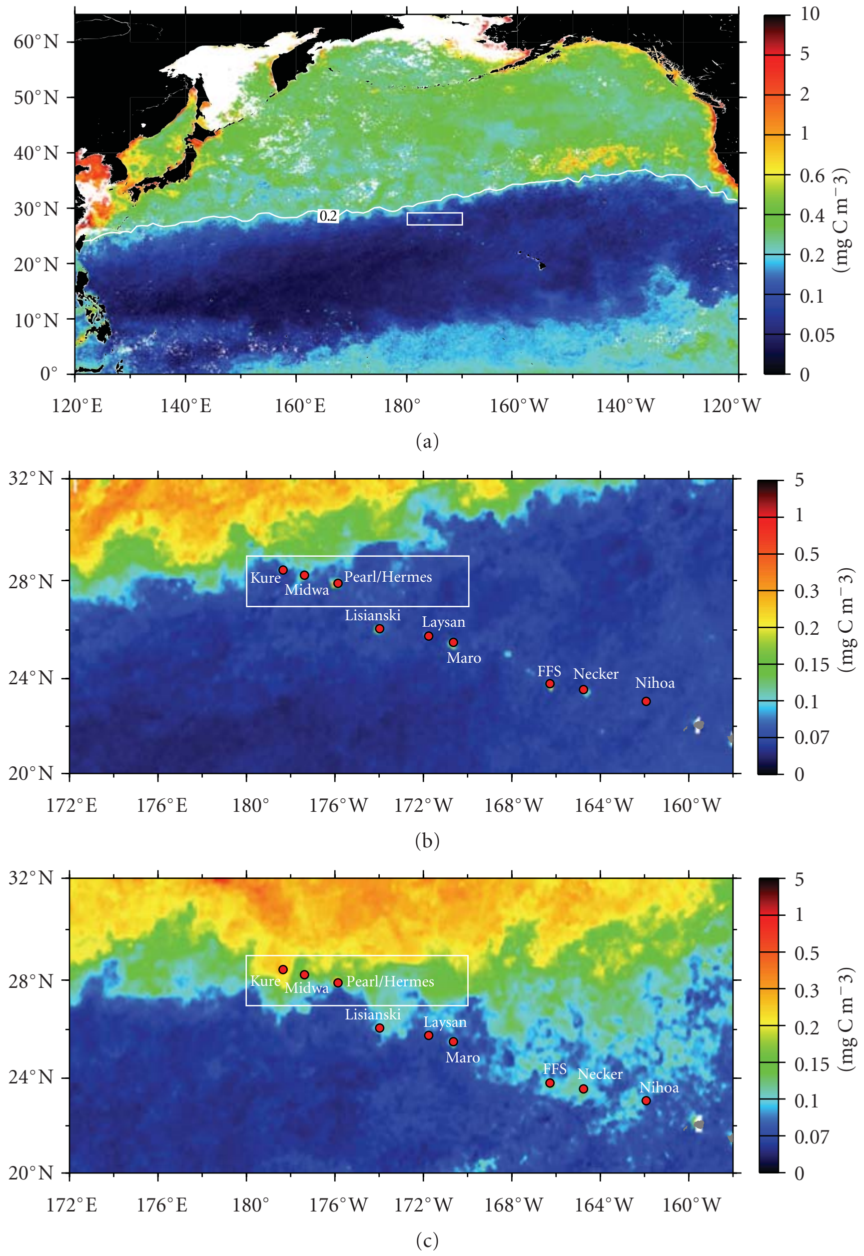
Changes in the PDO (i.e., the interdecadal shift between warm and cool surface waters in the North Pacific) will also result in atmospheric and oceanic changes that could impact productivity and circulation in Hawaiian waters, potentially resulting in ecosystem regime shifts. The intensification of the Aleutian Low Pressure System during 1977–1988, characteristic of the positive phase of the PDO, may have resulted in increased deep mixing, leading to more nutrients in the mixed layer and ultimately enhanced ecosystem productivity [96]. After this event ended, productivity in the NWHI diminished. In the late 1980s, 30%–50% declines were documented for seabird reproductive success, monk seal pup survival and spiny lobster recruitment [96]. Between the mid-1990s and 2010, the PDO has gone through another cycle of positive and negative modes, but similar shifts in productivity have not been repeated. This lack of repeatability may disprove the existence of a relationship between PDO and productivity, or the relationship may be more complicated, as a result of time lags and complex ecosystem interactions.

ENSO and PDO oscillate between two well-defined alternate states or modes; however, the global climate change signal is expressed as an increasing temporal trend. One impact attributed to this trend is increased vertical stratification in the subtropical gyre. This leads to a reduction in nutrients mixed into the euphotic zone and reduced primary production. Based on satellite remotely sensed estimates of surface chlorophyll, the least productive areas of major oceans (i.e., the core of the subtropical gyres) have expanded over the past decade [97]. Though the time series of SeaWiFS chlorophyll data are limited to the past 12 years, this trend could be responsible for long-term reduction of carrying capacity in the NWHI ecosystem. Further research is required to determine whether the change in productivity is responsible for the lack of recovery in seals, oysters, and lobsters.

8. Implications and Recommendations for Ecosystem-Based Management

Marine ecosystem-based management (EBM) is designed to protect ecosystem integrity and to achieve long-term sustainability [98–101]. Specific objectives of EBM often include the maintenance of viable populations and the restoration of depleted resources [102, 103]. Marine mammals, bivalves, and lobsters are often considered keystone species [104, 105] and may be essential in maintaining ecosystem integrity [106, 107], as the removal of apex predators, suspension feeders, and grazers has diminished the capacity for resilience in other systems [1]. Even the loss of a single species within these functional groups reduces overall biodiversity and may be detrimental to natural ecological dynamics [6, 108]. Therefore, while single species are not the target of protection, they remain important to management considerations [109].

Management interventions, such as fishery or area closures, are often enacted to recover depleted taxa. We have shown that these actions do not automatically result in immediate or rapid population growth. Overexploitation can result in widespread impacts that resonate through the system for decades, especially if intra- and interspecies dynamics have changed, or if energy input has been reduced. In such instances, managers generally have three options: provide additional time for recovery, actively try to restore populations, or accept that irreversible change has occurred and adapt to the new, altered system [6]. We will consider each of these options as it pertains to the NWHI (which



(a)

(b)

(c)

Figure 4: Surface chlorophyll estimated from SeaWiFS ocean color for (a) March 2000 basin-scale, (b) March 2000 where northern atolls remain in low chlorophyll water, and (c) March 2004 where high-chlorophyll waters reach the northern atolls (http://oceancolor.gsfc.nasa.gov/SeaWiFS/).

since 2006 have been protected as the Papahānaumokuākea Marine National Monument) and provide suggestions for research and management.

Though it appears that adequate time has passed for seal, oyster, and lobster populations to recover from previous exploitation, we may need to alter our expectations of population growth following excessive take. For example, Hawaiian lobster and monk seal dynamics may be explained by metapopulation theory [110], in which survival and growth rates vary spatially among metapopulations, connected by gene flow [74, 111, 112]. Extinction and recolonization events may occur at broad spatial and temporal scales, most of which are beyond the scope of contemporary research. These natural troughs and peaks occur even in the absence of anthropogenic stressors but may be exacerbated by over-exploitation. Another possibility is that reef species have low-frequency recruitment pulses, perhaps linked to stochastic local environmental processes. Oyster and lobster populations, for example, may have very low annual recruitment, with the exception that once every 50–100 years, they experience a period of high recruitment. Such theories would suggest that it is difficult to sustain single-species fisheries in coral reef ecosystems. The Papahānaumokuākea Marine National Monument is one of the largest marine protected areas in the world. As no recreational or commercial extraction occurs within its waters, it provides a natural laboratory in which to evaluate the amount of time required for population recovery when anthropogenic impacts are controlled (with the exception of global pollution and climate change). Within a protected area such as this, research becomes the main management activity. Thus, we recommend focus on the following as topics for future study:

(i) long-term monitoring of multiple species to detect shifting population trends,

(ii) research on inter-specific interactions to determine how systems shift over time after a perturbation,

(iii) research on metapopulation dynamics to establish baseline levels of recruitment, connectivity and spatial/temporal shifts in abundance.

Another option is active management and restoration. At French Frigate Shoals, translocation of at-risk Hawaiian monk seals and removal of ten Galapagos sharks over four years reduced predation on pre-weaned and recently weaned pups from 31 in 1997 to 11 in 2003 [40]. The continuation and expansion of such initiatives should be considered. Monk seals and pearl oysters may benefit from captive breeding and eventual release, though the risks associated with such activities are high and must be thoroughly researched. Aquaculture of black-lipped pearl oysters from Pearl and Hermes Reef could aid in the recovery of the population [113]. Because bivalves settle in the presence of conspecifics [114], discarded shells left on the beach at Pearl and Hermes could be placed on the reef to encourage settlement. In addition, live adult oysters could be moved closer together to increase fertilization success as well as induce the settlement of larvae. These interventions could alleviate certain Allee effects, but other factors may contribute to the lack of population growth. If oceanographic processes influence carrying capacity, such management actions may be unsuccessful. Furthermore, well-intentioned attempts at restoration could have unintended and unpredictable ecological impacts of a magnitude comparable to those of overextraction. Therefore, this option requires:

(i) historical data on preimpact abundance (including traditional Hawaiian knowledge in the form of orally transmitted histories, chants, and genealogies),

(ii) knowledge of climate patterns,

(iii) flexibility (i.e., adaptive management) to mitigate unforeseen complications.

Managers may be limited to the third option: lowering their expectations of productivity in the altered system. Coral reefs have been described as oases of biodiversity in oligotrophic, oceanic deserts [49]. They may foster intense competition among species within the same functional group, such that when one species is depleted via exploitation, another fills its niche and prevents subsequent recovery. This paradigm of coral reef dynamics suggests low resilience of any one species but high functional group resilience; thus, focus on the preservation of trophic guilds is appropriate. However, catastrophic phase shifts (e.g., over-fishing of herbivorous fish followed by a sea urchin disease epidemic led to algal-dominated reefs in the Caribbean) stress the need to maintain highly diverse functional groups in order to sustain healthy ecosystems [115]. The NWHI can serve as a natural laboratory to examine hypotheses regarding factors thought to confer resistance or resilience (e.g., species diversity, genetic diversity, diversity within trophic guilds, and functional redundancy) without a plethora of confounding local impacts and stressors. As such, it provides a “control” for comparison with reefs elsewhere in Hawai‘i and throughout the world. Therefore, appropriate objectives for EMB are:

(i) maintenance of food-web dynamics and intricacies,

(ii) investigation of ecosystem function and energy flow, including research at and across all trophic levels to quantify productivity and address redundancy,

(iii) assessment of capacity for resilience against potential anthropogenic disturbances, such as climate change, pollution, or invasive species.

9. Conclusions

Though far from pristine, the NWHI coral reef ecosystem is not beyond repair. We recommend that managers continue to provide time for recovery while permitting minor interventions for research and restoration purposes. The examples discussed in this paper require that we change the way we think about the recovery of previously exploited populations. Time should be considered in the context of the slow gradual changes and sudden shifts characteristic of natural processes. Ecosystems do not operate at a single stable state and may not recover to the original wilderness condition after a disturbance. Populations that fail to recover should not be considered isolated events, but rather interpreted as the loss of essential ecosystem components that possibly reflect broad-scale changes. The NWHI coral reef ecosystem provides an important cautionary lesson: a perturbed ecosystem does not automatically revert to its previous state when stressors are removed. This message, utilized as an educational tool, will be important in informing marine management in the Papahānaumokuākea Marine National Monument and throughout the world.

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Research Article

Conservation Status of Marine Biodiversity in Oceania: An Analysis of Marine Species on the IUCN Red List of Threatened Species

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Given the economic and cultural dependence on the marine environment in Oceania and a rapidly expanding human population, many marine species populations are in decline and may be vulnerable to extinction from a number of local and regional threats. IUCN Red List assessments, a widely used system for quantifying threats to species and assessing species extinction risk, have been completed for 1190 marine species in Oceania to date, including all known species of corals, mangroves, seagrasses, sea snakes, marine mammals, sea birds, sea turtles, sharks, and rays present in Oceania, plus all species in five important perciform fish groups. Many of the species in these groups are threatened by the modification or destruction of coastal habitats, overfishing from direct or indirect exploitation, pollution, and other ecological or environmental changes associated with climate change. Spatial analyses of threatened species highlight priority areas for both site- and species-specific conservation action. Although increased knowledge and use of newly available IUCN Red List assessments for marine species can greatly improve conservation priorities for marine species in Oceania, many important fish groups are still in urgent need of assessment.

1. Introduction

Spread over approximately 43 million square kilometres of the Pacific Ocean, Oceania is comprised of thousands of small coral atolls and islands surrounded by vast areas of open ocean. Oceania is characterized by areas of high species diversity and endemism, both in the terrestrial and marine realms [1–3].

The Pacific islands of Oceania support an estimated nine million people [4], many of which rely heavily on marine resources for food and income generation. In many small island nations, the entirety of the population lives within the coastal zone, and marine resources may represent the only source of protein for human consumption. This is highlighted by fish consumption statistics, with annual rates estimated at 50 kg per person, as compared to eight kg for people living in continental countries such as Australia [5].

By nature of its small island geography, Oceania is particularly susceptible to changes impacting biodiversity [6, 7]. Depleted populations cannot always be easily replenished by neighbouring areas, and some species may be prone to localized extinctions, such as those with restricted ranges [8] or widespread species with low abundance and high ecological specialization [9]. Threats to marine conservation include habitat degradation, overfishing, invasive species introductions, and climate change. High human dependency on marine resources and increasing population size mean that pressures on coastal ecosystems in Oceania are only expected to increase [7]. An additional challenge is the management of 16 million square kilometres of ocean that fall outside of any country's exclusive economic zone (EEZ). This vast expanse of ocean is only governed under international high-seas legislation of questionable effectiveness [7].

Pacific islanders have traditionally made use of a number of marine conservation methods, including rights-based fishing (restricted entry), closed seasons, closed areas, size restrictions, and gear restrictions [10]. Historically, these traditional systems played an important role in sustaining fisheries in the region. The importance of local subsistence fisheries continues, with landings from this sector accounting for 80% of coastal fisheries production [11]. However, many of the traditional systems have broken down through the process of Western colonization and introduction of cash economies [12] and many coastal areas, including coral reef ecosystems, are threatened by overexploitation and development [13].

Given its remote nature, scientific knowledge of the region is poor, and conservation work is limited and biased towards more developed countries. In a preliminary review of all the plants and animals present in Oceania published on the 2008 IUCN Red List of Threatened Species, almost one-third are in threatened categories [14]. However, the vast majority of these Red List assessments are for terrestrial organisms. Here we provide a more comprehensive analysis of the status of marine biodiversity in Oceania by examining the conservation status of 1190 marine taxa that have been assessed to date under the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species. Our analyses highlight the current state of knowledge of marine species at risk, major threatening processes, and important research and conservation needs within the region.

2. Methods

2.1. Description of Study Scope. For this study, Oceania is defined as all of Micronesia (Palau islands to Wake and Kiribati), Polynesia (Tuvalu, Tonga, Kermadec Islands, north to the Hawaiian Islands and east to Rapa Nui) excluding the main islands of New Zealand, and the Melanesian island chains of New Caledonia, Vanuatu, Norfolk Island and Fiji (Figure 1). The Melanesian areas of New Guinea and the Solomon Islands were excluded because biogeographically these are more similar to the Coral Triangle region [15].

A species was determined to occur in the Oceania region if its range overlapped with any part of the described study area and there existed documented occurrences of the species' presence in the region. To date, the IUCN Red List Categories and Criteria [16] have been applied to 1190 marine species present in the Oceania region, including all marine mammals, sea birds, sea turtles, reef-building corals, mangroves, seagrasses, sea snakes, sharks and rays, and five perciform coral reef fish families or subfamilies (Table S1). IUCN has partnered with numerous institutions and organizations to complete Red List assessments for these species, such as SeagrassNet, BirdLife International, and several IUCN Species Specialist Groups including those for Cetaceans, Pinnipeds, Marine Turtles, Sharks and Rays, Corals, and Groupers and Wrasses.

Since 2002, the IUCN Red List process has moved away from only assessing select species of assumed high vulnerability or ecological importance and has created a number of different global species assessment initiatives to comprehensively assess complete groups or clades of species for inclusion on the IUCN Red List of Threatened Species. For example, all marine mammals were assessed under the Global Mammal Assessment initiative that assessed the world's approximately 5500 species of mammals, all of the world's seabirds were assessed under a comprehensive assessment of the world's bird species through BirdLife International, and over 20,000 marine species, including all key primary habitat producers (mangroves, seagrasses, corals) and all marine fishes, are currently in the process of being assessed through the Global Marine Species Assessment.

2.2. IUCN Red List Assessment Methodology. All Red List species assessments are based on standardized IUCN Red List methodology [16]. The vast majority of assessments are conducted in Red List Workshops focusing on a taxonomic group or geographic region that bring together the world's leading scientists to share and synthesize species-specific data, and to collectively apply the IUCN Red List Categories and Criteria. Red List assessments for Oceania species presented here represent the combined work of hundreds of scientific experts in at least 14 global Red List Assessment workshops. During Red List Assessment workshops, species are evaluated one at a time by the group of experts present, with outside consultation and followup conducted when additional information is needed but not available at the workshop. Information on taxonomy, distribution, population trends, ecology, life history, past and existing threats, and conservation actions for each species is recorded and reviewed for accuracy. Under the guidance of IUCN Species Programme scientists, quantitative species information is then used to determine if a species meets the threshold for a threatened category under at least one IUCN Red List Criterion. In order for species accounts to be finalized and published on the IUCN Red List of Threatened Species, each species must have a minimum of two Assessors (e.g., those scientists that provided key data and worked with IUCN Species Programme to create the initial species assessment) and two Evaluators (e.g., those scientists that reviewed the final account for data accuracy and correct application of Criteria); however, in many cases the number of Assessors and Evaluators for many species was much higher. All species data and results of Red List assessments, including the names of the scientists that contributed to the 1190 species assessed in Oceania either as Assessors or Evaluators, are freely and publicly accessible under each species account on the IUCN Red List of Threatened Species [17]. This IUCN Red List process consolidates the most current and highest quality data available and ensures peer-reviewed scientific consensus on the probability of extinction for each species.

The IUCN Red List Categories and Criteria are the most widely accepted system for classifying extinction risk at the species level [18–21]. The IUCN Red List Categories are comprised of eight different levels of extinction risk: Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR),

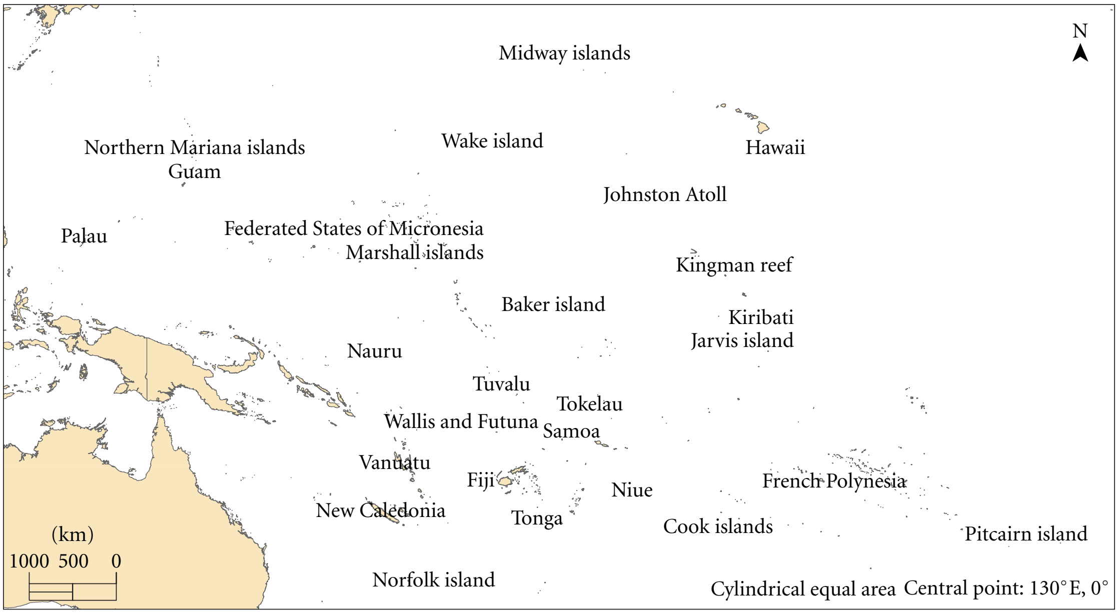


Figure 1: Major islands and regions of Oceania.

Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), and Data Deficient (DD). A species qualifies for one of the three threatened categories (CR, EN, or VU) by meeting a quantitative threshold for that Category in one of the five different available Criteria (A–E). A category of Near Threatened is assigned to species that come close to, but do not fully meet all the thresholds or conditions required for a threatened Category under Criterion A, B, C, D, or E. A category of Least Concern is assigned when there are no known threats to a species, or quantification of known threats for a species does not come close to meeting any of the threatened Category thresholds. A category of Data Deficient is assigned when there is insufficient information available to adequately apply the Criteria, such as taxonomic uncertainty, lack of key biological information, or inability to adequately quantify the impact of known threats.

The IUCN Criteria (A–E) that underpin the IUCN Red List are designed to be transparent, reproducible, and conservatively flexible in the handling of uncertainty [16]. The Criteria are a standardized methodology that can be applied consistently to any species from any taxonomic group [16, 22]. Each of the five Criteria is based on extinction risk theory [22] and fall within one of two paradigms of elevated extinction risk: (1) species with small population sizes that are inherently at higher risk of extinction and/or are undergoing decline, and (2) species with widespread or large populations that are declining faster than they are able to recover.

Criterion A measures extinction risk based on exceeding a threshold of population decline (30% for Vulnerable, 50% for Endangered, and 80% for Critically Endangered) over a timeframe of three generation lengths, a measure of reproductive turnover rate, in the recent past. For species with large, widespread population sizes, this is often the most applicable Criterion. As many marine species have large distributions, compared to terrestrial species, over 90% of species in Oceania that were determined to be in threatened categories were assessed under Criterion A. Taxa-specific methodology for application of Criterion A to species relies on first defining an appropriate generation length for the species group, and then determining the best proxy or surrogate available to estimate population decline over time (e.g., estimates of population size from survey samples, habitat loss, fishery statistics, etc). Generation length, defined as the average age of parents of the current cohort, is a measure of species reproductive turnover and is best calculated from a life table with appropriate age- and sex-specific information on survival and fecundity. However, when these data are not available, other methods can be used to estimate generation length [23]. It is recognized that there are inherent difficulties for calculating generation length in particular for very long-lived taxa, for taxa with age-related variation in fecundity and mortality, or for species with variable reproductive traits under different environmental or population stressors, such as overfishing [23–26].

Criterion B measures extinction risk based on a small geographic range size (extent of occurrence <20,000 km^2 or area of occupancy <2,000 km^2 to meet the lowest threshold for Vulnerable) combined with continued decline and habitat fragmentation. Criterion C is applied to species with small population sizes estimated to be less than 10,000 mature individuals, with continued decline. Therefore, Criterion B and C are most applicable for species with small range sizes or small population sizes, which are also undergoing decline. Criteria D is designed to capture the inherent risk of extinction of species with extremely small population sizes. Under Criterion D, species can qualify for a threatened category if the global population is estimated to be less than 1,000 mature individuals or occupies an area of less than 20 km^2. Criterion E is applied to species with extensive population information that allows for population declines to be appropriately modeled over time. Although few species have this quantity of data available for reliable modeling, it can be appropriate for some species of commercial marine fish [27].

The description and guidelines for the use of IUCN Red List Criteria are publicly available [23]. Details of how the Criteria have been interpreted and applied to different marine groups are described in several recent publications on marine mammals [28], reef-building corals [29], mangroves [30], sharks and batoids [31, 32], groupers [33], sea birds, and sea turtles [34–36].

2.3. Spatial Analyses. Spatial analyses were conducted for all species based on digital distribution maps compiled during IUCN Red List Workshops and from partner organizations. However, distribution maps were not available for all species of sea birds, and therefore all spatial analyses were conducted without the inclusion of sea bird species.

All digital distribution maps were first created based on a minimum convex polygon connecting points of known presence. To improve accuracy and standardize analyses, each polygon was cut to either a shore fish basemap or left as a pelagic species polygon, depending on whether the species is found primarily above 200 m depth or below 200 m depth. In general, the vast majority of shore fish, sea snake, mangrove, coral, and seagrass polygons were cut to the shore fish basemap created from a combined 100 km shoreline buffer and maximum depth of 200 m, based on 2-minute spatial bathymetry data available from NOAA National Marine Fisheries Service (ETOPO1). This "cookie-cutter" method allows for standardization of analyses and better visualization for near shore and shallower water species. Species that could occur in deeper waters, including the vast majority of marine mammals, sea turtles, sharks, and rays were left as entire polygons. Overall, this approach helps to improve the accuracy of subsequent analyses by standardizing species ranges and by excluding large areas of open ocean where a shallow water species would never occur.

For analyses of species richness and proportion maps, all species polygons were stacked and analyzed using a 10 km × 10 km square grid. This grid sizewas chosen as it avoids over-estimation of ranges for small-rangeendemic species. The grid database is a presence or absence record and if a very limited range endemic has a range smaller than the grid size, the species would be recorded in a larger area than it actually occupies and this could skew biodiversity per unit area estimates. Some limited range endemics actually occupy small areas and the 10 km by 10 km grid size is the smallest manageable resolution that was practical. Final maps were converted into a raster of 10 km × 10 km cell size to visualize biodiversity patterns. Presence and percentage of each species range within a marine protected area was estimated based on overlay with the World Database of Protected Areas [37].

3. Results and Discussion

3.1. Summary of IUCN Red List Status of Marine Species. Seventeen percent of all marine species (196 species) assessed to date in Oceania are in threatened (Critically Endangered, Endangered or Vulnerable) categories (Table 1). Of the 196 threatened species, 70% (140 species) are reef-building corals, 13% (26 species) are sharks or batoids, 6% (11 species) are sea birds, 3% (6 species) are shore fish, 3% are marine mammals (6 species), 2% (5 species) are sea turtles, and less than 1% are sea snakes (1 species). Another 16% (187 species) are listed as Near Threatened, indicating that over one-third (383 species) of all species assessed in Oceania are listed in threatened or Near Threatened categories. Fifty-eight percent of all species assessed in Oceania (690 species) are listed as Least Concern, and approximately 10% (117 species) are listed as Data Deficient. It is important to note that species listed as Least Concern or Data Deficient can still be impacted by a number of local and regional threats, but the impact of threats on the species' population was either unknown or unquantifiable (listed as Data Deficient), or if threats were operating on a species, they were determined to be below the threshold required for classification in a threatened or Near Threatened category (listed as Least Concern).

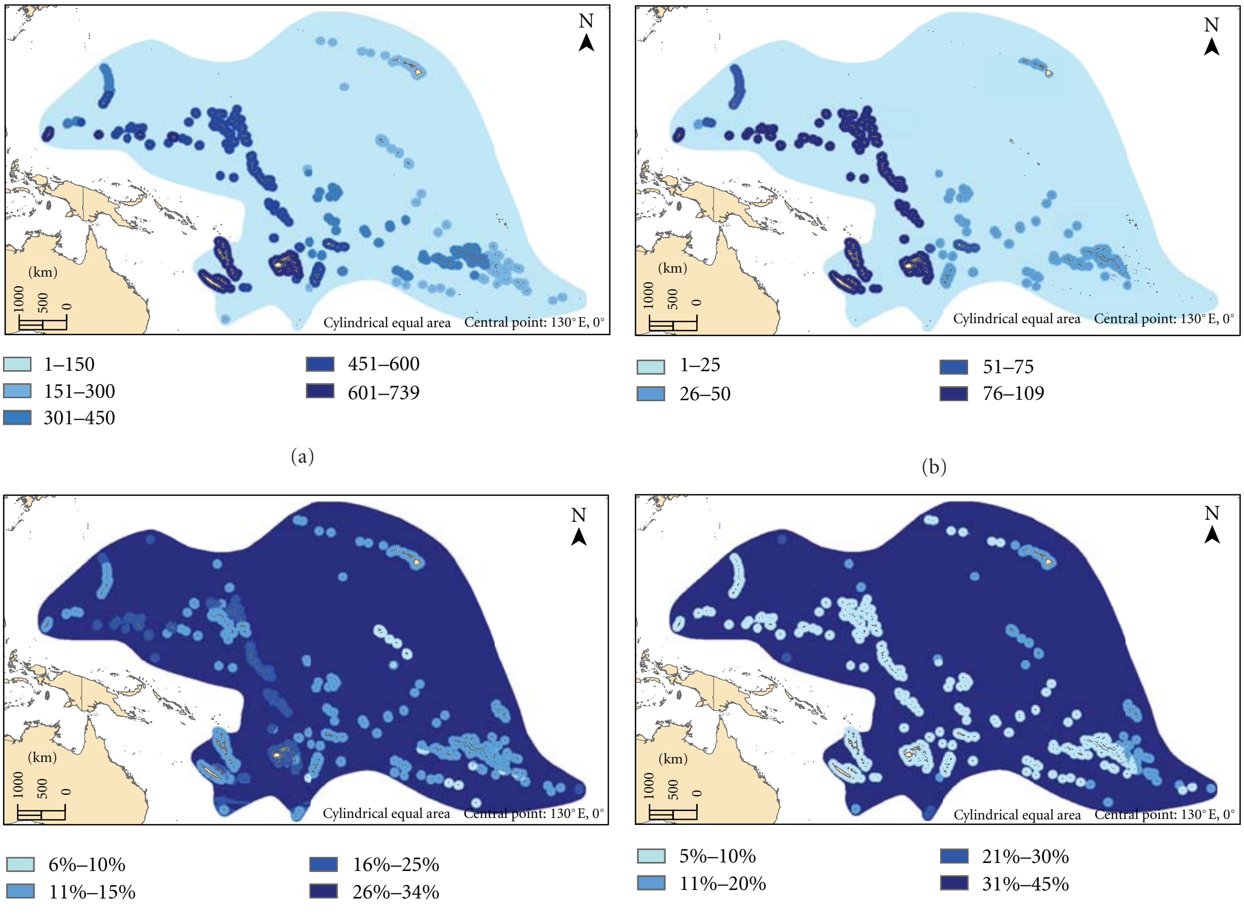
Although approximately 1 in 5 (17%) of marine species in Oceania were classified in a threatened category, it is not clear if this region is more or less threatened than other regions, as comprehensive analyses of marine species in other regions are not yet available. However, a preliminary study of all of the 519 marine bony fishes, sharks, and rays present in the Mediterranean Sea showed that approximately 8% are in threatened categories [38]. Similarly, approximately 9% of all bony fishes, sharks, and rays (108 of 1162 species) assessed in the Eastern Tropical Pacific were preliminarily assessed in threatened categories [39]. Although the vast majority of bony fish species still need to be assessed in Oceania, preliminary results are similar to other regions, with approximately 6% (32 of 512 species) of sharks, rays, and bony fish assessed found in threatened categories.

Although marine species are still vastly underrepresented on the IUCN Red List of Threatened Species (of the 58,000 species currently listed on the 2010 IUCN Red List of Threatened Species less than 7% or 3,800 species are marine), approximately 36% of terrestrial species, 27% of freshwater species, and 19% of marine species are in threatened categories [17]. A preliminary study of threatened species in Oceania found that approximately 28% were in threatened categories [14]; however, this study was not exclusively marine and assessed only five groups (all mammals, amphibians, birds, freshwater crabs, and hard corals). A comprehensive assessment of marine species is necessary for understanding conservation priorities in the region.

With regard to spatial patterns, marine biodiversity is highest in the western portion of Oceania (Figure 2(a)), including New Caledonia, Vanuatu, Fiji, Tuvalu, western Kiribati, and the Federated States of Micronesia. This pattern is consistent with general biogeographic patterns observed in the Indo-West Pacific with species diversity gradually declining with distance from the Coral Triangle [15]. This western Oceania region also has the highest numbers of threatened species assessed to date, with over 100 species

Table 1: Numbers and proportions of species of the different marine groups assessed to date for the IUCN Red List of Threatened Species in Oceania (CR: Critically Endangered, EN: Endangered, VU: Vulnerable, NT: Near Threatened, LC: Least Concern, DD: Data Deficient).

Kingdom	Phylum	Class	Order	Group	CR	EN	VU	NT	LC	DD	Total Oceania Species	no. of Oceania Endemics	% Oceania Endemism	no. of global species	% Threatened (CR, EN, VU) in Oceania	% DD in Oceania
Plantae	Angiospermae	Monocotyledons	Alismatales	Seagrasses			1		13	1	15	1	7%	72	7%	7%
Plantae	Magnoliophyta	Magnoliopsida	*Multiple*	Mangroves				1	23		24	0	0%	70	0%	0%
Animalia	Cnidaria	Anthozoa	Scleractinia	Corals	1	6	133	141	217	34	532	14	3%	845	26%	6%
Animalia	Chordata	Chondrichthyes	Chimaeriformes	Chimaeras					1	4	5	0	0%	174	0%	80%
Animalia	Chordata	Chondrichthyes	Rajiformes	Batoids	1	2	3	5	8	3	22	2	9%	511	27%	14%
Animalia	Chordata	Chondrichthyes	*Multiple*	Sharks	1	2	17	21	15	19	75	8	11%	357	27%	25%
Animalia	Chordata	Actinopterygii	Perciformes	Groupers (Epinephelinae)			4	10	32	14	60	4	7%	161	7%	23%
Animalia	Chordata	Actinopterygii	Perciformes	Angelfishes (Pomacanthidae)				1	41		42	8	19%	86	0%	0%
Animalia	Chordata	Actinopterygii	Perciformes	Butterflyfishes (Chaetodontidae)				1	55	3	59	9	15%	128	0%	5%
Animalia	Chordata	Actinopterygii	Perciformes	Parrotfishes (Scaridae and Odacidae)			1	2	37		40	4	10%	109	3%	0%
Animalia	Chordata	Actinopterygii	Perciformes	Wrasses (Labridae)			1		191	17	209	44	21%	503	0%	8%
Animalia	Chordata	Reptilia	Squamata	Seasnakes			1	1	15	2	19	4	21%	70	5%	11%
Animalia	Chordata	Reptilia	Testudines	Sea Turtles	2	2	1				5	0	0%	7	100%	0%
Animalia	Chordata	Aves	*Multiple*	Sea Birds	2	1	8	4	31	1	47	6	13%	190	24%	2%
Animalia	Chordata	Mammalia	*Multiple*	Marine Mammals	1	3	2		11	19	36	0	0%	132	17%	53%
				Total	8	16	172	187	690	117	1190	104			17%	10%



(a) (b) (c) (d)

Figure 2: (a) Range and number of marine species assessed in this study (species richness), (b) species richness of all marine species assessed in threatened categories: Critically Endangered, Endangered, or Vulnerable, (c) proportion of species assessed in threatened categories, and (d) proportion of all species assessed as Data Deficient. (Sea birds were excluded from all analyses as maps were not available for all species).

now in threatened categories in some of these same areas (Figure 2(b)). This region also has a higher number of Data Deficient species, with between 35 and 50 species listed as Data Deficient in New Caledonia, Vanuatu and Fiji (data not shown). The greater absolute number of threatened and Data Deficient species in the western portion of the study area is partly a reflection of the higher biodiversity in that area.

The proportions (not absolute value) of species in threatened (Figure 2(c)) and Data Deficient (Figure 2(d)) categories offer a different perspective, highlighting regions with more threatened or Data Deficient species relative to the total amount of species present. Areas of open ocean showed the highest proportion of species in these categories, indicating that deeper water or pelagic species (e.g., >200 m), such as marine mammals, sea turtles, sharks and rays are the most threatened and Data Deficient groups. Compared to other taxa assessed to date, these species may be more threatened because they are longer-lived and slower to reproduce. Additionally, many have global or Indo-Pacific distributions, and have experienced widespread population declines throughout their range. Knowledge of the nature and extent of regional threats to these deeper water or pelagic species is essential for their mitigation within Oceania. A higher proportion of deeper water species are also listed as Data Deficient, primarily as these species are generally harder to study in the wild, and less information is known on their population trends, reproductive biology, and impact of known threats.

3.2. Highly Migratory and Wide-Ranging Species. Comprehensive assessments were completed for all sea turtles, sharks and rays, marine mammals, and sea birds in the region. Among these, sea turtles have the highest proportion of threatened species of any group, with all five of the species present in Oceania, Loggerhead (*Caretta caretta*), Green (*Chelonia mydas*), Leatherback (*Dermochelys coriacea*), Hawksbill (*Eretmochelys imbricata*), and Olive Ridley (*Lepidochelys olivacea*), listed in threatened categories. Threats to all sea turtle species occur globally and at all stages of their life cycle. Marine turtles lay their eggs on beaches, which are subject to threats such as coastal development and sand mining. The eggs and hatchlings are threatened by pollution and predation by introduced predators such as pigs and dogs, as well as collection by humans. Sea turtles have traditionally been used in the Pacific Island for their meat and eggs, their shells used for decoration, fishing lures and hooks, and for sale and opportunistic by-catch by fishers targeting shellfish and sea cucumbers [40–43]. At sea, marine turtles are faced with threats from targeted capture in small-scale subsistence fisheries, by-catch by long-line and trawling activities, entanglement in marine debris, and boat strikes. Their life history characteristics, particularly late sexual maturity and long juvenile stage, combined with the many threats from human activities in the sea and on land contribute to their high risk of extinction [34]. In addition, global climate change is now considered to be a serious, if not entirely understood, threat that is contributing to the loss of nesting beaches [44], possibly skewed sex ratios [45], and loss of foraging grounds [46].

Approximately one-fourth of all sharks and batoids found in Oceania are in threatened categories. Like sea turtles, the threats to the majority of these species occur globally, and only 10 of the 97 species of sharks and rays present in Oceania are endemic to the region. The primary threat to sharks and rays (batoids) is their capture in nets from both targeted and accidental catch. Most shark species grow slowly, mature late, produce few young, and have low rates of population increase, making them highly vulnerable to depletion with a low capacity for recovery from overexploitation [32]. Shark fisheries have proliferated around the world during recent decades, in response to increasing demand for shark products and as traditional fisheries come under stronger management. Millions of sharks are caught each year for their fins which are used to make the Asian delicacy shark fin soup [34]. Many subsistence and small-scale fisheries for sharks occur in the Oceania region. Typically, the meat is used for domestic consumption and the teeth and jaws are sold as curios in the tourist industry [47]; however, catches are poorly documented. Sharks are also commonly taken in the Oceania region as by-catch of commercial tuna and other pelagic long-line or purse seine fisheries, which retain primarily shark fins for the international trade [47–49]. The two most threatened shark and ray species found in Oceania, Harrison's Deepsea Dogfish (*Centrophorus harrissoni*) and the Narrowsnout Sawfish (*Pristis zijsron),* both listed as Critically Endangered, have ranges primarily outside of the region, but with records from a few locations within Oceania including New Caledonia and Fiji.

Approximately 25% (19 of 75 species) of sharks and 80% (4 of 5 species) of chimaeras are listed as Data Deficient. For many shark species, little is known about their reproductive biology and quantitative data is lacking on the impact of fisheries on their populations. For example, approximately 50% of the estimated global catch of chondrichthyans is taken as by-catch which does not appear in official fishery statistics and is rarely managed [50]. Most chimaeras are not well-studied, as they are primarily deep-water species that occur in temperate waters. For the few species that are thought to occur in Oceania, little is known about their distribution, reproduction, or the potential impact of fishing activities on their populations.

Almost one-fifth of marine mammals present in Oceania are in threatened categories, and over 50% (19 of 36 species) of marine mammals in Oceania are listed as Data Deficient, again because threats to many of these pelagic and/or highly migratory species cannot be adequately quantified [28]. No marine mammals are known to be endemic to Oceania, and major threats to these species are global or historic. The primary threats to marine mammals in Oceania and around the globe are accidental mortality through entanglement in fishing gear, the effects of noise pollution from military and seismic sonar, or boat strikes [28, 51]. In many regions, including Oceania, marine mammals are also threatened by habitat loss from coastal development, loss of prey, or other food sources due to poor fisheries management, and historical or current effects of hunting [34]. Hunting of large whales does not occur in the region, and countries including Cook Islands, Fiji, French Polynesia, Samoa and Niue have declared whale sanctuaries [52]. However, several Pacific Island countries have recently joined the International Whaling Commission and voted with Japan in favor of commercial whaling. Dolphin hunts have occurred traditionally throughout Oceania, and still remain in the Solomon Islands where they are thought to be contributing to population declines [53, 54]. Dugongs, *Dugong dugon*, are also traditionally hunted in many areas for their meat, bones, and skin [55, 56]. Although there are no estimates of the numbers of dugong caught, the species is likely very vulnerable to hunting and other human impacts due to its restricted coastal habitat, dependence on sea grasses, and low reproductive rates [57]. The most threatened marine mammal in Oceania is the Hawaiian monk seal, *Monachus schauinslandi*, listed as Critically Endangered. Mortality rates from birth to maturity of monk seals in the northwestern Hawaiian Islands are very high, and disproportionally impact juveniles. Causes of mortality are thought to include food limitation, predation on suckling and recently weaned pups, and entanglement in marine debris. There are currently less than 600 mature individuals of this species, and declines are expected to continue into the near future despite the species being primarily found within the Northwestern Hawaiian Islands National Marine Monument [58].

Twenty-three percent (11 of 47 species) of all sea birds in Oceania are in threatened categories. Major threats to seabirds across the globe include mortality in long-line fisheries and gill-nets, oil spills, and the impact of invasive species such as rodents and cats at breeding colonies. Additional threats to breeding sites of seabirds are habitat loss and degradation from coastal development, logging, and pollution [59]. In Nauru and Tonga, seabirds have traditionally been caught for food, but it is unclear whether this constitutes a threat [60]. Some sea bird species are vulnerable to by-catch, usually in longline fisheries in the Oceania region. The most common species caught are albatrosses, petrels, shearwaters, and fulmars [61]. Many of these occur only in passage through Oceania and are typically more abundant in temperate areas. However, for those species that are endemic, even infrequent fisheries-related mortality may have a significant effect on populations [61]. Very little information is available on the numbers and species of sea birds that are by-caught [62]. Globally, albatrosses are one of the most threatened families of birds, and both species found in Oceania are listed as Vulnerable. Five of the six Oceania endemic sea birds: Little White Tern (*Gygis microrhyncha),* White-throated Storm Petrel *(Nesofregetta fuliginosa),* Fiji Petrel *(Pseudobulweria macgillivrayi),* Henderson Petrel *(Pterodroma atrata),* Collared Petrel *(Pterodroma brevipes*), and the Hawaiian Petrel (*Pterodroma sandwichensis*) are in threatened or Near Threatened categories. These species have restricted ranges and their nesting sites are threatened by introduced species such as rats, pigs, mongoose, and feral cats. The Fiji petrel, listed as Critically Endangered, is the most threatened sea bird in the region, with the remaining population estimated to be less than 50 individuals [63].

3.3. Sea Snakes. As a group, sea snakes and the impact of perceived threats to their survival are not well understood. Much of what is currently known about sea snakes is from their capture in fisheries by-catch. However, many species of sea snakes prefer near-shore, shallow waters, including estuaries and brackish water habitats, which are areas that are often highly impacted by coastal development and aquaculture. Fifteen of the 19 sea snakes species found in Oceania are also found throughout the Pacific. Of these nonendemics, all are listed as Least Concern except one species listed as Data Deficient. The four species that are endemic to Oceania have relatively restricted ranges, and at least two of these species are exposed to a number of different threats. The Flat-tail Sea Snake (*Laticauda schistorhynchus)* is currently known only from Niue and is listed as Vulnerable. The Yellow-lipped Sea Snake (*Laticauda frontalis)*, listed as Near Threatened, is thought to be endemic to Vanuatu with some records also from the Loyalty Islands of New Caledonia. Both of these species occur primarily in shallow waters and are impacted by coastal development and habitat destruction throughout their small ranges and are especially vulnerable as females of both species need to come onto land to deposit their eggs [64].

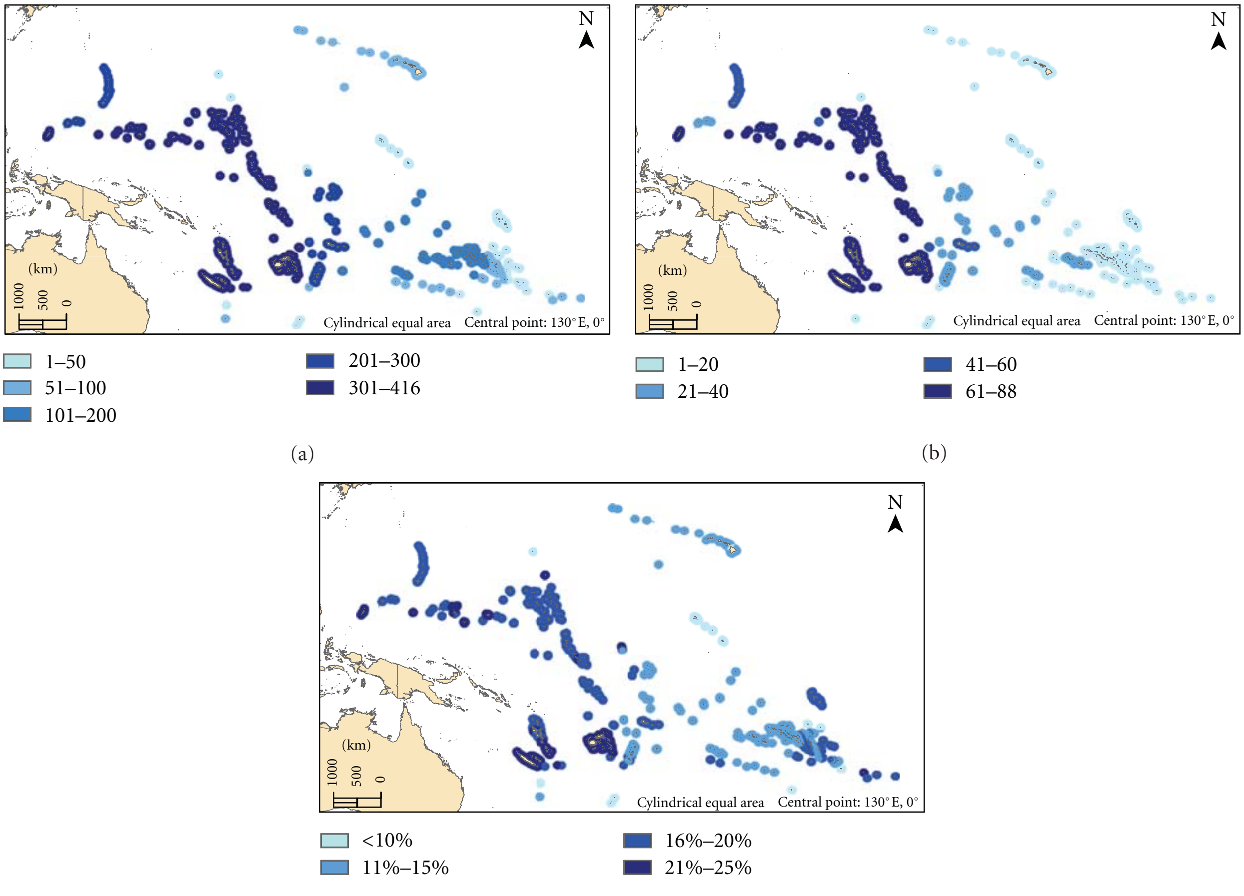
3.4. Primary Habitat Producers. Of the coral, seagrass, and mangrove species present in Oceania, corals are by far the most threatened group. Only one seagrass, *Halophila hawaiiana* listed as Vulnerable, is in a threatened category. This shallow water seagrass is endemic to the Hawaiian Islands and is declining due to invasive algal species, shoreline development, and beach replenishment. All of the mangrove species present in Oceania are widespread in the Pacific and are listed as Least Concern, with the exception of *Rhizophora samoensis*, listed as Near Threatened, which is declining due to the loss of mangrove habitat primarily in the eastern Pacific portion of its range [30]. In general, the Oceania region has lower species diversity and few threatened species of mangrove and seagrasses compared to other regions, such as the Coral Triangle or the Eastern Tropical Pacific [30, 39].

As previously mentioned, reef-building corals comprise the highest proportion (70%) of all threatened species currently assessed in the Oceania region. In terms of marine ecosystems, coral reefs harbor the highest concentration of marine biodiversity and are declining worldwide due to a myriad of threats [29] including ocean acidification, coastal development, sedimentation resulting from poor land-use and watershed management, sewage discharges, nutrient loading and eutrophication from agro-chemicals, coral mining, overfishing, and destructive fishing practices. Overall, 25% of all coral species present in Oceania are in threatened categories (133 of 532 species), and another 26% are in Near Threatened categories.

In Oceania there is generally a lower percentage of destroyed or critically declining reef compared to other regions of the world [65], although sedimentation, coastal development and destructive fishing practices are still major threats in the region. The majority of coral species found in Oceania are also found in the Coral Triangle region, which has the highest proportion of threatened coral species and reef decline [29]. Due to a greater absolute number of coral species in the western portion of Oceania, there is also a higher number of threatened species (Figures 3(a) and 3(b)). However, the proportion of threatened coral species is high not only in some western Oceania countries such as New Caledonia, Vanuatu, and Fiji, but also in some eastern regions such as within French Polynesia (Figure 3(c)). There is also higher coral species endemism in eastern Oceania, such as in Hawaii (data not shown). Nine of the 14 coral species endemic to Oceania are in threatened or Data Deficient categories. Of special concern are *Porites pukoensis*, listed as Critically Endangered, and *Montipora dilatata*, listed as Endangered, both of which are only known from a few dozen colonies or less in Hawaii.

3.5. Bony Shore Fishes. Only 410 species of bony fish have been assessed in Oceania to date, all of which belong to fish groups associated with coral reef habitat. Compared to other taxa assessed in Oceania, bony fishes have lowernumbers of threatened species, with only four groupers, one parrotfish, and one wrasse species in threatened categories. Threats to these species are primarily from population declines due to overfishing. Eight percent (34 species) of bony fishes assessed to date are listed as Data Deficient (the majority of which are groupers) as population declines, and the impact of fisheries could not be adequately quantified. Many species of grouper are highly targeted throughout the world, especially for the live fish trade, and have high commercial value. Like many large-bodied fish species [24], groupers are considered to be especially vulnerable to overfishing given their long life span, late sexual maturation, and aggregation-spawning in many species. Many species of parrotfish are also targeted in recreational, artisanal, and commercial fisheries throughout their range. The Green Humphead Parrotfish, *Bolbometopon muricatum,* listed as Vulnerable, is highly sought after in many parts of Oceania, and severe declines in local populations have led to the implementation of improved management measures including minimum size limits, banning of night spearfishing, and required catch permits in US territories in the Oceania region [66].

Like marine species diversity in general, coral reef fish diversity is also higher in western Oceania (Figure 4(a)), especially in New Caledonia, Vanuatu and Fiji, with a trend



(a)

(b)

(c)

Figure 3: (a) Species richness of coral species present in Oceania, (b) species richness of coral species in threatened categories, and (c) proportion of coral species in threatened categories.

of declining number of species moving eastward from the Coral Triangle [15]. The number of threatened bony fishes assessed to date is therefore also higher in these areas (Figure 4(b)). However, the proportion of threatened and Data Deficient bony fishes show a different pattern with slightly higher proportions of threatened shore fishes outside of western Oceania such as around Kiribati and Micronesia (Figure 4(c)) and higher proportions of Data Deficient shore fish in other areas such as around French Polynesia (Figure 4(d)). This apparently random pattern is most likely because of the very low proportion of total shore fishes that have been assessed to date, particularly groups with high numbers of species endemic to Oceania. Compared to the widespread or primary habitat producing species, bony fishes assessed to date have a relatively higher proportion and number of endemic species in Oceania, with 69 of the 410 species (17%) considered endemic to the region. Of these, the wrasses and angelfish have the highest endemism with approximately 20% of Oceania species endemic to the region. None of the assessed endemics have been placed in a threatened category because they mostly appear to be present in high abundances and with few major threats. However, large numbers of small, limited range endemic shore fishes that may be threatened have not yet been assessed. This includes species groups with high numbers of endemic shore fishes in Oceania, such as damselfishes, gobies, and blennies. In general, species with small range sizes and/or population sizes are inherently more at risk for extinction than more widespread species [22], and the highest rates of extinction have been recorded for endemic species on isolated islands [67, 68]. However, widespread species that are low in abundance and exhibit some degree of specialization can also have a greater risk of local extinction [9], especially in areas of intensive localized threats such as overfishing, pollution, or habitat loss. It will be important to assess all shore fishes in order to get a complete picture of conservation status of bony fishes in Oceania.

3.6. Threatened Marine Species Conservation in Oceania. The Oceania region is politically and culturally complex, with 10 independent island nations, 3 self-governing or autonomous territories, and 10 territories or jurisdictions with varying degrees of autonomy and association with one of five metropolitan countries (Australia, France, New Zealand, the United Kingdom, or the United States). Independent island nations in Oceania with specific national laws or ordinances

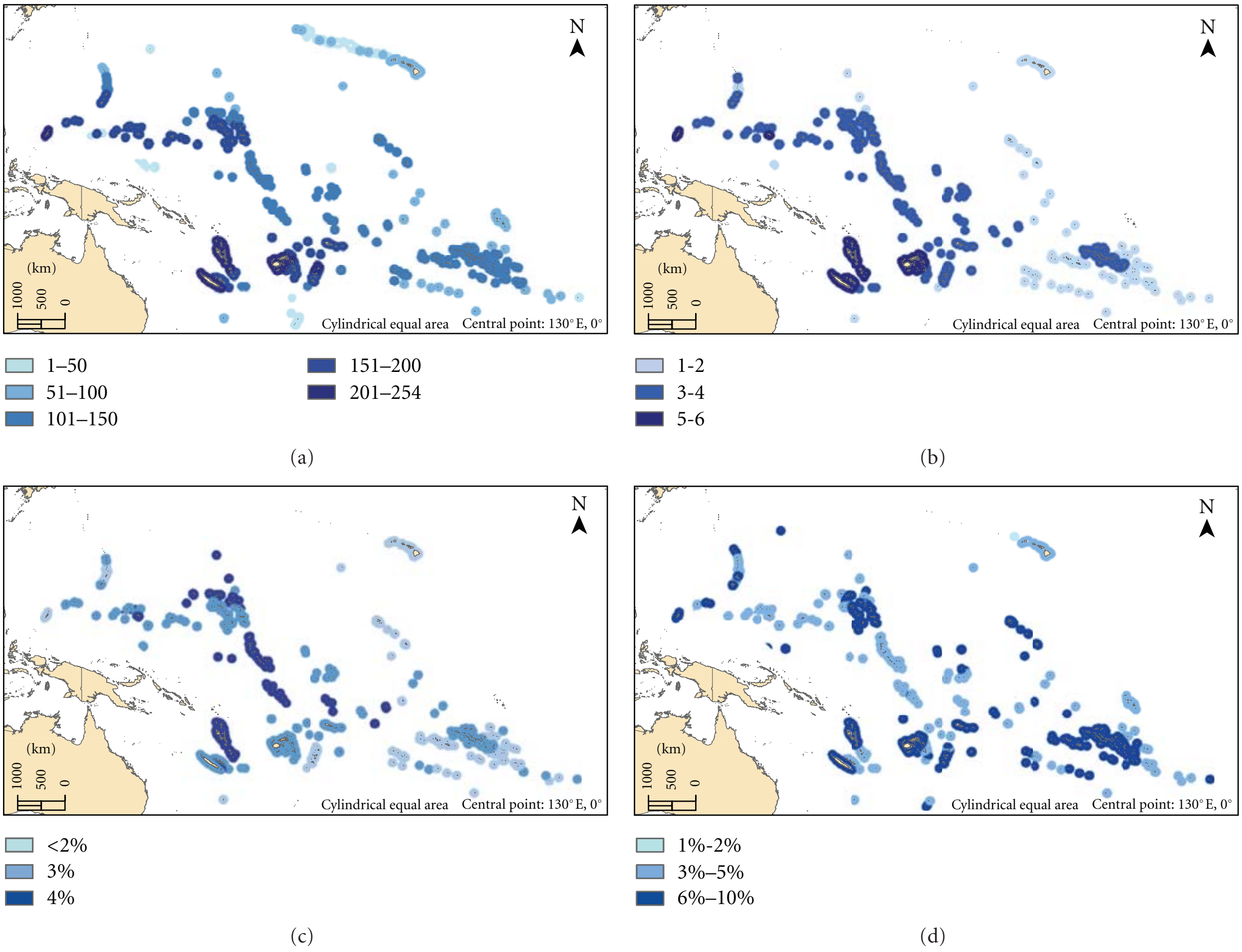


Figure 4: (a) Species richness of bony coral reef fish species assessed in Oceania, (b) species richness of bony shore fish species assessed in threatened categories (Critically Endangered, Endangered, or Vulnerable), (c) proportion of all bony coral reef fish species assessed in threatened categories, and (d) proportion of all bony coral reef fish assessed as Data Deficient.

related to the protection of threatened species include Fiji, the Marshall Islands, the Federated States of Micronesia, Palau, Tonga, and Vanuatu [69]. Amongst the various national laws, the designated species to be protected range from a few species of sea turtles to any species declared by the state to be endangered or threatened [70]. The Secretariat of the South Pacific Environmental Programme (SPREP) plays an important role in unifying regional conservation efforts, and a number of regional conventions have been developed (e.g., Apia Convention 1976, Noumea Convention 1986, and Waigani Convention 1995) but none to date are specifically designed for the protection of threatened or endangered species. Similarly, some but not all countries are signatories to international treaties and conventions which include protection for some species of threatened coral, shark, or whale species, such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), the Convention on the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean, and the International Convention for the Regulation of Whaling. Finally, it is important to note that the degree of enforcement of national laws and regional or international conventions among countries and territories in the Oceania region is likely to be highly variable.

Of the 43 million km^2 of ocean in the Oceania region, approximately 2% (865,000 km^2) is found within designated marine protected areas (MPAs), although the degree of protection for species and enforcement of MPA regulations is also highly variable in the region. Nearly all of the 1190 species assessed in Oceania have a distribution that overlaps with at least one MPA area within its range. Only 5 of the 196 threatened species in Oceania do not have ranges that overlap with a MPA in Oceania. These are an Acroporid coral (*Acropora willisae,* VU), a Faviid coral (*Leptastrea aequalis* VU), Cooke's Petrel (*Pterodroma cookie* VU), the Fairy Tern (*Sterna nereis*, VU), and the Doubleheader Wrasse (*Coris bulbifrons* VU). These species are therefore of high concern, as there is currently no protection for these species in Oceania.

The majority of threatened species identified in this study receive poor MPA protection. Of the 196 threatened species in Oceania, 93% (182 species) have less than 10% of their range within an MPA. Threatened species with the best MPA coverage include three Acroporid corals (*Montipora patula, Montipora flabellata,* and *Monitpora dilatata*) and the Hawaiian monk seal (*Monachus schauinslandi*) which are all endemic to the Hawaiian islands and have between 50%–75% of their range within the Northwestern Hawaiian Islands Marine National Monument. The only record of the widespread Oil Shark (*Galeorhinus galeus*) in Oceania is also in the northwestern Hawaiian Islands, and therefore a high percentage (80%) of this species known range is within an MPA. The percent of MPA protection that a species receives relative to its distribution is not in itself a measure of effective protection, but must be accompanied by enforcement of MPA regulations and continued monitoring of population trends.

There is extensive debate on the size and design of MPAs and MPA networks for species conservation [71] due to the large variation in marine species life history strategies, connectivity, and asymmetry in their distribution. A comprehensive dataset of threatened marine species in Oceania can support the management of current MPAs by providing information on threats to individual species, and the gaps to mitigating these threats. This information can also be used to prioritize areas for the designation of new MPAs. For example, many of the currently identified threatened species in Oceania are pelagic and wide-ranging. Protection of these species through pelagic MPAs may be easier to enforce than catch or gear restrictions for fisheries, particularly in international waters and in countries with limited regulatory capacity, though there are challenges for the effective implementation of such areas [72]. Although MPAs are insufficient to address certain threatening processes, such pollution or climate change that may occur outside of MPA boundaries, Red List data can help to identify the protection measures needed to ensure viable populations of threatened species in Oceania.

3.7. Benefits and Limitations of Marine Species Assessments in Oceania. Around the world, the presence of threatened species is often used to refine marine conservation priorities, such as the designation of critical habitat or key biodiversity areas, no-take zones, and marine protected areas, or to support policies that regulate resource use [18, 19, 73]. Protection of IUCN Red List threatened species in Oceania is currently very limited, mainly because before now IUCN Red List assessments were only available for a few dozen megafauna species, such as the marine mammals, some sharks, and the sea turtles. As the majority of threats to these highly migratory or wide-ranging species occur globally, it is difficult to identify priority sites for conservation action for these species in Oceania, with the exception of mitigating local threats at breeding, foraging, or nesting sites. Similarly, the protection afforded by high seas legislation for these species has been very limited to date.

With the release of the 2010 IUCN Red List of Threatened Species, 1190 Red List Assessments for a wide range of marine species in the region are now available, including many endemic species, in addition to wide-ranging species with low abundance and/or high specialization of habitat. The availability of data on threatened species across multiple taxonomic and trophic levels allows for the development of more effective conservation priorities at the national and regional level, in particular by identifying areas with high concentrations of threatened species. Research priorities can also be focused on regions where many Data Deficient species are found. In addition, species-specific conservation targets can be developed that prioritize threatened endemic species as well as widespread species in the highest threat categories that have high specialization or are undergoing rapid decline in Oceania.

However, compared to terrestrial species, marine species assessments in Oceania especially for bony fish, are still severely lacking [12]. It is estimated that there are over 2,000 bony shore fish species present in Oceania, of which only around one-fifth have been fully assessed through the IUCN Red List process. Without completion of all marine bony fishes, conservation priorities based on knowledge of threatened species will be biased toward mega charismatic and/or widespread species (such as marine mammals, sharks and rays, sea turtles, and sea birds), or primary habitat producers (corals, mangroves and seagrasses). It will also be difficult to identify comprehensive species- and site-specific conservation priorities especially as (1) bony fishes form the foundation for regional economies and human livelihoods throughout Oceania, (2) more than 20% of the remaining 1,600 species of bony fish lacking IUCN Red List assessments are considered endemic to the region, and (3) the vast majority of the species assessed to date are impacted by threatening processes across their global range, which does not necessarily translate to the development of effective mitigation at the regional level.

Of particular concern are key coral reef associated endemic species, such as damselfishes. As many of the coral species in Oceania are threatened, the deterioration of reef structure and ability of these ecosystems to sustain other organisms, including reef-dependent shore fishes may be compromised [74]. Assessments are also urgently needed for species of importance in artisanal and industrial fisheries, such as tunas (Scombridae), emperor fishes (Lethrinidae), snappers (Lutjanidae), mulletfish (Mugilidae), and jacks and pompano (Carangidae) [75]. It is estimated that more than 200 species of marine shore fishes are consumed in artisanal and subsistence fisheries in the Oceania region [76]. Additionally, there are over 200 vessels of various nationalities including the US, Japanese, Korean, and Taiwan China operating purse seining vessels in the Pacific Islands region, representing about 40% of all the large tuna seiners in the world [76].

In addition to shore fishes, other noticeable gaps include seaweeds and marine invertebrates such as sea cucumbers, echinoderms, and worms. Additional comprehensive information on the distribution and conservation status of marine fishes and other key marine groups in Oceania will only continue to provide meaningful analysis and improve the ability to implement effective conservation planning and resource management at the national or regional level [77, 78].

4. Conclusion

Marine resources form the foundation for the livelihoods and economies of Pacific islanders and nations in the Oceania region. As of 2010, 1190 species present in Oceania have been assessed by the IUCN Red List of Threatened Species to determine their population status and probability of extinction, widely expanding the taxonomic breadth and knowledge of threatened species in the region. Almost one-fifth of the marine species assessed in Oceania are in threatened categories due to population decline from a myriad of threats including habitat degradation, overfishing, invasive species introductions, and oceanic environmental changes associated with climate change. High dependency on marine resources and a growing population size in Oceania indicate that pressure on marine resources is only expected to increase.

Urgent action is required to address some of the immediate conservation issues identified by already completed species Red List assessments in Oceania. These include the protection of breeding grounds of highly threatened endemic seabirds that are affected by invasive predators, the monitoring and mitigation of threats to the Critically Endangered Hawaiian monk seal, the implementation of national and high seas policies to reduce the overexploitation of many shark species in targeted fisheries and by-catch, and the halting of destructive fishing practices and the negative impacts of coastal development on coral reefs.

Although Oceania is one of the first regions of the world to be included in a comprehensive analysis of IUCN Red List assessments for marine species, the status of the vast majority of the 2,000 marine shore fish species present in Oceania is still largely unknown. IUCN Red List assessments for these species, especially for important species in artisanal or industrial fisheries and for those found in coral reefs, are urgently needed. Current protection of threatened species in Oceania is very limited and primarily focused on widespread megafauna. Data currently available on the IUCN Red List in addition to subsequent assessments for all remaining marine fish will form the foundation for more effective identification of both site and species-specific conservation and research priorities. In addition to increased species data availability, effective conservation of threatened species in Oceania will also require additional mechanisms to disseminate species data and knowledge, to expand national and regional laws for protected species, and to improve marine protected area management and enforcement.

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Research Article

Coral Diversity and the Severity of Disease Outbreaks: A Cross-Regional Comparison of *Acropora* White Syndrome in a Species-Rich Region (American Samoa) with a Species-Poor Region (Northwestern Hawaiian Islands)

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The dynamics of the coral disease, *Acropora* white syndrome (AWS), was directly compared on reefs in the species-poor region of the Northwestern Hawaiian Islands (NWHI) and the species-rich region of American Samoa (AS) with results suggesting that biodiversity, which can affect the abundance of susceptible hosts, is important in influencing the impacts of coral disease outbreaks. The diversity-disease hypothesis predicts that decreased host species diversity should result in increased disease severity of specialist pathogens. We found that AWS was more prevalent and had a higher incidence within the NWHI as compared to AS. Individual *Acropora* colonies affected by AWS showed high mortality in both regions, but case fatality rate and disease severity was higher in the NWHI. The site within the NWHI had a monospecific stand of *A. cytherea*; a species that is highly susceptible to AWS. Once AWS entered the site, it spread easily amongst the abundant susceptible hosts. The site within AS contained numerous *Acropora* species, which differed in their apparent susceptibility to infection and disease severity, which in turn reduced disease spread. Manipulative studies showed AWS was transmissible through direct contact in three *Acropora* species. These results will help managers predict and respond to disease outbreaks.

1. Introduction

Ecosystem resilience can be defined as the capacity of a system to absorb disturbance and reorganize so as to retain the basic ecosystem services [1, 2]. Regime shifts in ecosystems are increasingly common as a consequence of human activities that erode resilience. This is especially apparent for coral reefs worldwide, which are in decline primarily due to overharvesting, pollution, disease, and climate change [3–6]. Active and adaptive coral reef management is critical if we are to maintain these ecosystems, which requires an understanding of those processes that support coral reef resilience. A critical component underlying ecosystem resilience is the diversity of functional groups and their response to disturbance [1, 2]. A functional group is a collection of species that perform a similar function, irrespective of their taxonomic affinities [6, 7]. For example, herbivores such as reef fish and sea urchins, are an important functional group, which help to maintain the balance between corals and algae. Coral reefs that have high species diversity would have a higher capacity to absorb a disturbance since the loss of any one species could potentially be compensated for by the actions of others (functional redundancy). In the Caribbean, overfishing reduced the abundance of important fish herbivores, but this was initially compensated for by a corresponding increase in sea urchin populations [8–10]; when sea urchin populations subsequently collapsed from a disease outbreak [11], this led to massive losses of corals [12]. Resilience also requires variability in the response of the species within functional groups to the perturbation (response diversity) [1, 2]. If all species respond in a similar manner then functional redundancy is lost. Coral reefs with a high diversity of species should therefore be more resilient to change, with a greater probability that some component of the species pool will be able withstand a specific stressor allowing for functional redundancy and response diversity.

The capacity of coral reefs to withstand the impacts of coral disease is of increasing concern. Coral disease has severely altered coral reefs in the Caribbean [13–17] and is increasing on reefs across the Indo-Pacific [18–25]. Models of global climate change predict that disease outbreaks, worldwide, will continue to increase through time [3, 4, 26–28], and it is therefore important that managers are given sufficient information to predict how coral reefs may respond to future disease events in terms of their resistance and resilience. A basic premise of epidemiology is that increased host abundance enhances disease transmission, both initially into a population and subsequently within it, resulting in increased disease severity [29–31]. As such, the diversity-disease hypothesis predicts that low host species diversity can result in an increase in disease severity of specialist pathogens, since low host richness can, through relaxed interspecific competition, increase relative abundances of one or more susceptible hosts [32, 33]. The diversity-disease hypothesis is well supported in plant-pathogen systems [34–39] as well as some animal disease systems [40–43]. This hypothesis has not yet been adequately tested within the coral reef environment (but see [44]); however given examples from terrestrial ecosystems, coral reefs in species-rich regions should be more resistant and/or resilient to coral disease than reefs in species-poor regions. If so, then species diversity might be a good indicator for managers in predicting the outcome of disease events on reefs and an impetus for managing for species diversity. Within the Indo-Pacific, marine organisms exhibit a longitudinal biodiversity gradient with species-richness declining with increasing distance from the Indo-Australian Archipelago [45–47]. For example, over 500 coral species are found in the Indonesian-Philippines centre of diversity compared to less than 80 species within Hawaii [48, 49]. Presumably, impacts of disease on coral reefs could be more severe in low diversity regions, especially for those diseases, which are more host specific such as *Montipora* white syndrome [50] or *Acropora* white syndrome [20], which have only been observed in the field affecting corals of a specific genus (e.g., *Montipora* and *Acropora,* respectively). However, little is known regarding the relationship between coral disease severity and coral species richness.

We present the first study to examine the role that biodiversity may play in influencing the impact of coral disease outbreaks, by comparing the dynamics of *Acropora* white syndrome (AWS) on a reef in a species-poor region (Northwestern Hawaiian Islands) (reef coral species = 80) [49] with a reef in a species-rich region (American Samoa) (reef coral species = 276) [51]. AWS is a coral disease that results in progressive tissue loss and which has caused extensive coral mortality in many regions throughout the Indo-Pacific [19, 20, 22]. AWS was first documented within the Northwestern Hawaiian Islands at French Frigate Shoals in 2003 [20] and studies on the disease were initiated in 2005. AWS was documented on Tutuila in American Samoa in 2004 [22] and in 2008 we conducted a parallel study on AWS dynamics. Our objectives were to (1) compare how differences in biological variables between the two regions influence the impact of disease events (e.g., the number of susceptible host species (species-richness), host, abundance (colony density and percent cover), and size class structure of the host coral; (2) document the initial AWS outbreak levels (prevalence) and subsequent disease spread (incidence) in each region; (3) compare the virulence (degree of colony mortality) of AWS on individual colonies between regions and among different host species; (4) determine whether AWS is transmissible and investigate any variation in transmissibility among host species.

2. Methods

2.1. Description of Sites. The Northwestern Hawaiian Islands (NWHI) are a chain of small rocky islands, atolls, coral islands, and reefs that span 1,800 km over more than five degrees of latitude in the northwestern portion of the Hawaiian Archipelago. The research site was located at French Frigate Shoals (23° 50′N, 166° 10′W), which is a crescent-shaped atoll approximately 27 km in length with a well-formed barrier reef and lagoon [52]. The NWHI are now part of the Papahānaumokuākea Marine National Monument. The territory of American Samoa has a total land area of 76.1 square miles and includes five volcanic islands (Tutuila, Aunu'u, Ofu, Olosega, Ta'u) [53]. The research site was located in Vatia on the north side of Tutuila (14° 14′S, 170° 40′W). These two regions were opportunistically chosen for comparison as each had reported outbreaks of AWS and were accessible for study.

2.2. Disease Prevalence and Incidence. Within each region, preliminary visual surveys were conducted to identify sites which were dominated by *Acropora* sp. and that had an ongoing AWS outbreak. When multiple outbreak sites were found, those sites having the highest AWS levels were chosen for the study. The Northwestern Hawaiian Islands was surveyed in May 2005 and resurveyed in May 2006. American Samoa was surveyed in June 2008 and was resurveyed in September 2009.

At each outbreak site, two 25 m transect lines were laid end-to-end and separated by approximately 3 m. The substrate at the start of each transect (and every 5 meters thereafter) was marked with either a numbered cow tag or a steel pin ensuring that future surveys could be conducted over the same area on the reef. Coral colony density and size class structure were documented by recording *Acropora* colonies by size class along the transect lines. All *Acropora sp.*, with a colony center within one meter on either side of the transect line (25 m × 2 m), were enumerated and placed into one of seven size classes: <5 cm, 5–10, 10–20, 20–40, 40–80, 80–160, and >160 cm. These protocols have been used successfully in other studies to document size class structure within the NWHI [54–57]. Colonies were identified to species whenever possible. A second diver surveyed a wider area along the

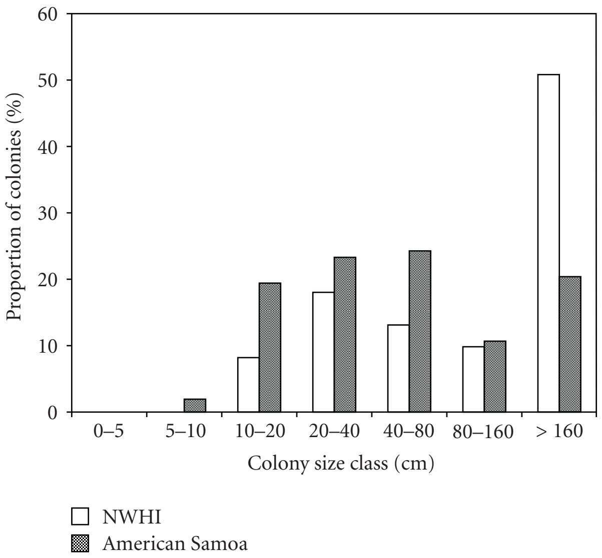

Figure 1: Mean size class structure of *Acropora* colonies within transects at the *Acropora* white syndrome outbreak sites in American Samoa and the northwestern Hawaiian Islands. Two 25 × 2 m belt transects were surveyed at each site.

belt transect (25 m × 6 m) for colonies exhibiting signs of AWS and measured coral cover using the point-intercept method, recording the substrate type at 50 cm intervals along the transect. Time constraints underwater prevented the enumeration of all coral colonies within the wider belt transects surveyed for disease. Therefore, we estimated the total number of colonies surveyed for disease based upon the mean number of colonies m^{-2} found within the narrower (25 × 2 m) belt transects. Biological variables (average percent coral cover, colony density, and colony size class structure) and disease levels (number of AWS affected colonies and prevalence of AWS) were determined from diver surveys. To determine disease incidence (number of new cases), surveys were repeated one year later but it was not possible (poor weather and logistics) to reassess biological variables (% coral and colony counts) in American Samoa and so only the number of new AWS colonies within the transects were enumerated.

2.3. AWS Virulence (Degree of Tissue Loss). To determine the progression of lesions, AWS-affected colonies that were initially identified within (or just outside) the belt transects, were tagged with either a colored cable tie or a numbered cow tag, photographed with a digital camera and the location on the reef mapped. The percentage of the colony surfaces that appeared diseased, healthy, or dead were scored *in situ* to provide a semiquantitative measure of AWS severity. Twenty infected colonies were tagged within the NWHI and 18 colonies were tagged in AS. The following year, the tagged colonies were relocated, photographed, and scored for tissue loss.

2.4. Differential Disease Susceptibility: Field Pattern and Transmissibility. Within AS, we determined whether there were differences in susceptibility to AWS among *Acropora* species, by examining disease prevalence among species and using a Chi-Square Goodness of Fit test to compare the abundance of each species within the transect (% coral cover) with their respective contribution to total disease prevalence. Field patterns of AWS were indicative of a communicable agent, so manipulative experiments were conducted to test whether AWS is transmissible through direct contact or indirectly via the water column. We examined three *Acropora* species (*A. cytherea, A. clathrata, and A. hyacinthus*) to gather preliminary evidence as to whether there were differences in transmissibility among coral species. Experiments were conducted under static conditions using a paired design in which two aquaria (experimental and control) were used, with each aquarium containing two fragments of healthy *Acropora sp.* in 0.2 μm-filtered seawater. In the experimental tank, an infected fragment was placed in direct contact with one healthy fragment (direct transmission) and the other healthy fragment was placed 10 cm away (water-borne transmission). In control aquaria, a healthy fragment replaced the infected fragment, so as to control for lesions created by healthy coral-to-coral aggressive interactions. All fragments were examined daily for signs of acute tissue loss and photographed. Experiments were run until disease transmission occurred (tissue loss observed) on any of the fragments (touching or nontouching) or for a maximum of 8 days (time constraints). Water quality was maintained through daily partial water changes and each aquarium was aerated with a bubbler to simulate water motion. Aquaria were held under natural light and ambient temperatures (26–28°C). A total of eight experimental replicates with controls were conducted: one run for *A. clathrata,* three runs for *A. cytherea,* and four runs for *A. hyacinthus.*

3. Results

3.1. Biological Variables and AWS Prevalence and Incidence. The site within the NWHI was dominated by a larger size class of *Acropora* colonies resulting in higher *Acropora* cover but lower colony density as compared to the AS site (Table 1; Figure 1). Only one species of *Acropora* (*A. cytherea*) was found at the site in the NWHI in contrast to the AS site in which at least six different *Acropora* species (*A. cytherea*, *A. clathrata, A. abrotenoides, A. c.f. humilis, A. c.f. gemmifera, Acropora* sp.) were identified. Both the initial prevalence and incidence (number of new cases) of AWS were higher in the NWHI relative to AS. Twenty-six AWS affected *Acropora cytherea* were initially identified within the NWHI survey area (prevalence = 14.2%) as compared to 13 AWS colonies from at least 6 different species (*A. cytherea*, *A. clathrata, A. abrotenoides, A. c.f. humilis, A. c.f. gemmifera,* and *Acropora* sp.) in AS (prevalence = 4.2%). In year two, 16 and four newly infected colonies were found in the NWHI and AS, respectively. This represents a 61.5% increase in disease in the NWHI and a 30.8% increase in AS.

3.2. AWS Virulence (Amount of Tissue Loss). In the NWHI, we were able to relocate 17 of the twenty marked colonies

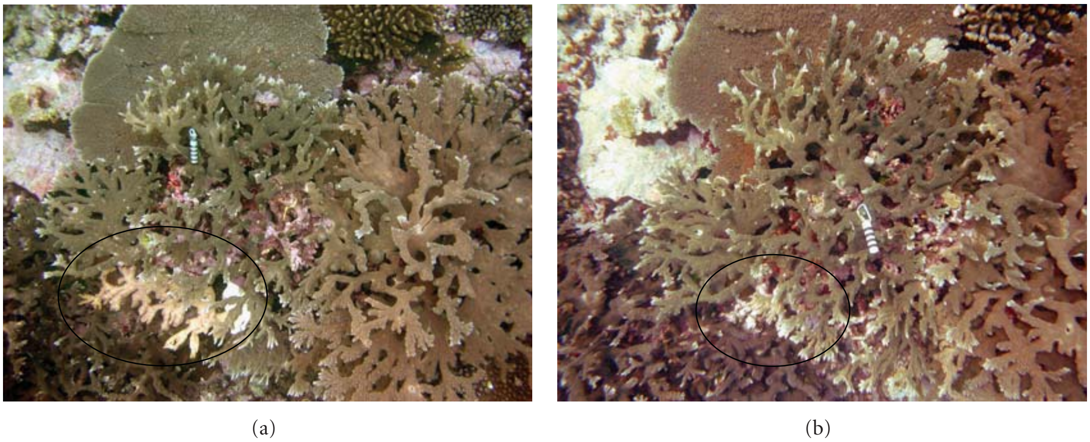

FIGURE 2: Example of minimal mortality from AWS in a resilient *Acropora* species (*A. abrotenoides*) in American Samoa. (a) A colony affected by AWS in 2008 and (b) shows the same colony in 2009; affected area circled.

FIGURE 3: Example of complete mortality from AWS in a highly susceptible *Acropora* species (*A. clathrata*) in American Samoa. (a) The colony affected by AWS in 2008 and (b) shows the same colony in 2009.

TABLE 1: Differences in biological variables and disease levels and incidence at outbreak sites within the northwestern Hawaiian Islands (NWHI) and American Samoa (AS).

Region	NWHI	AS
depth (m)	9.1	9.1
# *Acropora* species within transects	1	6+
Avg. Acropora cover (%)	52.9	31.3
Avg. Acropora density (#/m^2)	0.61	1.03
est. # *Acropora* colonies surveyed	183	309
Dominant colony size class within transects	>160 cm	40–80 cm
# AWS colonies year 0	26	13
# new AWS colonies year 1	16	4

and all (100%) showed signs of disease progression with the average increase in area of tissue loss on individual colonies being 46.2% (SE ± 5.5). Within AS, 14 of the 18 marked colonies were relocated and the change in area of tissue loss ranged from +15% (e.g., regrowth of tissue) (Figure 2) to 100% mortality (mean loss = 27.4% SE ± 8.9%) (Figure 3). The initial severity (% of colony dead or diseased) of the AWS-affected colonies was similar in both regions averaging 37.1% (SE ± 3.1%) within the NWHI compared with 32% (SE ± 7.7%) in AS. The mean disease severity increased in both regions after one year, indicating that the disease had progressed on individual colonies but mean severity was higher in the NWHI (83.2% SE ± 6.2%) as compared to AS (59.4% SE ± 12.4). Within the NWHI, case fatality rate was 58.8% with 10 out of 17 colonies showing 100% mortality. Within AS, 7 out of 14 colonies (*A. clathrata, A. cytherea,* and *Acropora* sp.) suffered 100% mortality (case fatality rate = 50%).

3.3. Differential Disease Susceptibility: Field Pattern and Transmissibility. At the site in AS, AWS prevalence varied among species but no clear relationship was found between AWS prevalence and differences in host abundance as measured by coral cover among affected species (X^2 = 41.02,

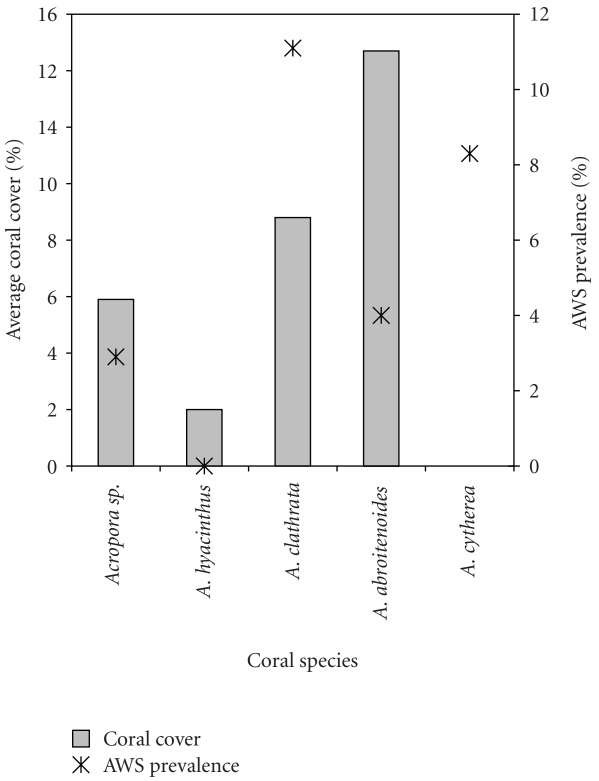

Figure 4: Differences in *Acropora* white syndrome prevalence among coral species and their respective average abundances within transects. Data are from the 2008 survey at the outbreak site within American Samoa. Note that colonies of *A. cytherea*, although present within the belt transect, did not occur directly underneath the transect line and so the percent of cover was measured as zero.

df = 3, $P < .001$; Figure 4). *A. clathrata* had the highest disease prevalence (11.1%) but only comprised 8.8% of the coral cover. Similarly, *A. cytherea* had the second highest prevalence (8.3%) yet made up <1% of the coral cover. In contrast, *A. abrotenoides* had the highest contribution to coral cover (14.7%) but only showed a 4% AWS prevalence. AWS was found to be transmissible through direct contact between AWS-affected and healthy coral fragments in six out of eight experimental runs (75%). *A. clathrata* ($n = 1$) and *A. cytherea* ($n = 3$) demonstrated 100% successful direct transmission. Two of the four trials with *A. hyacinthus* resulted in disease transmission. Tissue loss was only observed in one fragment (*A. cytherea*) out of eight nontouching coral fragments within treatment aquaria. There were no signs of tissue loss recorded in any of the eight control aquaria. The time required for disease transmission to occur ranged from 1–4 days. Lesions appeared as acute tissue loss similar to that observed for AWS lesions in the field.

4. Discussion

Consistent with the diversity-disease hypothesis, this study found that an outbreak of AWS resulted in a greater degree of damage to the reef in the species-poor region of the NWHI compared with the species-rich region of AS. The site within the NWHI had higher host abundance, which would facilitate disease transmission but specifically, the site was composed of a monospecific stand of large colonies of *Acropora cytherea*, a coral species that our study showed to be highly susceptible to AWS. Consequently, the incidence of disease within the NWHI was more severe than in AS initially and over time. The outbreak site in the NWHI also suffered greater coral mortality as evidenced by the higher case fatality rate and the greater amount of tissue loss (disease severity) on individual colonies.

The outbreak site within AS was also an *Acropora*-rich area, but it contained at least six different species of *Acropora*. Disease prevalence varied among the coral species and these differences were not explained by host abundance. The branching coral *Acropora abrotenoides* appeared to be less susceptible to AWS with prevalence lower than would be expected based on the abundance of this species. *A. abrotenoides* was also resilient to the disease and the few colonies that were infected in 2008 were found to have suffered minimal colony mortality in 2009. In contrast, the plating corals, *A. clathrata* and *A. cytherea,* both showed extensive colony mortality from the disease and had a higher prevalence than would be expected based on their abundance on the reef suggesting that these species were especially vulnerable to AWS. Species-specific differences in disease susceptibility were also supported in aquaria studies examining the transmissibility of AWS. Although sample sizes were small and so must be interpreted with caution, we did find that AWS transmission was more successful in *A. cytherea* (three out of three trials) than with *A. hyacinthus* (two out of four trials). A similar pattern was observed in the field with *A. hyacinthus* occurring within the transects at the outbreak site but no colonies were infected with AWS. Numerous studies have found differences in disease susceptibility among coral genera and *Acropora* sp. are emerging as one of the most vulnerable coral genera to diseases [19, 22, 58]. This study reveals that differential disease susceptibility can also occur between species within a genus.

Although the dynamics of disease etiology are complex and can be affected by a number of factors, our study suggests that species-richness may be important in determining the extent of damage occurring on a coral reef due to disease. We found that differential disease susceptibility among *Acropora* species (response diversity) in AS-reduced disease spread and virulence. Susceptible species formed a smaller component of the AS ecosystem, decreasing successful disease transmission and thereby minimizing damage from the disease outbreak. The underlying process is a function of host abundance and indeed several studies have demonstrated a positive relationship between coral abundance and disease prevalence [23, 50, 59, 60]. However, it must also be noted that we were comparing disease outbreaks between regions during different years and so other factors could have also affected disease outcomes. For example, thermal stress has been found to affect coral disease processes [4, 59] and if temperatures had varied between the two study years more so in one region than the other then that might explain differences in disease spread. However, the SST did not vary much between the two years of the studies in either region (http://coral-reefwatch.noaa.gov/satellite/current/sst_series_24reefs.html). Disease outbreaks in populations of susceptible hosts can often be more severe early on when host density is highest [29–31] and so timing of the initial disease outbreak might have contributed to the differences found between AS and NWHI. We know that the outbreak in the NWHI occurred at the study site in 2003, as it is one of our monitoring sites [20]. Therefore, we know that the disease had been ongoing for 2 years when our study was initiated in 2005. The AS site was not a monitoring site and so we do not know when AWS first appeared. However, our surveys found little evidence of past coral mortality such as would be expected from a prior disease event suggesting that AWS had recently emerged. Based on these observations, a more rapid disease spread would have been expected in AS rather than the NWHI. Hence, regardless of other potential cofactors, the interspecific variability in susceptibility to AWS found in AS still offers the most reasonable explanation for the differences we observed in AWS virulence and spread among regions.

The relationship between species diversity and disease severity may not be valid for diseases that affect multiple host genera. For example, Ward et al. [44] examined the diversity-disease hypothesis on coral reefs along the Mexican Yucatan Peninsula and found no relationship between disease prevalence and measures of host diversity. However, they included many diseases found to affect multiple host genera, such as black band disease which is known to affect 19 Caribbean shallow-water coral species and 45 Indo-Pacific coral species [17]. For coral diseases with low host specificity, a negative relationship between species-richness and abundance of susceptible hosts would no longer apply since multiple species or genera can be affected by disease.

For managers, this information is essential for predicting and responding to diseases outbreaks. It is of utmost importance that reef managers know the species-richness and community composition of those coral reefs under their jurisdiction and are aware of which coral diseases might affect their reefs, host susceptibility and have insight into the ecology underlying those diseases (etiology, mode of transmission, etc). Support of research to understand local coral disease processes should be encouraged, and in species-poor regions, such as the Northwestern Hawaiian Islands, a proactive approach is required to develop the capacity to respond to disease outbreaks rapidly and efficiently as disease outbreaks are likely to result in high mortality. Most critical is research in understanding disease causation in corals, since only through understanding this aspect can diseases be effectively managed.

Disease management in other wildlife systems is routinely used and include actions such as culling, vaccination, or habitat alteration which minimize the spread of disease and the resulting mortality [61]. A recent example of this was management of avian botulism in endangered Laysan ducks in the NWHI by draining affected ponds thereby reducing the amount of bacteria in the environment that causes botulism [62]. For coral disease, much less is known about the causes or ecology of the diseases and so the development of management actions is far more difficult [63]. However, some coral disease management has been successfully implemented. For example, in the Florida Keys, Hudson [64] treated black band disease (70% effective) by removing the pathogen by suction and covering the affected area with modeling clay (lesion occlusion). In Australia, Dalton et al. [65] found that mechanical removal of the advancing disease margin for *Turbinaria* colonies affected by a tissue loss disease ("white syndrome") was successful at halting the disease in 80% of the colonies. AWS might be effectively managed by either lesion occlusion or mechanical removal of affected parts depending on the severity of the disease on the colony and the colony morphology. Although information regarding the treatment of coral diseases is still limited, these two studies show that disease management can be accomplished in the marine environment. Further work should be encouraged in developing methods to manage coral disease as we also continue to understand disease processes.

Coral disease is a very real threat to global reefs. The findings in this study show that reefs in species-rich regions might be more resistant and resilient to those coral diseases, such as *Acropora* white syndrome, that are more host specific (genus level). More detailed studies are required to unravel the complex interaction of variables that affect disease dynamics, such that adequate and timely management actions can be taken to maintain these valuable coral reef ecosystems. Cross-regional comparisons, such as this one, are also of great value, so we might better understand the spread of disease across the Indo-Pacific and in identifying general patterns of disease dynamics on these reefs.

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Research Article

Comparative Effects of Different Disturbances in Coral Reef Habitats in Moorea, French Polynesia

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Degradation and loss of critical coastal habitats has significant ramifications for marine fisheries, such that knowledge of changes in habitat quality and quantity are fundamental to effective ecosystem management. This study explores changes in the structure of coral reef habitats, specifically changes in coral cover and composition, in Moorea, French Polynesia, to assess the independent and combined effects of different disturbances since 1979. During this period, reefs on the north coast have been subject to coral bleaching, severe tropical storms, as well as outbreaks of *Acanthaster*. Coral cover varied significantly among years, showing marked declines during some, but not all, disturbances. The greatest rates of coral loss coincided with outbreaks of *A. planci*. Moreover, successive disturbances have had differential effects among coral genera, leading to strong directional shifts in coral composition. *Acropora* is declining in abundance and coral assemblages are becoming increasingly dominated by *Pocillopora and Porites*. Observed changes in the cover and composition of corals are likely to have further significant impacts on the reef fish assemblages. Given that significant disturbances have been mostly associated with outbreaks of *A. planci*, rather than climate change, effective ecosystem management may reduce and/or delay impending effects of climate change.

1. Introduction

Disturbances play an important role in the structure and dynamics of marine communities and are a necessary part of ecosystem dynamics [1–4]. On coral reefs, moderate levels of disturbance make an important contribution to increasing biodiversity [5]. In many locations, however, natural acute "pulse" disturbances have combined with chronic "press" [6] anthropogenic stresses (e.g., overfishing, pollution and eutrophication) to cause excessive disturbance and degradation of coral reef environments [7, 8]. On a global scale, it is estimated that 30% of coral reefs have now lost >90% of reef-building corals and there is little to no prospect of recovery [9]. Moreover, 60% of coral reefs around the world may face a similar fate by 2030 [9, 10]. The loss of reef-building corals is likely to have major impacts on the biodiversity, productivity, and biological functioning of coral reef ecosystems [11, 12]. In some locations, changes in the structure and quality of benthic reef habitats are now the most important driver of changes in the abundance of reef fishes (including some large piscivorous species), having a greater influence than extractive fisheries [13, 14].

Major contributors to coral loss and coral reef degradation vary regionally [15], but most reef areas are exposed to multiple disturbances [12]. Areas in which coral reef degradation is most pronounced (the Caribbean, SE Asia, and the western Indian Ocean) are characterized by a long history of heavy exploitation of coral reef resources and other chronic disturbances [9], which may have increased vulnerability to recent acute disturbances, such as severe tropical storms [16–20], El Niño Southern Oscillation (ENSO) events [21, 22], coral bleaching events [23–28], high and low temperature extremes, freshwater plumes from heavy rainfall and runoff events [29], coral diseases [30], and outbreaks of coral predators (mainly, the corallivorous sea star *Acanthaster planci* in the Indo-Pacific, [31–39], and tidal fluctuations [40]). More importantly, coral loss and associated degradation of coral reef habitats is expected to worsen over the next 2-3 decades, due to climate related increases in temperature [41] and ocean acidification [42].

Effects of acute disturbances on coral assemblages vary greatly, both within and among different types of disturbance. Disturbances that result in an immediate loss of habitat complexity (e.g., severe tropical storms) tend to have a greater impact on fishes from all trophic levels, compared with disturbances that kill corals, but do not immediately compromise the structure of reef habitats (e.g., coral bleaching and outbreaks of *Acanthaster planci*) [12]. Disturbances of a similar type (e.g., cyclones) may also differ in terms of the spatial scale of impact on habitat, intensity, magnitude, and duration of effect [5, 6]. Moreover, responses to disturbances will vary among locations, according to the history of disturbances that have already modified community structure [3], the stage of recovery since the last major disturbances [43–45], as well as inherent differences in community structure at large geographical scales [46]. Despite these differences, increases in the diversity, frequency, and intensity of disturbances in many reefs throughout the world tend to be causing clear directional changes in the structure of coral reef habitats [8, 47]. In general, increasing disturbances cause declines in the abundance of habitat-forming corals, which may, in some situations, be replaced with macroalgae (e.g., [48]). Even if coral cover does not decline there may be marked changes in community structure of coral assemblages (e.g., [49]).

Effects of disturbances on coral composition depend on selectivity of effects, and differential vulnerabilities among major coral taxa (common families and genera). *Acropora*, for example, is the first and worst affected genera during coral bleaching [50, 51], outbreaks of *A. planci* [52], and cyclones [20], whereas massive corals, such as *Porites* and *Favia* are resistant to all but the most severe disturbances. Consequently, erect branching corals (e.g., *Acropora*) are increasingly being replaced with encrusting and/or massive corals (e.g., *Porites*) at locations with extreme disturbance regimes (e.g., the Arabian Gulf; [53, 54]), which greatly reduced habitat availability and topographical complexity of coral reef environments. *Acropora* and other branching corals are the predominant habitat used by most coral-dwelling fishes [55], while habitats with low complexity and topographic relief support far fewer fishes (e.g., [13, 38]) owing to the critical role of topographic complexity in moderating recruitment, competition, and predation [56]. It is important therefore, to assess whether changes in the structure of coral assemblages observed in the Arabian Gulf, may ultimately occur at other locations the Indo-Pacific, especially given projected increases in the severity and/or frequency of disturbance [41].

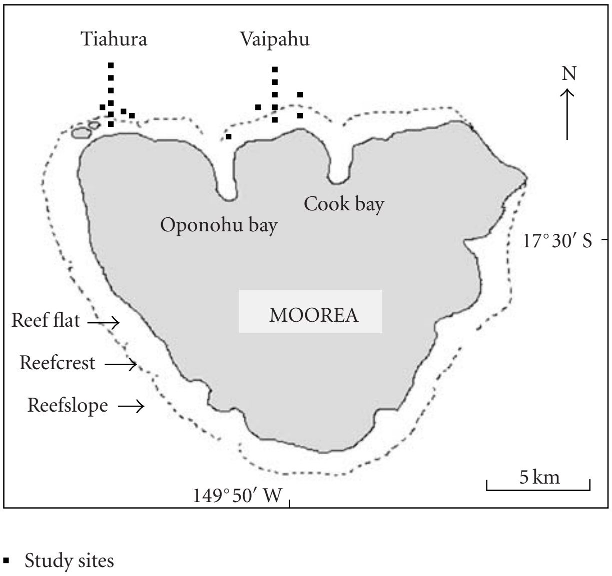


Figure 1: Map of Moorea (17°30′S, 149°50′W) in the Society Island, French Polynesia, showing the main study sites on the reef flat, reef crest and reef slope at Tiahura (North-West) and Vaipahu (North-East). Dashed lines represent the approximate extent of the reef front.

A critical limitation in understanding effects of persistent or recurrent disturbances on coral reefs is the lack of long-term data [12]. Most studies are conducted at very limited temporal and spatial scales [57], and there are a limited number of locations around the world where there has been sufficient research conducted over an extended period to provide information on long-term changes in coral composition associated with multiple and successive disturbances [12, 16, 58]. One of the major centers for coral reef research in the central Pacific is Moorea (17°30′S, 149°50′W) in the Society Islands, French Polynesia (National Science Foundation Long-Term Ecological Research program—http://www.lternet.edu/sites/mcr/; Program "Agencement Temporel des Populations et des Peuplements", USR CNRS-EPHE3278 CRIOBE). Changes in coral cover and composition (mostly to genus) have been documented in Moorea since the 1970s by [59] and Bouchon [60], focusing on Tiahura reef on the north-west corner of Moorea (Figure 1). Since that time, extensive coral reef research and monitoring has been undertaken at Tiahura reef (and to a lesser extent at Vaipahu, situated approximately 12 km east of Tiahura, Figure 1). During this period, coral assemblages have been subject to many acute (pulse) disturbances, which are purported to have caused major changes in the community structure of coral reef communities [49]. Most notably, multispecific coral bleaching has been reported every 3-4 years since 1983 (1984, 1987, 1991, 1994, 2002, 2003, and 2007), corresponding with periods when sea surface temperature increased above 29.2°C [16, 26, 58, 61]. Then, cyclones have been reported to occur in Moorea during two El Nino events in 1983 and 1991, but in general are rare in French Polynesia (Table 1). Finally, two outbreaks of crown-of-thorn sea star occurred in Moorea, the first from 1979 to 1985, and the second one which started in 2006 was still occurring in 2009 when the reef was resurveyed by Pratchett et al. (Table 1).

looseness=-1The purpose of this study was to assess the recent history of disturbances affecting coral reefs of Moorea, French Polynesia, based on extensive field-based research undertaken at this location since 1979. In addition to documenting the occurrence of distinct disturbance events, changes in cover and composition of reef-building corals were assessed following each major disturbance event. These data provide insights into the comparative effects of different disturbances, as well as revealing long-term effects of recurrent disturbances on coral reefs in the central Pacific. Assessing the major causes of coral loss is particularly important in establishing potential management strategies to address habitat-degradation (specifically, declines in habitat diversity and structural complexity) within ecosystem management frameworks.

2. Materials and Methods

To explore long-term changes in coral cover and community structure at Moorea, quantitative data were compiled from 15 studies conducted at Tiahura [16, 33, 49, 58, 62–70] and/ or Vaipahu [16, 62, 71, 72], located 2 kilometres apart on the north coast of Moorea [62]. Most of these studies (11 studies) directly compared changes in coral cover and composition through time, sampling coral assemblages between 2–17 years. This study also encompasses data from two previous studies, that document long-term changes in coral cover and composition [49, 58]. However, this study extends the temporal and spatial extent of these data sets. Most importantly, it includes knowledge of recent changes in coral cover and composition, from 2006–2009, during which time there was a major outbreak of *A. planci*.

To account for differences in sampling among specific habitats or depths, we pooled data across different reef zones (up to 7) to distinguish between: (i) shallow habitats (from 0 to 5 m), which encompass the barrier reef flat, the barrier reef crest, and the upper part of the outer-reef slope and (ii) deep habitats (10 to 30 m), encompassing the outer-reef slope. We calculated a mean coral cover for each of these habitats, at each site, and in each year. Whenever possible, we also considered the structure of coral communities, based on relative abundance of the major coral genera *Pocillopora*, *Acropora*, *Montipora,* and *Porites*. All other corals were then lumped into a single category, "others".

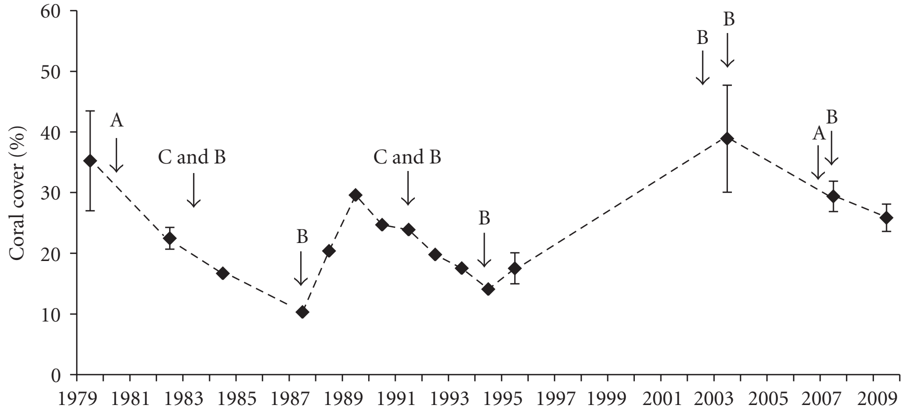
The temporal occurrence and severity of major disturbances such as coral bleaching events, cyclones, and outbreaks of *Acanthaster planci* (*A. planci*) was assessed based on a comprehensive review of published literature (Table 1). To relate changes in total coral cover to the occurrence of disturbances, we calculated annual geometric rate of change in total coral cover for each year, following Côté et al. [73]. Geometric rates of change in live coral cover are calculated based on the relative change in coral cover between respective samples, without assuming a linear decline in coral cover, which is necessary when comparing among different sampling intervals. The average annual rate of change was then compared among individual years in which different types of disturbances (bleaching, cyclones, and outbreaks of *A. planci*) occurred. It was not possible to partition effects of different disturbances that occurred simultaneously, though there were only three years (1983, 1991, and 2007), where multiple disturbances occurred within the same year. Unfortunately, however, both cyclones occurred in years with either bleaching (1991) or bleaching and outbreaks of *A. planci* (1983), making it difficult to assess the independent effect of these disturbances.

3. Results and Discussion

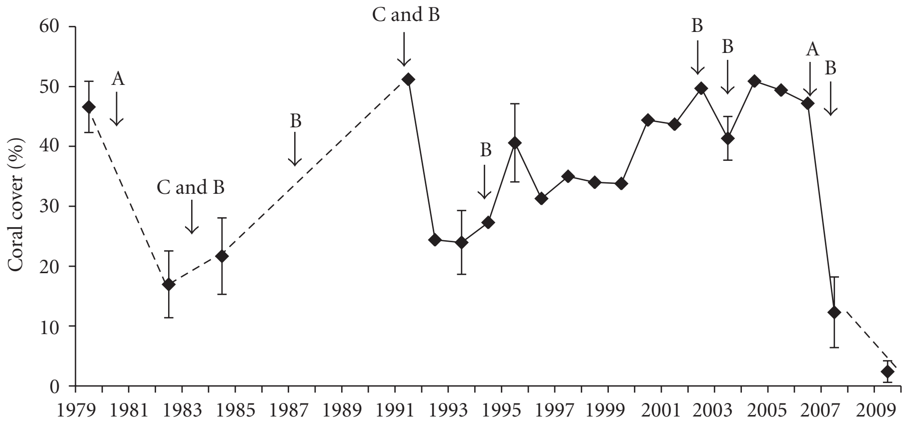
3.1. Episodic Disturbances and Changes in Coral Cover. Since 1979, Moorea has been subject to seven coral bleaching events, two cyclones and two major outbreaks of *Acanthaster planci* (Table 1). As such, coral assemblages have been subject to an average of one disturbance every 2.7 years. Coral cover has varied considerably throughout this period, starting with mean cover of 40.9% (±4.9 SE) in 1979, and ending with 16.5% (±5.9 SE) in 2009. Coral cover recorded in 2009 (especially on the reef slope) was the lowest that has been recorded since 1979. However, coral cover has not exhibited a systematic decline through time, rather live coral increased to >50% on outer reef slopes in 1991, and also in 2004, immediately prior to the most recent outbreak of *A. planci* (Figures 2 and 3). Although there is limited data on chronic disturbances affecting the study locations in Moorea (e.g., fishing pressure, sedimentation, and/or eutrophication), it appears that periodic depletion of live corals is largely explained by the occurrence of acute disturbances (Figures 2 and 3), including bleaching, cyclones, and outbreaks of *A. planci*, all of which have contributed to significant coral depletion elsewhere throughout the Pacific [7, 12].

The average annual rate of change in coral cover recorded in years during which acute disturbances were reported was −25.6 (±11.6 SE), compared to 1.5 (±1.8 SE) in years with no reported disturbances. Average rates of coral loss were significantly different among years in which bleaching was reported to occur, versus cyclones or outbreaks of *A. planci* (ANOVA, $F = 9.38$, $df = 3/96$, $P < .001$). Among the different types of disturbances, overall rates of coral loss (averaged across zones and locations) were greatest (mean = −33.2 ± 14.1 SE) during outbreaks of *A. planci*, and significantly higher than rates of coral loss recorded during bleaching events (Tukeys Post-Hoc, $J = 0.41$, $P = .003$). The two major cyclones affecting Moorea (in 1983 and 1991) were associated very high rates of coral loss, but these disturbances coincided outbreaks of *A. planci* and/or bleaching (Figures 2(a) and 2(b)), making it difficult to assess the individual contribution of cyclones to recorded coral loss. However, the average rate of coral loss across years with multiple disturbances was higher than for recorded during any single disturbance, suggesting that different disturbances may have additive effects on coral loss (Figure 4).

During the course of the study (1979-2009), there were two distinct outbreaks of A. planci. The first of these outbreaks began in 1979, with infestations of sea stars first observed on the deep reef slope at Tiahura reef [68]. This initial infestation seemed to have ended by 1986 at Tiahura reef [68], but there were significant ongoing outbreaks in southern parts of Moorea until 1987 [33], probably reflecting the movement of sea stars as well as increased settlement of larval sea stars spawned by infestations of reproductively



(a) Tiahura (0–5 m)



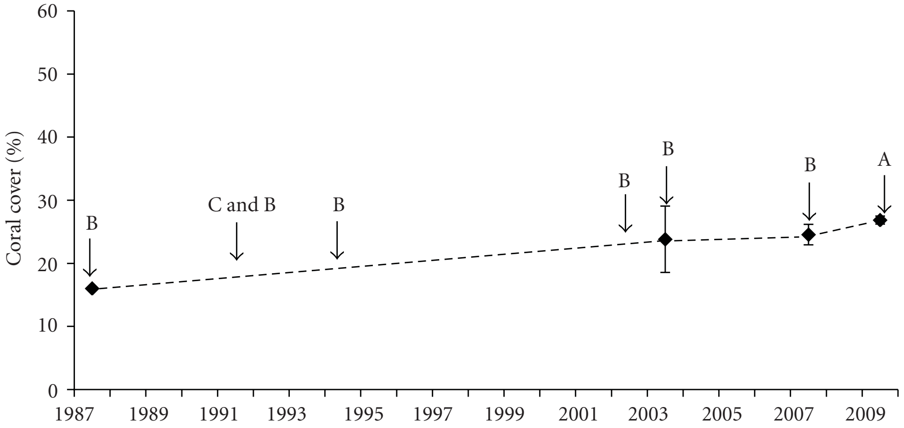
(b) Tiahura (10–30 m)

FIGURE 2: Interannual variation in mean (±SE) coral cover in (a) shallow habitats (0–5 m), and (b) deep habitat (0–30 m), and at the Tiahura reef, Moorea. Dashed lines indicate presumed trend across years for which no survey data are available. The occurrence of outbreaks of *A. planci* (A), coral bleaching (B), and cyclones (C) is shown.

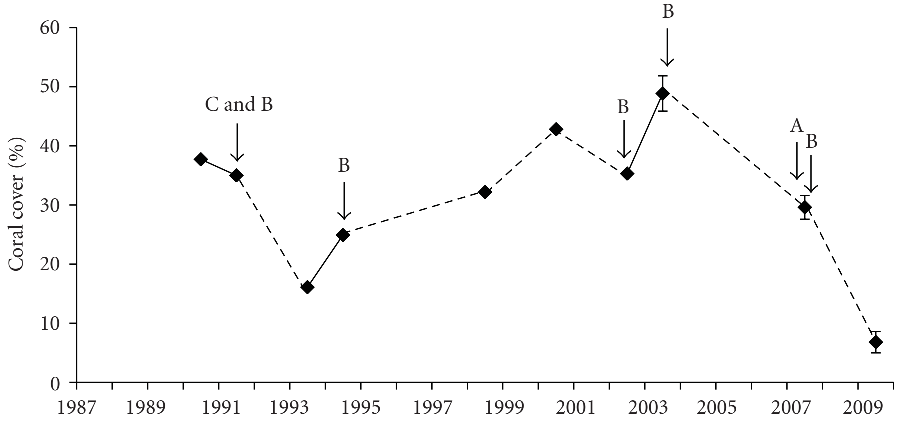
mature sea stars in northern Moorea, as reported by Pratchett [36] at Lizard Island on the northern Great Barrier Reef. The most recent and only second known outbreak of *A. planci* in Moorea started in 2006 [58], with high densities of sea stars again being recorded first on the outer-reef slope of Tiahura (23,000 sea stars km^{-2}, according to Lison de Loma et al. [74]) which was far higher than the density threshold of >1500 sea stars km^{-2}, considered to cause devastation to reef habitats by Moran and De'ath [75]. Accordingly, rates of coral loss recorded during outbreaks of *A. planci* were much higher on the reef slope, compared to the reef flat (Figure 4), which is consistent with observations of *A. planci* impacts elsewhere in the world (reviewed by Moran [76]).

Outbreaks of *A. planci* are one of the most significant biological disturbances on coral reefs [77] and remain the principal cause of short-term coral loss in the Indo-Pacific [15], often killing up to 90% of scleractinian corals, for example, on the Great Barrier Reef [36, 78, 79], in Guam [80], in Papua New Guinea [81] and in Japan [39]. After the first outbreak of *A. planci* in Moorea (1979–1986), coral cover at Tiahura increased rapidly and returned to predisturbance levels (46.6%) within less than 5 years. In other geographic locations, recovery of coral cover following outbreaks of *A. planci* has typically taken much longer (e.g., Great Barrier Reef—10 to 15 years, [82]; 10 to 20 years, [83]; 10 to 25 years, [84] and 20 to 40 years, [32]; Guam—11 years, [85]; 20 to 30 years, [86]). Coral recovery was even more pronounced in deep water where the coral cover increased from <20% in 1982 to 51% in 1991 (Figure 2(a)). This apparent resilience in coral cover on reefs in Moorea has been reported previously and may be attributable to consistently high rates of coral recruitment [58]. However, relatively rapid increase in total coral cover may belie fundamental changes in coral composition [49] and thereby habitat structure. Moreover, the amount of remnant corals on the reef slope in 2009 was much lower compared to the end of the first *A. planci* outbreak in 1982 (Figure 2), which may suggest that recovery from the latest outbreak of *A. planci* will take substantially longer [87].

Coral bleaching has occurred every 3-4 years at Moorea since 1983, but these mass-bleaching events have not caused consistent declines in live coral cover. The greatest rates of coral change recorded during bleaching years (1991 and 2007) both coincide with other disturbances (a cyclone and outbreak of *A. planci*, resp.), whereas in all other years that bleaching has been recorded, coral loss was negligible. Coral



(a) Viapahu (0–5 m)



(b) Viapahu (10–30 m)

Figure 3: Interannual variation in mean (±SE) coral cover in (a) deep habitat (0–30 m) and (b) shallow habitats (0–5 m) at the Viapahu reef, Moorea. Dashed lines indicate presumed trend across years for which no survey data is available. The occurrence of outbreaks of *A. planci* (A), coral bleaching (B), and cyclones (C) is shown.

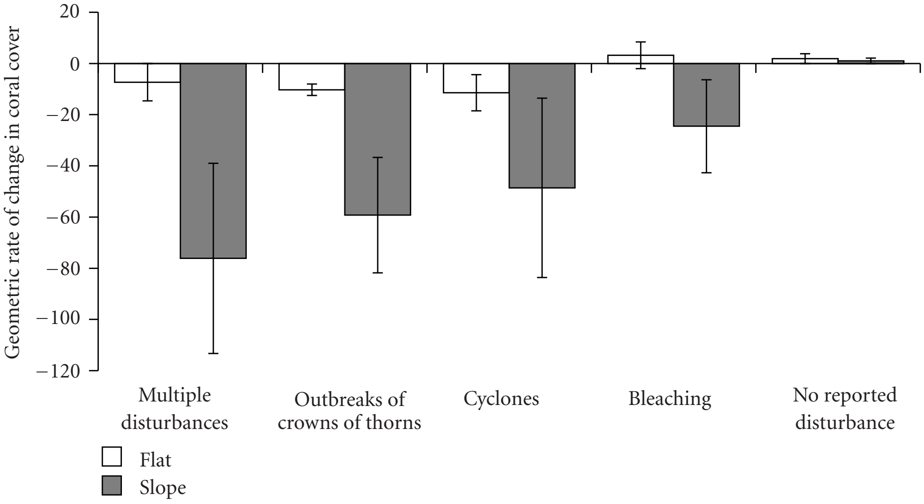


Figure 4: Variation in the mean (±SE) annual geometric rate of change in total cover of scleractinian corals, for years (between 1979 and 2008) during which outbreaks of *A. planci* (1979–1986, 2006–2008), cyclones (1983 and 1991), or bleaching (1983, 1987, 1991, 1994, 2002, 2003, and 2007) were reported.

TABLE 1: Episodic disturbances that have affected Moorea Island, and geometric rate of change in mean coral cover (Δ Coral cover) reported to occur between successive surveys spanning each disturbance.

Disturbances	Period	Reference(s)	Δ Coral cover
Bleaching Events	March–May, 1983	Williams and Bunkley-Williams [28], Glynn [22], Salvat [88]	−2.2 (±13.8 SE)
	March-April, 1987	Williams and Bunkley-Williams [28], Glynn [22], Salvat [88]	21.1 (±14.4 SE)
	March-April, 1991	Salvat [88], Gleason [72], Adjeroud et al. [58]	−43.9 (±24.2 SE)
	February–April, 1994	Hoegh-Guldberg and Salvat [26], Adjeroud et al. [16, 58]	15.3 (±6.9 SE)
	April–July, 2002	Adjeroud et al. [16, 58], Penin et al. [61]	4.9 (±9.9 SE)
	January–March, 2003	Carroll et al. (unpulished data)	−0.3 (±13.9 SE)
	February–April 2007	Adjeroud et al. [58], Pratchett et al. [62], Penin et al. (unpublished data)	−59.3 (±4.0 SE)
Cyclones	April, 1983	Harmelin-Vivien and Laboute [19]	−2.2 (±13.8 SE)
	December, 1991	Gleason [72]	43.9 (±24.2 SE)
Acanthaster planci outbreaks	1979–1986	Bouchon [60], Faure [33]	−12.2 (±4.5 SE)
	2006–2009	Lison de Loma et al. [74], Pratchett et al. [62]	−64.8 (±25.4 SE)

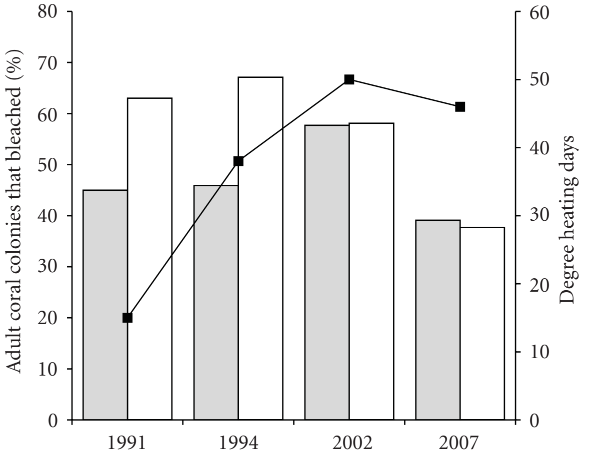
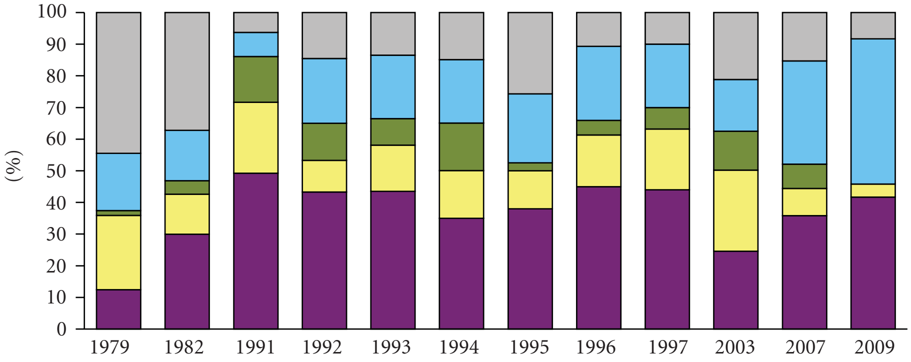


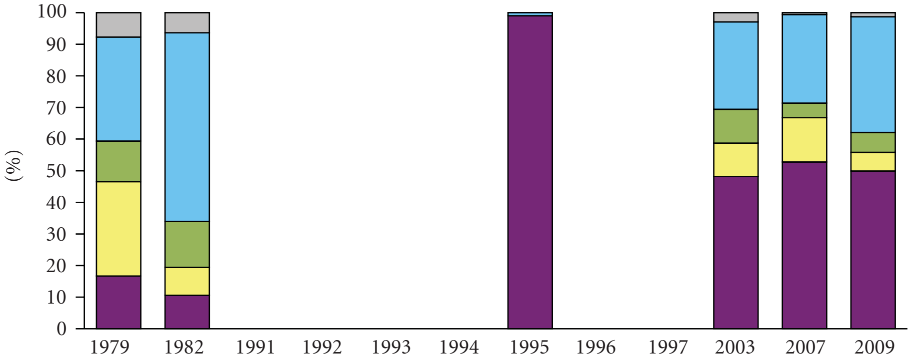
FIGURE 5: Percentage of adult coral colonies that bleached at Tiahura (grey bars) and Viaphu (white bars), versus the duration of temperature anomalies (degree heating days) during four episodes of mass-bleaching in Moorea. Degree heating days were calculated for the summer period (September–March) in each year that mass-bleaching was documented (generally between February and April), based on 4 km Pathfinder (NOAA) data for Tiahura Reef with backfilling and smoothing functions to eliminate null values.

bleaching generally occurs at Moorea whenever sea surface temperature (SST) exceeds the notional threshold of 29.2°C for more than several weeks [16, 26, 58, 61, 64]. There does not, however, seem to be any significant relationship between the extent of bleaching recorded during major mass-bleaching events (1991, 1994, 2002, and 2007) and the temporal duration of thermal anomalies (Figure 5). On the outer-reef slope at Tiahura and Vaipahu, the percentage of coral that bleached in 1991 was 45% and 63%, respectively, [72, 88], compared to 45.9% and 67.1% in 1994 [26], 57.7% and 58.1% in 2002 [61], and 39.1% and 37.7% in 2007 (Penin et al. unpublished data). As such, the severity of bleaching appears to have declined, even though the severity of temperature extremes (degree heating days) has increased among these bleaching events (Figure 5). Declines in the response of corals, despite similar or worsening thermal stresses, suggest that corals and/or the zooxanthellae may have acclimatized or adapted to increasing temperature, and may therefore, be less susceptible to future thermal anomalies [89, 90]. Alternatively, successive disturbances are likely to cause changes in the structure of coral assemblages, increasing the proportional abundance of species and genotypes that are most resistant to bleaching [25, 91]. If the latter is true, then severe bleaching and high rates of coral mortality may result with further increases in the severity and/or duration of temperature stresses.

3.2. Persistent Shifts in Coral Composition. Aside from causing marked changes in live cover, acute disturbances occurring in Moorea from 1979 to 2009 have caused significant and persistent shifts in coral composition (Figures 4(a) and 4(b)). In 1979, coral communities at Tiahura were mostly dominated by *Acropora* (Figures 4(a) and 4(b)). However, the *A. planci* outbreaks in late 1970s greatly affected *Acropora* corals which declined by 84.3% throughout the reef by 1982. While coral cover increased rapidly following the initial outbreak of *A. planci*, the postoutbreak coral composition was very different compared to the composition recorded in 1979 [60]. Berumen and Pratchett [49] described apparent recovery of coral cover despite marked temporal changes in coral composition as evidence that recurrent disturbances were causing a pronounced shifts in the structure of local coral assemblages. In 2003, *Pocillopora* was the most abundant genus in Moorea (Figures 4(a) and 4(b)), probably because it is less affected by coral bleaching, outbreaks



(a) Deep habitat (10–30 m)



(b) Shallowhabitat (0–5 m)

Figure 6: Interannual variation in relative abundance of major coral genera at Tiahura reef, Moorea Island.

of *A. planci* [92, 93], and tropical storms [49], especially compared to *Acropora* corals. *Pocillopora* corals increased in their relative abundance after the initial outbreak accounting for 30% and 49.2% of the coral cover on the reef slope (10 to 20 m) in 1982 and 1991, respectively, and remained the dominant coral until 2009 (Figure 4(a)). Similarly, in shallow waters habitats, the dominant coral genera changed from *Acropora* to *Porites* after the first outbreak of *A. planci* in 1982 (Figure 4(b)).

Acanthaster planci selectively feed on certain coral species, mostly *Acropora* [93, 94]. Accordingly, the proportional cover of *Acropora* (relative to all other genera) declined from (26.5%) in 1979, before the first reported outbreak of *A. planci*, down to 11.0% in 1982 (Figure 4). Further changes in coral composition were apparent in 1991, whereby the prevalence of *Acropora* coral was further diminished, probably due to their disproportionate susceptibility to both coral bleaching and storm damage [72]. Both *Pocillopora* and *Porites* have tended to increase in prevalence through time at the expense of *Acropora* corals and other coral genera (Figure 4). The most recent outbreak of *A. planci* (2006–2009) has further reduced proportional and absolute abundance of *Acropora* corals which accounted for only 4.2% of the coral cover in deep habitat and 5.9% in shallow habitat in 2009 (Figure 4, [62]). In contrast, *Porites* and *Pocillopora* corals accounted for 45.8% and 41.7% of the coral cover in deep habitat, respectively, and 36.6% and 49.9% in shallow habitat in 2009. Despite an increase in proportional cover of *Porites* and *Pocillopora* corals, absolute cover of these genera has also declined during the latest outbreak of *A. planci*. This is consistent with observed feeding habitats of *A. planci* whereby starfishes will tend to consume more of their less preferred prey corals when the overall abundance of the preferred prey drops [94].

Although not measured in Moorea, declines in the abundance of branching corals, especially *Acropora* and *Pocillopora*, are likely to cause reductions in diversity and topographical complexity of coral reef habitats [95]. This will, in turn, affect many other reef-associated species [13, 96]. *Acropora* and other branching corals are the predominant habitat used by coral-feeding and coral-dwelling species, and specialized species may disappear following declines in abundance of these microhabitats [96, 97]. Moreover, any declines in habitat diversity and complexity are likely to reduce the number of species that cooccur in coral reef habitats [13, 38], owing to the role of topographic complexity in moderating competition and predation [56]. In Moorea, these effects may be partly offset, by increases in the abundance of *Pocillopora* (Figure 6). However, declines in abundance of *Acropora* from 1979 to 2003 have already caused significant declines in the abundance of (coral-feeding) butterflyfishes that specialize on *Acropora* [49], and these fishes (*C. reticulatus* and *C. trifascialis*) may now be facing localized extinction (especially on the reef slope) given further declines in abundance of both *Acropora*, as well as other potential coral prey.

4. Conclusion and Management Implications

Coral reefs on the north coast of Moorea have been subject to several periods of extensive coral loss since 1979, caused by outbreaks of *A. planci*, cyclones, and/or bleaching. The greatest rates of coral loss recorded occurred during two major outbreaks of *A. planci* in 1979–1982 and 2006–2009, which caused particularly severe coral loss on the outer-reef slope. Moreover, coral loss was greatest among *Acropora* corals, thereby contributing to a marked shift in the composition of coral assemblages. Until now, effects of coral bleaching on local coral cover appear to have been fairly minor, especially compared to outbreaks of *A. planci*. However, projected increases in ocean temperatures, as well as ocean acidification, may yet cause significant coral loss in Moorea, and throughout the Pacific [98]. Hoegh-Guldberg et al. [98] predict that average coral cover on reefs in the Pacific will decline by 30%–40% in the coming decades, due to increasing effects of global climate change. Moreover, robust species such as *Porites* and *Favia* are expected to replace branching species, mostly *Acropora,* as the dominant coral genera [98].

Coral reef ecosystems are fundamental to coastal fisheries, and the provision of fresh seafood, throughout the Pacific. However, increasing disturbances, and the associated degradation of coral reef habitats threaten to undermine the capacity of these ecosystems to yield sufficient food and resources [99]. Climate change will, therefore, represent a major challenge for Pacific countries in the coming decades. However, in locations where major cause(s) of coral loss relate to more direct anthropogenic disturbances (e.g., fishing and eutrophication), improved local management may serve to reduce and/or delay effects of climate change. There is considerable controversy relating to the role of anthropogenic activities in causing and/or exacerbating outbreaks of *A. planci*. However, on the Great Barrier Reef, it is suggested that outbreaks result from increased nutrient loads [100] and/or overfishing of predatory fishes [101, 102]. There is a potential, therefore, that reduced fishing and/or improved water quality will minimize the occurrence and impacts of outbreaks of *A. planci*. In this instance, ecosystem management may provide an effective strategy to reduce a major contributor to coral loss in Moorea, and thereby improve ecosystem resilience to future climate change.

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Research Article

Ecosystem-Based Management in Fiji: Successes and Challenges after Five Years of Implementation

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In 2005, a network of 3 large, district-wide marine protected areas (MPAs) and 17 village-managed closures (*tabu*) was established in Kubulau District, Fiji. Underwater visual census (UVC) data of fish biomass and benthic cover were collected between 2007 and 2009 and analysed with PERMANOVA and ANOSIM to assess differences between closed and open areas. High reef fish biomass (>1000 kg/ha) within closures, significantly elevated over open areas, was consistently observed from: (1) tabu areas on naturally productive reefs within visual distance from villages; and (2) the large, long-term permanent closure located away from fishing pressure. Factors that may have contributed to low fish biomass within closures include small size of closures; noncompliance with management rules; and disclosure of management success to fishers from villages with high reliance on fisheries products. Future success of the network depends on improving awareness of management rules and ensuring implementation within a broader ecosystem framework.

1. Introduction

While the tropical western Pacific is a recognized hotspot for global marine biodiversity [1, 2], rapid loss of species and stocks are imminent as Pacific Island nations rely heavily on inshore and offshore fisheries for economic development and sustenance [3]. In the Fiji Islands, although fisheries data are often uncertain, there has been a high level of pressure on coastal fisheries in the past few decades [4]. Of the 410 traditionally managed fishing grounds (*qoliqoli*), at least 70 are considered overexploited while a further 250 are fully developed [5]. Rising prices for fish and fishery products have contributed to declines in artisanal catches from 1996 to 2002 [6], while percentages of catches sold are increasing: catch per unit effort (CPUE) from recent surveys of village catch from locations across Fiji suggests that >70% of catch is being sold [7].

In recognition of declines in coastal fisheries and marine biodiversity, there has been a global movement to increase the amount of area in the oceans under some form of protection [8]. The benefits of marine protected areas (MPAs) are recognized to include increases in abundance and biomass of targeted species [9], which may lead to increased recruitment [10, 11] and migration of adults into neighbouring areas [12]. These benefits, however, rely strongly on effective compliance and enforcement as well as selection of appropriate size and spacing of MPAs within a network. Furthermore, most positive and lasting effects have been observed in permanent no-take areas compared with partial protection [13] or periodically harvested areas [14].

Over the past two decades, hundreds of communities in the western Pacific have established locally managed marine areas (LMMAs) to control the perceived decline of marine natural resources [15]. The primary tool applied for the management of coastal marine resources within LMMAs is the use of traditional temporary closures, where the local community chooses the location, size, and management regime for their closed area. These areas tend to be small, averaging just 0.2–3.3 km^2 for the Cook Islands, Fiji, Papua New Guinea, Samoa, Solomon Islands, and Tonga [15]. Because their boundaries tend to fall within the secure, customary tenure of one village or clan, they are typically easy to manage because there are no overlapping governance constraints and their location is often within visual distance from villages [16]. However, while the benefits of many, small reserves can theoretically maximize fisheries yields [17], there may be a threshold size below which potential benefits of protection are outweighed by negative edge effects. Furthermore, the reserves must be placed in appropriate habitat that will maximize fisheries production. There is strong evidence to support reduced fish biomass in habitats characterized by macroalgae and unconsolidated sediments [18], which are typically found on fringing reef flats and backreef lagoons where traditional closures are often established.

In Fiji, an alternative, complementary approach was initiated in Kubulau District in 2005, representing one of the first efforts in Oceania to design and implement an ecologically functional MPA network. Traditional-style periodic closures were combined with large, permanent, no-take reserves in a network design using ecosystem-based management (EBM) principles, with approximately 30% of the qoliqoli area under closure to maximize fisheries and biodiversity benefits [19]. Initial placement of MPAs was based on baseline biological surveys and design criteria which considered size, spacing, and representation of habitats and critical processes (e.g., spawning aggregations) in a multispecies framework [20, 21]. The design was subsequently modified following extensive socioeconomic assessments and consultations with resource owners in order to spread cost and maximize compliance. An ecosystem-based management plan was completed for the protected area network in Kubulau District and qoliqoli [22] and was endorsed by the hierarchy council of chiefs (*Bose Vanua*) in July 2009. The planning process was informed by extensive scientific and socioeconomic research as well as local and traditional ecological knowledge. Conceptual modeling methods were used to define conservation targets, threats, and management strategies [23] both for the qoliqoli and the adjacent catchments lands in order to embed the MPA network in a broader management framework [24].

This study evaluates the biological and socioeconomic factors that have contributed to the effectiveness of the MPAs within the Kubulau network to achieve their goal of increasing fish biomass following the first five years of management. In particular, we ask (1) which factors are responsible for positive responses of fish populations to management and (2) which factors have contributed to a lack of response in certain cases. Based on the results, we present recommendations for adaptive management of the network to both improve long-term fisheries yields while conserving the unique biodiversity of Kubulau.

2. Methods

2.1. Study Region and Management Institutions. Kubulau District, located in Bua Province, Vanua Levu (Fiji), has a population of approximately 1,000 spread between ten villages, seven of which are located on the coast. The catchments of Kubulau district have between 70%–80% forest covered with relatively intact hyrodologic connectivity between terrestrial, freshwater, and marine areas [25]. The area of Kubulau's qoliqoli is 260 km^2 and its MPA network comprises 17 community-managed MPAs (*tabu*) sites and 3 district-wide MPAs (Namena, Namuri, Nasue), totalling approximately 80 km^2 (Figure 1). Kubulau qoliqoli includes portions of globally significant areas of marine biodiversity [26]. Marine fish diversity estimates from rapid surveys in 2003, including reefs from Kubulau, showed comparable biodiversity to sites in Indonesia and Papua New Guinea [27], while endemic fish represented nearly 5% of all observed reef fish species in 2009 [28].

While the state maintains ownership of the seabed and overlying waters throughout Fiji, the *Fisheries Act* explicitly recognizes traditional fishing rights within qoliqoli boundaries by customary land owners [29]. A qoliqoli resource management committee (KRMC) was established in Kubulau in 2005, made up of representatives from each village whose management decisions require authorization from the Bose Vanua. The resource management committee makes broad decisions over regulations for the qoliqoli (including the district MPAs), while village chiefs retain the rights to determine gear restrictions, lifting of temporary closures, and other local regulations in individual village tabu areas [29]. The main management rules for the Kubulau tabu areas and district MPAs evaluated in this study are listed in Table 1.

2.2. Biological Monitoring Surveys. Surveys of fish and benthos were carried out in Kubulau qoliqoli in 2007, 2008, and 2009, with specific methods described below.

2.2.1. Fish Surveys. Underwater visual census (UVC) was carried out at closed and open sites within the qoliqoli to measure fish abundance and size of the following families: Acanthuridae, Balistidae, Carangidae, Carcharhinidae, Chaetodontidae, Ephippidae, Haemulidae, Kyphosidae, Labridae, Lethirinidae, Lutjanidae, Mullidae, Nemipteridae, Pomacanthidae, Scaridae, Scombridae, Serranidae (groupers only), Siganidae, Sphraenidae, and Zanclidae, plus *Chanos chanos* (Chanidae) as it is a targeted food fish. Surveys were carried out in January 2007, April-May 2008, and April-May 2009 at closed and open sites adjacent to Namena MPA, Namuri MPA, Nasue MPA, Nakali tabu, and Yamotu Lase tabu (2007 and 2008 only), as indicated in Figure 1. Measurements of fish size (total length in 5 cm size classes for fish less than 40 cm and exact size over 40 cm) and abundance were recorded along five replicate 5 m × 50 m belt transects at deep (12–15 m) and shallow depths (5–8 m) at forereef sites and at reef tops (0.5–2 m) and shallow depths at backreef sites. A power analysis conducted in late 2008 indicated that changing the sampling design to increased sample size of *forereef-only* sites would improve the ability to detect differences related to management [28]. As a consequence, only data from forereef sites from datasets prior to 2009 were utilised for all analyses, and only forereef sites were surveyed in 2009.

Observer bias was investigated by assessing the mean number of fish species counted per transect, resulting in the exclusion of data from one observer from Kubulau 2007 surveys (19/346 transects) and data from one observer from Kubulau 2008 surveys (4/391 transects) who routinely counted significantly fewer species than other observers.

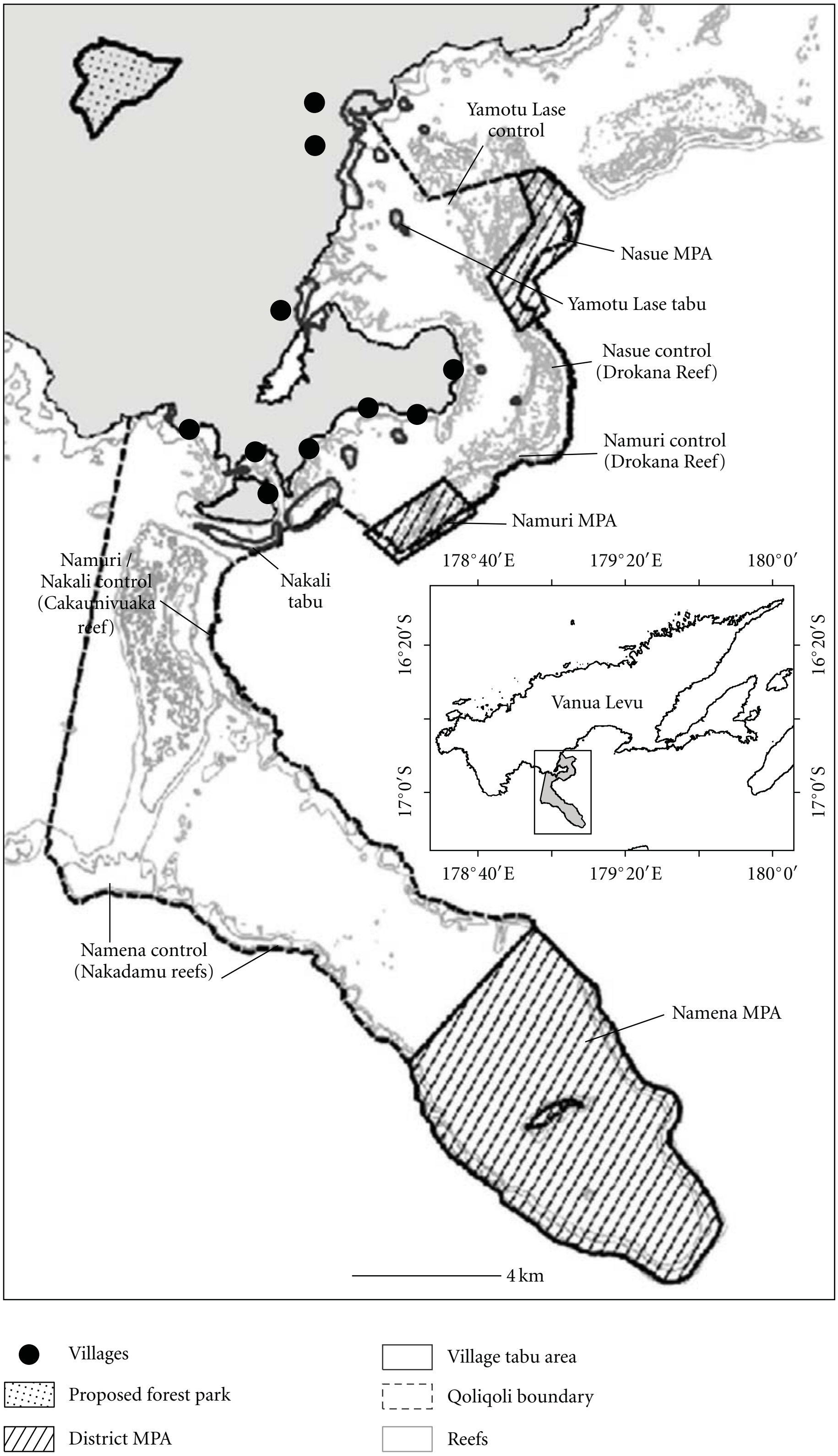


Figure 1: Location of MPAs, tabu areas, and adjacent fished areas used as control sites within the Kubulau traditional fishing grounds. Inset map shows the location of Kubulau qoliqoli on Vanua Levu, Fiji.

Table 1: List of MPA type, governance, date of establishment, size, and major management rules from the Kubulau Ecosystem-Based Management Plan [22]. KRMC = Kubulau Resource Management Committee.

MPA	Type	Management authority	Year est.	Size (km^2)	Major rules
Yamotu Lase	Tabu	Village chief of Nakorovou	2005	0.13	(1) Fishing using lines and nets, and diving for trochus and beche-de-mer is prohibited (2) Use of anchors within the tabu area is prohibited (3) May be opened each year for Saint Teresa feast day, 1 Oct, as authorized by village chief (4) All other qoliqoli rules apply
Nakali	Tabu	Village chief of Navatu	2005	0.77	(1) Taking any aquatic animal, including fish and beche-de-mer is prohibited (2) May only be opened up to three times per year, preferably in January, June, and November (3) All other qoliqoli rules apply
Nasue	District MPA	KRMC	2005	8.14	(1) Taking any aquatic animal, including fish and beche-de-mer is prohibited (2) Use of anchors within the marine reserve is prohibited, except during authorised research (3) All other qoliqoli rules apply
Namuri	District MPA	KRMC	2005	4.25	(1) Taking any aquatic animal, including fish and beche-de-mer is prohibited (2) Use of anchors within the marine reserve is prohibited, except during authorised research (3) All other qoliqoli rules apply
Namena	District MPA	KRMC	1997	60.61	(1) Taking any aquatic animal, including fish and beche-de-mer is prohibited (2) Removing anything, living or nonliving, from Namena Reserve is prohibited (3) The reserve may only be opened by the Bose Vanua for the funeral of the Tui Kubulau or the Tui Nadi (4) Diving, snorkeling, or kayaking without a marine reserve user tag is prohibited (5) Marine recreation providers, including dive operators, must comply with the Namena Marine Reserve Recreational Guidelines (6) Use of anchors within the marine reserve is prohibited, except during authorised research (7) All other qoliqoli rules apply

Biomass was calculated from size class estimates of length (L) and existing published values from Fishbase [30] used in the standard length-weight (L-W) expression $W = aL^b$, with a and b parameter values preferentially selected from sites closest to Fiji (e.g., New Caledonia). If no L-W parameters were available for the species, the factors for the species with the most similar morphology in the same genus were used [31]. If a suitable similar species could not be determined, averages for the genus were used. As many of the L-W conversions required fork length (FL), a length-length (L-L) conversion factor was obtained from Fishbase where necessary to convert from total length (TL) recorded during

Table 2: Maximum published weights from Fishbase [30] applied to listed species sighted above the indicated threshold size.

Species	Threshold size (cm)	Max published weight (kg)
Trianedon obesus	180	34
Carcharhinus melanopterus	75	13.6
Carcharhinus amblyrhynchos	150	33.7
Chanos chanos	80	14

the surveys to FL before biomass estimation. Because the L-W formula resulted in some grossly overestimated weights for fishes that substantially change morpholog as they age, maximum weights were used for certain species when these fish were sighted above threshold sizes (Table 2).

2.2.2. Benthic Substrate Composition. Benthic life-form categories were recorded along the same 50 m transects surveyed for fish assemblages at 0.5 m intervals as described by English et al. [32]. Life-form classes were combined into 6 functional strata: unconsolidated substrate (US: rubble, sand, silt); reef matrix (RM: dead coral, reef pavement, crustose coralline algae, coralline algae); macroalgae (MA: all fleshy macroalgae >2 cm, including cyanobacteria); live hard coral (LC: including *Millepora* and *Tubipora*); other soft substrate (OT: including soft corals, sponges, ascidians, anemones); and turf algae (TA: ≤2 cm height on reef pavement).

2.3. Socioeconomic Surveys. Measures of poaching levels in Kubulau qoliqoli were gauged in two ways. First, in November-December 2008, 51 households were surveyed across 8 villages in Kubulau. Respondents were asked how often they encounter people fishing in breach of MPA rules (regularly, sometimes, rarely, never), and, if they do witness offences, who are the offenders. Secondly, within the four villages (Raviravi, Navatu, Kiobo, Nakorovou) participating in weekly catch per unit effort (CPUE) monitoring between May 2008 and June 2009, fishers were asked to draw on a map the locations where they caught fish. The maps did not show the boundaries of the tabu areas or district MPAs.

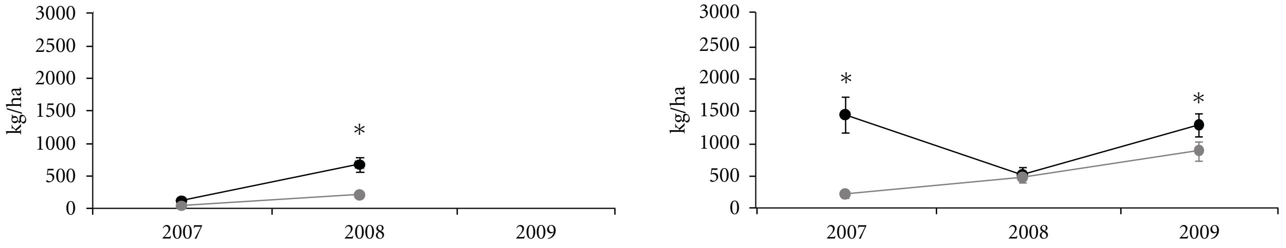
2.4. Metrics of Fishing Pressure. Based on the results of the socioeconomic surveys and a literature review, potential surrogates of fishing pressure in Kubulau were assigned for each site, including: proximity to adjacent districts of Wailevu and Wainunu; visibility from Kubulau villages; and distance from Kubulau villages weighted by weekly fish consumption (ω). The proximities to Wailevu and Wainunu were calculated as the distance (km) from each site to the closest point on either qoliqoli boundary through boat passages using a minimum number of turn points. Distances from villages were measured as the perpendicular distances (km) from each village to the site: this was weighted based on the frequency of fish consumption in each village as assessed from the 2008 household surveys described above where respondents were additionally asked on how many days of the previous week they consumed caught fin fish, based on the formula:

$$\omega = \frac{\sum_i^N (d_i * (1/c_i))}{N}, \tag{1}$$

where c is the mean number of days per week fish was consumed in the ith village, d is the perpendicular distance from the ith village to the site, and N is the total number of villages ($N = 9$ as there was no fish consumption data available for Nasasaivua). All distances were measured in ArcView 3.2a software. Visibility was given a weighted, ranked score as to whether fishers could be spotted from land: 1 = not visible; 6 = can be seen from 1 location or from people walking along coastal fringe; 11 = can be seen from 2 locations; 16 = can be seen from >2 locations.

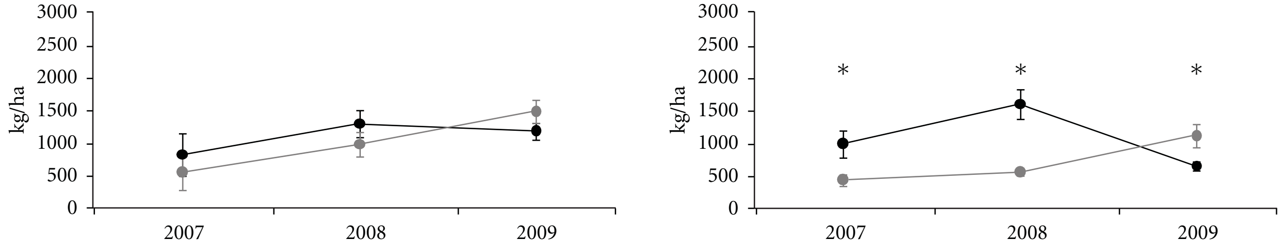
2.5. Statistical Analyses. A nonparametric Friedman ANOVA was performed using Statistica version 8 software to assess differences in responses across villages of how often infringements were observed. All other statistical analyses described below were performed in PRIMER version 6 software with PERMANOVA extension [33]. To assess whether fish biomass had increased within the MPAs, PERMANOVA analyses were conducted with 999 permutations using log 10 Modified Gower resemblance matrices of total fish biomass summed at the transect level [34, 35]. Year and protection status were fixed factors and outputs from within-year results are presented. To assess potential differences in benthic structure that may influence fish community assemblages [18], one-way Analysis of Similarity (ANOSIM) [36] was performed on a similarity matrix calculated with Euclidean distances between square-root transformed mean percent benthic strata cover for each site from 2009 data only, as there was insufficient replication at the site level in 2007 and 2008.

Fish community patterns from the 2009 data were investigated using multidimensional scaling (MDS) plots of a Bray-Curtis resemblance matrix of fish biomass data per species for each site. Data were fourth-root transformed to reduce the influence of large, schooling species, and rare fish species (found at 2 sites or fewer) were removed from the dataset prior to the calculation of the resemblance matrix. Repeated runs of the BVSTEP procedure within BEST were used to identify the most common subset of fish species with the highest correlation (≥0.95) to the Bray-Curtis similarity matrix for the full suite of species [37]. Significance of the output ρ_s statistic was tested using the permutation method of Clarke et al. [38], run over 999 permutations. To evaluate whether the factors likely to affect



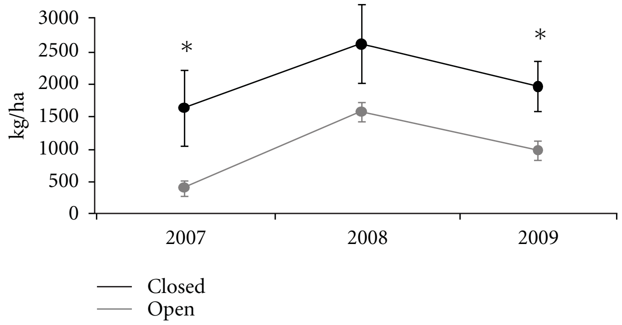
(a) Yamotu Lase

(b) Nakali



(c) Nasue

(d) Namuri



(e) Namena

Figure 2: Mean total fish biomass (kg/ha) in closed (black) and adjacent open (grey) areas of: (a) Yamotu Lase tabu; (b) Nakali tabu; (c) Nasue MPA; (d) Namuri MPA; and (e) Namena MPA for survey periods between 2007 and 2009. Error bars are ±1 standard error. $*$ denotes significant difference to at least $P < .05$ with PERMANOVA test.

fishing intensity could explain the patterns in fish biomass structure, a RELATE analysis was conducted to evaluate agreement between the Bray-Curtis resemblance matrix of fish biomass and a resemblance matrix of normalized fishing pressure variables calculated using Euclidean distance [39]. Significance of the output ρ_s statistic was tested over 999 permutations.

3. Results

Observations of reef fish biomass recovery varied across MPAs. On forereef areas within the village-managed tabu areas, total reef fish biomass was significantly greater than in adjacent fished locations in 2008 only for Yamotu Lase (Figure 2(a) and Table 3(a)) and in 2007 and 2009 (but not 2008) for Nakali (Figure 2(b) and Table 3(b)). Mean total fish biomass was never observed to be significantly higher in the Nasue district MPA than on adjacent fished reefs (Figure 2(c) and Table 3(c)). For the Namuri district MPA, total reef fish biomass was significantly greater within the closed area in 2007 and 2008, but significantly greater in the open areas in 2009 (Figure 2(d) and Table 3(d)). Mean total reef fish biomass was consistently highest from closed sites within the large, offshore Namena district MPA and was significantly greater than open areas on control reefs in 2007 and 2009. Although mean total reef fish biomass inside Namena district MPA was the highest recorded from any reef area in the Kubulau qoliqoli in 2008 (2642.73 kg/ha), the variability across transects (SE = 601.25 kg/ha) was also the highest observed, mostly due to the presence of large, schooling carangids occurring on some but not all transects.

ANOSIM results comparing benthic composition at the site level showed no overall difference between open and closed sites in the Kubulau qoliqoli (global $R = 0.076$; $P = .171$). When benthic composition across the 6 major strata was compared between reefs, there were only strong, significant differences between open sites on the Nakadamu reefs used as control for Namena MPA and Cakaunivuaka reef used as control for the Nakali MPA (Table 4), which were not directly compared for fish biomass.

Fish community structure based on species biomass is significantly different ($\rho_s = 0.387$; $P = .001$) from

Table 3: PERMANOVA results of differences in fish biomass inside and adjacent to the following MPAs: (a) Yamotu Lase; (b) Nakali; (c) Nause; (d) Namuri; (e) Namena. Mean total fish biomass in closed and open areas is reported in kg/ha. Significant differences of $P \leq .05$ (derived by permutation analysis) are indicated in bold.

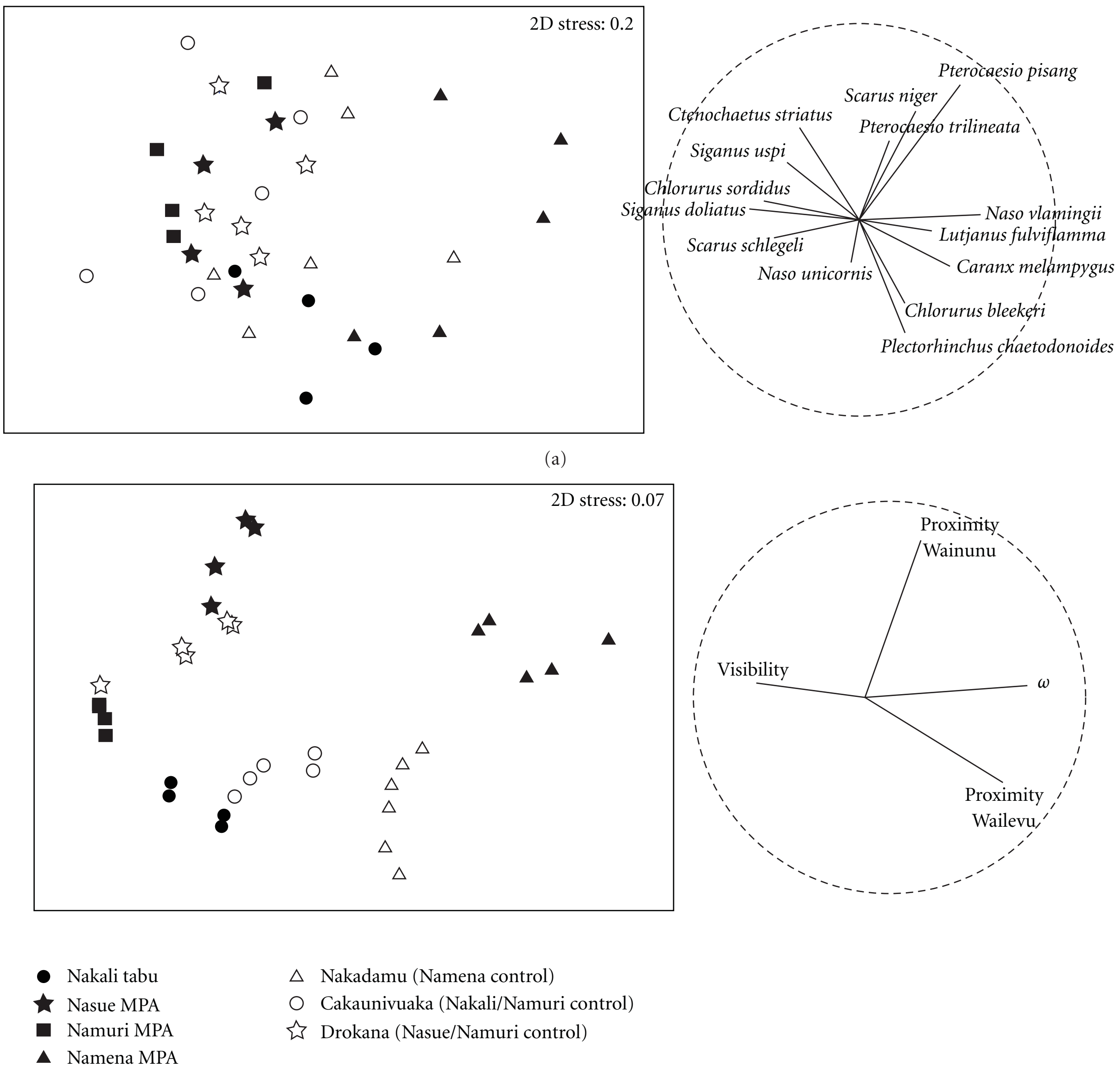
MPA	Closed	Open	*t*	*P* (perm)
(a) Yamotu Lase				
2007	119.46	40.12	1.608	.126
2008	**673.64**	**215.36**	**2.633**	**.007**
(b) Nakali				
2007	**1449.71**	**224.64**	**4.639**	**.001**
2008	521.25	485.81	0.057	.953
2009	**1296.97**	**897.14**	**2.873**	**.006**
(c) Nasue				
2007	831.35	560.29	0.610	.530
2008	1309.59	993.84	1.307	.168
2009	1194.76	1498.94	1.411	.187
(d) Namuri				
2007	**1015.97**	**461.91**	**2.832**	**.008**
2008	**1625.72**	**585.39**	**5.265**	**.001**
2009	**673.47**	**1143.99**	**2.288**	**.025**
(e) Namena				
2007	**1660.11**	**436.12**	**2.666**	**.014**
2008	2642.73	1602.71	1.168	.243
2009	**1994.50**	**1009.31**	**3.004**	**.003**

Table 4: *R* values from pairwise comparisons from one way ANOSIM of benthic strata across 2009 closed (C) sites within and open (O) sites adjacent to Kubulau MPAs. Significant differences at $P < .05$ are in bold.

	Namena C	Namena O	Namuri C	Namuri O	Nasue C	Nasue O	Nakali C
Namena C	—						
Namena O	0.056	—					
Namuri C	−0.175	0.167	—				
Namuri O	−0.131	0.063	0.000	—			
Nasue C	−0.131	−0.032	0.094	−0.24	—		
Nasue O	0.077	−0.093	0.500	0.019	−0.259	—	
Nakali C	0.206	0.155	0.448	0.063	0.135	0.074	—
Nakali O	0.190	**0.383**	0.463	−0.019	0.074	0.407	−0.056

the underlying structure that would have been predicted from the surrogate measures of fishing pressure alone (Figure 3). The protected Namena MPA sites, which are distant from Kubulau villages and adjacent districts, are in general agreement with the fishing pressure model in that they are more distant from the majority of other sites in both MDS plots in Figure 3. However, the Nakali tabu fish communities, which responded strongly to management in 2009, clustered more closely with the Namena closed sites, despite the fact that Nakali is located close to Wainunu District and to Kubulau villages that consume a lot of fish. The position of Namena and Nakali closed sites in Figure 3(a) is best explained by high biomass of fusiliers (e.g., *Pterocaesio pisang*), important food fish such as *Naso unicornis*, *N. vlamingii*, *Caranx melampygus*, *Plectorhinchus chaetodonoides*, and *Lutjanus fulviflamma*, and important reef cleaners such as *Scarus niger* and *Chlorurus bleekeri*. The position of the other more clustered sites from Nasue, Drokana, Namuri, and Cakaunivuaka is best explained by high biomass of schooling and solitary grazers: *Ctenochaetus striatus*, *Siganus doliatus*, *S. uspi*, *Chlorurus sordidus*, and *Scarus schlegeli*, with secondary or no importance as food fish.

There were no significant differences between villages in response to how frequently the respondents observed infringements of MPA rules in the Kubulau qoliqoli (Friedman's ANOVA: $\chi^2_{4,7} = 5.833$; $P = .559$), with most respondents reporting that they sometimes or rarely witnessed offences. Of the 33 respondents who answered the question of who was committing offences, 75.8% ($n = 25$) replied that they were nonresource rights owners coming from outside the Kubulau qoliqoli. Only 9.1% ($n = 3$) reported that the offenders came exclusively from within Kubulau; however notably, only 2 of the 8 residents of Navatu village responded



(a)

(b)

Figure 3: MDS plots showing distances between sites for (a) mean fish species biomass, coupled with vector trajectories for fish species that best explained variation among sites; and (b) potential fishing pressure, coupled with vector trajectories for all fishing pressure surrogates. Dark circles = Nakali tabu; open circles = Nakali/Namuri control (Cakaunivuaka reef); dark stars = Nasue MPA; open stars = Nasue/Namuri control (Drokana reef); dark square = Namuri MPA; dark triangle = Namena MPA; open triangle = Namena control (Nakadamu reefs).

to this question: Navatu residents have been repeatedly caught fishing within the Namena MPA. Synthesis of catch locations from CPUE surveys showed multiple instances of fishing activity from within MPA boundaries by local Kubulau fishers, in particular within: Nasue district MPA; Namuri district MPA; Yamotu ni Oqo, Bovici and Bagata (Kilaka's village tabus); and Rewa Bota, Yamotu Lase and Yamotu Vutia (Nakorovou's village tabus; Figure 4).

4. Discussion

Many different factors can potentially influence whether or not MPAs and MPA networks are effective in reaching their conservation and management goals. These factors can include, but are not limited to: degree of protection (permanent no-take, periodic opening, partial closures); awareness of and degree of compliance with MPA rules; visibility from land; design of MPAs and MPA networks; benthic habitat condition; frequency and intensity of current and historical disturbance (e.g., land-based pollution, bleaching, tropical cyclones, crown-of-thorns outbreaks); and longevity of protection [9, 16, 18, 19]. As the goals of the Kubulau tabus and MPAs were primarily to increase size and abundance of food fish, we evaluate the results of our surveys in the context of the above factors to determine where management has been effective and where there needs to be improvements.

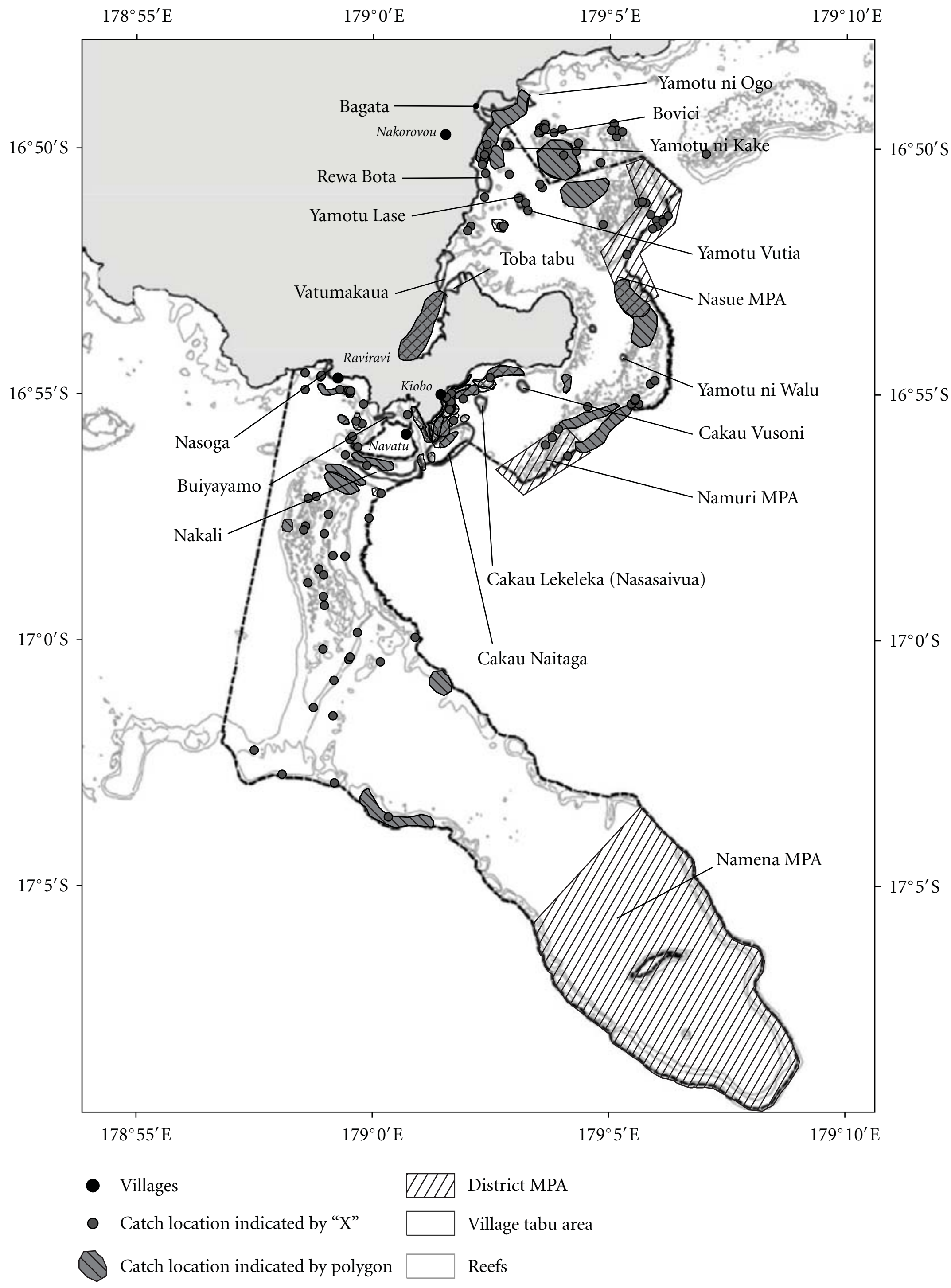


Figure 4: Fishing locations (grey circles and shaded grey polygons) recorded by Kubulau fishers from Raviravi, Navatu, Kiobo, and Nakorovou fishers between May 2008 and June 2009. CPUE locations, District MPAs, and tabu areas are labelled.

We additionally discuss how the MPA network can be adaptively managed within an EBM framework to respond to these improvements.

4.1. Small, Village-Managed MPAs. Monitoring the effectiveness of the small tabus has been challenging, largely because they may be too small to fit well-replicated survey sites within their boundaries (e.g., Bartlett et al. [40]), thus preventing rigorous statistical analysis. For example, only 1 survey site with 5 replicate transects could be placed inside the Yamotu Lase tabu ($0.13\,\mathrm{km}^2$) without the risk of pseudoreplication. Even with this low statistical power, 2008 data indicate

Table 5: Comparison of mean fish biomass (kg/ha) evaluated from underwater visual census (UVC) at protected and fished sites in the Indo-Pacific.

Location	Fish group	Mean Biomass range (kg/ha)	Source
Kubulau, Fiji (Namena)	Total fish protected	1647–2633	This study
	Total fish open	1009–1758	
Kubulau, Fiji (Namuri/Nasue)	Total fish protected	673–1626	This study
	Total fish open	462–1499	
Kubulau, Fiji (Yamotu Lase)	Total fish protected	119–674	This study
	Total fish open	40–215	
Vatu-i-Ra, Fiji	Total fish	~550–900	[27]
Northern Lagoon, New Caledonia	Targeted fish along terrestrial gradients	148–447	[44]
North Efate, Vanuatu	Vulnerable fish protected	508–669	[40]
	Vulnerable fish open	175–296	
	Less vulnerable fish protected	307–381	
	Less vulnerable fish open	261–302	
Ahus Island, Papua New Guinea	Total fish protected	~225	[45]
	Total fish open	~120	
Muluk, Papua New Guinea	Targeted fish protected	378	[41]
	Targeted fish open	301	
Karkarotan, Indonesia	Targeted fish protected	139	[41]
	Targeted fish open	101	
Apo Island, Philippines	Targeted fish protected†	~250–1200	[14]
	Targeted fish open	$\lesssim$100–850	
Line Islands, Kiribati and USA	Total fish along human impact gradient	1300–5300	[46]

positive significant differences in total reef fish biomass compared to adjacent fished areas. Further examination of the data from 2008 shows that although the ranges of total fish biomass in the small, community-managed tabu of Yamotu Lase are comparable to the ranges reported for the small periodically closed areas on inshore, fringing reefs adjacent to Muluk village of PNG [41], Karkarotan village of Indonesia [41] and in Efate, Vanuatu [40] (Table 5), overall mean biomass is low compared with both fished and some unfished barrier reef areas in Kubulau qoliqoli. Secondly, the mean biomass of fish primarily targeted for consumption comprised only 21.6% of the total biomass recorded within the tabu, which is a substantially lower percentage than in the Namena MPA where primary targets comprised 72.0% of the total fish biomass. The low values for primary food fish may be due to the fact that the management rules for Yamotu Lase include a provision for an annual harvest for the feast of Saint Theresa (Table 1) and that local fishers have themselves reported fishing inside the MPA (Figure 4). Repeated harvests and sustained fishing pressure may reduce the size structure of fishing communities, resulting in fewer, smaller individuals [42, 43].

The Nakali tabu, while also small ($0.77\,\text{km}^2$), supported over ten times the total fish biomass as the Yamotu Lase tabu in 2007. This is likely due to the natural geomorphology of the reef system in which the offshore barrier is located within 1 km from land and is regularly flushed with high currents through the Naisonisoni Passage. High currents along reef walls provide important fluxes of zooplankton, upon which planktivorous fish feed [47], some of which (e.g., schooling damselfish) are prey for larger-bodied carnivores. The currents may also bring nutrients supporting algal growth upon which large herbivores (e.g., *Naso unicornis*) feed. *N. unicornis* are preferred food fish of many Fijian fishers and were sighted in large numbers and sizes at all sites within Nakali. By 2008, however, sites in Nakali no longer supported greater biomass than adjacent fished areas and there was significantly more fish outside the MPA. This is most likely because the village of Navatu harvested the tabu three times between survey periods, which is within the community-declared management provisions of the Nakali tabu (Table 1). Despite the high frequency of harvests, the natural features of the reef may be highly resilient to exploitation as reef fish populations, in particular of primary food fish, had recovered substantially by 2009. In addition, the close proximity of the tabu to Navatu village facilitates compliance as offenders would be visible from shore.

Given the strong community buy-in across Fiji to the establishment and maintenance of small tabu areas [15], it is important to maintain the cultural traditions that support the management of existing small tabu areas and the establishment of new sites. However, management support networks like the Fiji LMMA network would do well to increase awareness among community members of the potential consequences of harvesting to ensure that periodic openings of tabus are done in a limited and controlled manner only according to provisions in management plans. Further, when establishing new sites for tabu placement, conservation partners should aid communities to select the most naturally productive and resilient areas where possible, which can be identified using the methodologies of Green and Bellwood [48] and Obura and Grimsditch [49].

4.2. Large, District-Managed MPAs. The results from the larger MPAs located <10 km offshore (Nasue, Namuri) in Kubulau are equivocal. For example, total fish biomass inside Nasue MPA was never significantly greater than on adjacent fished reefs. The MPA is located relatively close to the mouth of the Yanawai River, which in the past has discharged runoff from the upstream Mt. Kasi gold mine. However, the mine is no longer operational and there did not appear to be any significant difference in benthic composition from sites inside and adjacent to the MPA, suggesting little current terrestrial influence [50]. Based on the responses from perceptions surveys in Kubulau, external poaching from the adjacent Wailevu District is likely to play a critical role in influencing the total fish biomass and species composition within the MPA. The Nasue MPA shares a boundary with the neighbouring Wailevu qoliqoli, and Wailevu fishers have been repeatedly caught fishing in the MPA, a problem compounded by the fact that the MPA is not visible from any of the villages in Kubulau. External poaching has been a common occurrence across sites within the FLMMA network when adjacent communities hear about local management success. The heavy fishing pressure has affected fish community structure by removing important food fish, leaving the reefs dominated by opportunistic grazers (e.g., *Ctenochaetus striatus*, *Chlorurus sordidus*) and nontargeted species. In order to combat this problem, the Kubulau Bose Vanua and KRMC have resolved to stage meetings with their neighbours from both Wailevu and Wainunu to both raise awareness of the management rules in the Kubulau EBM plan and to assist the districts to establish their own protected area networks and management rules.

The Namuri MPA appeared to be effectively protecting marine resources in 2007 and 2008, with significantly higher total fish biomass inside compared with adjacent fished areas. The opposite pattern was observed from 2009 surveys, provoking some concern that when Kubulau fishers were made aware of the exceptionally high biomass inside Namuri MPA during a management planning workshop in February 2009, they may have proceeded to covertly fish the area. Indeed, the monitoring sites within Namuri all had exceptionally low consumption-weighted distance-to-village scores (ω), indicating that they are near numerous villages whose residents frequently consume fish and would therefore be susceptible to high levels of fishing intensity without management (Figure 3(b)) or if management rules were ignored. Thus, in an attempt to use the monitoring data to foster discussions related to management implementation, its public presentation may have had detrimental consequences for the fishery [51]. To resolve these issues, more careful attention needs to be paid with respect to dissemination of sensitive monitoring information which in the future should likely only be shared during restricted meetings with the KRMC and Bose Vanua.

The Namena MPA demonstrated the strongest results in terms of increasing food fish biomass. The upper range of mean total fish biomass observed in Namena (2643 kg/ha; Table 3(e)) falls within the range of values reported for Palmyra atoll in the northern Line Islands, which is considered to have relatively intact trophic structures and minimal impact from humans (Table 5) [46]. The Namena MPA has been informally established as a permanent no-take protected area since 1997, when the high council of chiefs both banned commercial fishing from the qoliqoli and set up the reserve around the reefs of Namenalala Island [29]. The longevity and permanence of the closure has enabled recovery of large-bodied piscivores such as carangids, serranids, and lutjanids, which have low growth and recruitment rates and are highly vulnerable to overfishing [52]. Increases in biomass of these taxa from growth alone may take a decade to observe, as opposed to biomass increases from successful adult fish attraction following the closure of an MPA, which can occur rapidly over 1–3 years [53–55]. At 60.6 km^2, Namena is the largest MPA in Fiji, covering an extensive barrier reef system that extends outward into the deep waters of the Vatu-i-Ra passage. High currents flush the reef, supporting an abundance of top predators, including schools of hammerhead sharks which draw dive tourists from around the globe. Like in the Nakali tabu, these naturally favourable habitats may promote rapid recovery of exploited populations [21].

Given that there is international dive tourism in Namena which brings revenue to the communities of Kubulau through the payment of user fees to dive in the MPA, there is high incentive from the communities to enforce the MPA regulations. The chiefs of Kubulau have empowered the owners of Moody's Namena Resort, located within the reserve, to patrol the area, and trained community fish wardens may board vessels suspected of illegal fishing activity [29]. Due to this vigilance, there is unlikely to be poaching for subsistence fishing from fishers coming from the mainland given the high price of boat fuel: fishers would only be attracted to the area if they have guaranteed access to a market to sell their catch. While villagers say that this still remains a potential problem, the extent of illegal fish extraction for sale prior to surveys in 2009 did not appear to be overly compromising the biological effectiveness of Namena.

5. Conclusion

In the Kubulau MPA network, the factors which appear to have the most influence on the success of management to provide protection of exploited species included: size; placement of reserves in naturally productive habitats; visibility from land; distance from potential poachers; degree and longevity of protection. Some key recommendations to improve and expand MPA networks to other sites in Fiji include the following.

(i) MPAs need to be larger than the home ranges of targeted fish species. Recent fish tagging studies from the Coral Coast of Fiji have shown that *Lethrinus* spp. can move up to 700 m and do so mostly at night [56]. Therefore, MPAs should be at least double this length on both sides in order to ensure that fish are not caught while foraging.

(ii) Though some studies have observed limited increases in fish biomass and abundance despite periodic opening [40, 41], the ability of fish populations to recover from harvests is likely to depend both on the frequency and intensity of harvest events [57]. Permanently closed areas provide the maximum level of protection and degree of recovery. Russ and Alcala [58] make a strong argument for permanent closures as a precautionary principle because the "benefits accrue slowly but are lost quickly" with repeated fishing events.

(iii) MPA placement can enhance success when factors such as natural geomorphology and oceanographic features of the region promote rapid recovery. Placement in high visibility areas can also promote compliance, though visibility need not always imply that they be placed within direct sight of villages. Visibility can be improved by frequent enforcement patrols, though resourcing is required for boats and fuel. Resource management committees must therefore place priority on financing enforcement activities through their varied sources of revenue.

(iv) Lastly, management of MPAs cannot occur in isolation of potential disturbance from outside the fisheries management areas (e.g., from land-based threats or commercial fisheries operating in adjacent, connected areas). MPA management needs to be placed into the context of a broader ecosystem framework in order to reduce local threats to reef systems and therefore improve resilience [24]. Within Kubulau and across Fiji, EBM requires close collaboration between upland and lowland villages as well as engagement of stakeholders across multiple sectors, including fisheries, forestry, agriculture, tourism, and cultural heritage.

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Research Article

Marine Protected Areas, Multiple-Agency Management, and Monumental Surprise in the Northwestern Hawaiian Islands

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Large, regional-scale marine protected areas (MPAs) and MPA networks face different challenges in governance systems than locally managed or community-based MPAs. An emerging theme in large-scale MPA management is the prevalence of governance structures that rely on institutional collaboration, presenting new challenges as agencies with differing mandates and cultures work together to implement ecosystem-based management. We analyzed qualitative interview data to investigate multi-level social interactions and institutional responses to the surprise establishment of the Papahānaumokuākea Marine National Monument (monument) in the northwestern Hawaiian Islands (NWHI). The governance arrangement for the monument represents a new model in US MPA management, requiring two federal agencies and the State of Hawai'i to collaboratively manage the NWHI. We elucidate the principal barriers to institutional cotrusteeship, characterize institutional transformations that have occurred among the partner agencies in the transition to collaborative management, and evaluate the governance arrangement for the monument as a model for MPAs. The lessons learned from the NWHI governance arrangement are critical as large-scale MPAs requiring multiple-agency management become a prevalent feature on the global seascape.

1. Introduction

Coral reef ecosystems comprise less than 0.1% of ocean space [1], but they are disproportionately important with regards to the critical role they play in tropical cultures worldwide [2]. In the Pacific, the history and cultural heritage of island societies are closely intertwined with coastal ecosystems [3], and coral reefs have long provided critical ecosystem goods, services, and sociocultural values that are the basis for Pacific Islanders' livelihoods, cultural practices, and traditional lifeways [4–6]. The social benefits that coral reefs provide are threatened, however, by a relatively small set of proximate, or direct, human activities that include overexploitation, land-based pollution, biological invasions, disease, and threats associated with climate change [7–9]. The principal response to reef ecosystem decline and degradation has been an increased focus on the implementation of marine protected areas (MPAs), which reserve ocean space for conservation. MPAs serve primarily as a mechanism for ameliorating exploitation pressure, but often provide the institutional nexus by which other threats are addressed. MPAs exhibit a variety of forms but generally share a common goal to preserve resources and the ecosystems in which they are embedded.

Traditionally, the establishment of MPAs has focused on relatively small-scale reserves at the community level that focus on specific conservation targets (e.g., habitats or species). Attention has increasingly turned, however, to the establishment of large-scale MPAs and networks of marine reserves to achieve conservation goals at regional scales [10]. Conservation on regional scales allows for protection of larger proportions of marine habitat and different habitat types, spans the ranges utilized by errant marine megafauna, and preserves the dynamic biological processes required to maintain ecosystem integrity and resilience [11–13].

The establishment of MPAs has also become a primary focus as a means for implementing ecosystem-based management (EBM) in marine environments [14]. Marine EBM is defined as an integrated approach to the management of both social and ecological systems as opposed to traditionally fragmented sectoral approaches [15, 16]. Though many frameworks for EBM have been advanced, the social dimensions of marine EBM have been identified as including governance arrangements, institutional dynamics, stakeholder engagement, and adaptive management [17–20]. Comparatively less research has focused on these social dimensions versus the biological science of marine reserves, but it is a growing field that has been spurred on by an increased recognition of the importance of social science approaches in defining the pathways toward sustainable governance of linked social-ecological systems [21–27].

Large-scale MPAs face different challenges in governance and management than local and community-level MPAs, including multiple-agency management, overlapping statutory responsibilities and juridical zones, socioeconomic and political pressures, and a broader and more diverse constituency [28]. Compared with small-scale MPAs, however, relatively little literature has focused on the governance and management of large-scale MPAs, though some notable exceptions exist [28–32]. As marine EBM gains traction as the accepted approach in MPA management and planning [14, 18, 30], natural resource management institutions are considering new means by which to integrate EBM. Management transitions to EBM approaches are complicated by differing statutory responsibilities, existing governance arrangements and institutional processes, all of which mediate the pathways that institutions utilize in environmental planning and management. Understanding the challenges that human institutions must meet to effectively navigate change is necessary if MPAs are to be social as well as biological successes [21, 30, 33, 34]. This is particularly important considering the increased prevalence of multiple-agency management structures associated with large-scale MPAs, where new challenges are presented as agencies with differing mandates and cultures work collaboratively to synthesize sectoral-based approaches into comprehensive EBM frameworks.

We investigated multilevel social interactions and institutional dynamics that characterized the management transition from the proposed national marine sanctuary to the surprise establishment of the Papahānaumokuākea Marine National Monument (monument) in the northwestern Hawaiian Islands. The objective of our research was to assess how the monument's multiple-agency governance structure and resultant management transition to institutional co-trusteeship have affected the institutional dynamics of natural resource agencies. We were also interested, in a more applied context, in identifying the major barriers to effective multiple-agency management, the solutions that have been employed to address these barriers, and more broadly, in assessing the governance arrangement for the monument as a model for MPAs. First, we provide a brief overview of the Northwestern Hawaiian Islands and the governance arrangement for the monument. Next, we briefly describe our interview-based research approach and methodology for analyzing qualitative data. Subsequently, we present the results of our research, summarized in a series of tables of coded interview responses and supported by summaries of direct quotations from respondents. We conclude with a discussion on the management transition to institutional co-trusteeship, the efficacy of the multi-agency governance structure as a model for marine conservation and offer policy prescriptions for improvement in multiple-agency management and planning for ecosystem conservation.

2. Ecosystem Protections and Management in the Northwestern Hawaiian Islands

The Northwestern Hawaiian Islands (NWHI) are a chain of islands, atolls, and shoals spanning approximately 2,000 kilometers to the northwest of the inhabited Main Hawaiian Islands (MHI), which together comprise the Hawaiian Archipelago in the central Pacific Ocean (Figure 1). Human habitation of the NWHI is restricted to a small population at Midway Atoll National Wildlife Refuge (∼70) and Tern Island at French Frigate Shoals (∼5); additionally, researchers, cultural experts, and other visitors inhabit various islands and atolls seasonally. Islands in the southeast portion of the chain were inhabited prior to European contact by Polynesian societies [35, 36], and Native Hawaiians recognize the islands as a sacred ancestral homeland from which life arises and to which spirits return after death [37].

Biologically, the various island, atoll, and coral reef habitats in the region support a rich array of species and populations, including a high proportion of coral reef species endemic to the Hawaiian Archipelago [39–41]. Coral reefs in the NWHI experienced impacts associated with exploitation and other human activities starting in the 19th century, but over the past 50+ years reef ecosystems have been in a recovery mode [42]. With the exception of a few populations of vulnerable marine megafauna (e.g., the Hawaiian monk seal, *Monachus schauinslandi*) and some species that were commercially overexploited (e.g., lobsters, pearl oysters), intact populations now characterize the predator-dominated reefs in the NWHI [43].

Ecosystem protections predating the monument in the NWHI have a more than 100-year history and have been adequately summarized elsewhere [28, 44, 45]. The monument was established in 2006 by presidential proclamation under the American Antiquities Act of 1906 and includes the entire NWHI coral reef ecosystem [46, 47]. The proclamation created the largest protected area under US jurisdiction (362,073 km^2), an area almost the size of the State of California (Figure 1). In 2010, the monument was inscribed as a UNESCO World Heritage Site for both natural and cultural value. Pursuant to the proclamation, full protections were to take effect in 2011 with the closure of the last remaining fishery (bottomfish fishery). In January 2010, however, the National Marine Fisheries Service signed an agreement with the remaining bottomfish fishers to surrender their federal fishing permits in exchange for compensation; as a result, all commercial fishing ended in January 2010. Extraction is now limited to subsistence take by visiting scientists,

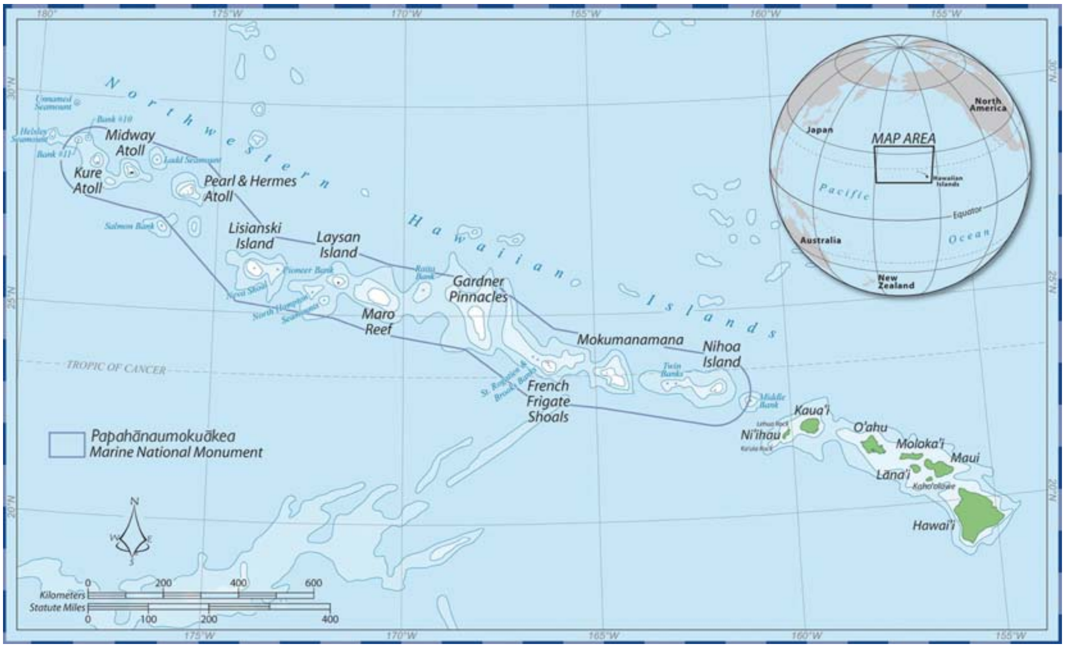

Figure 1: Map showing the Hawaiian Archipelago, comprised of the inhabited high islands of the main Hawaiian Islands and the uninhabited reefs, banks, and atolls of the Northwestern Hawaiian Islands. The boundary for the Papahānaumokuākea Marine National Monument is indicated in black. Map courtesy of the NOAA Papahānaumokuākea Marine National Monument Office.

residents of Midway Atoll and Native Hawaiian cultural practitioners, as well as minimal extraction for research purposes. Due to the limited number of permitted entries and negligible extraction for research, the monument is primarily considered a no-take reserve. Beyond exploitation impacts, NWHI coral reef ecosystems are threatened by human activities beyond the agencies' regulatory authority or the boundaries of the protected area. These threats include sea-level rise, biological invasions, marine debris, ocean acidification, coral bleaching, ship-based pollution, research impacts, contaminants associated with past occupations, and other threats [48, 49].

The proclamation establishing the monument was a major surprise to natural resource managers and stakeholders involved in the NWHI Coral Reef Ecosystem Reserve (a proto-sanctuary designation) [28], who had been engaged in a 5+ year planning process for a national marine sanctuary designation [28, 50]. The proclamation and associated regulations created a requirement for federal agencies to consult with each other in managing the NWHI. Following the proclamation, a memorandum of agreement (MOA) signed by the managing institutions established an institutional "co-trusteeship" of the protected area, requiring two federal agencies (the National Oceanic and Atmospheric Administration [NOAA] and the US Fish and Wildlife Service [USFWS]) and the State of Hawai'i to manage the monument collaboratively as "co-trustees" (Figure 2). Though ostensibly the proclamation and MOA named three agencies as co-trustees, in actuality the co-trusteeship is comprised of seven different partner agencies that include different divisions of the primary co-trustee agencies as well as the Office of Hawaiian Affairs (Figure 2). Each of the co-trustee agencies has a long management history in the NWHI [45], and agencies have worked collaboratively in the past. But most of these collaborations were project specific, such as the multiple-agency approach to reducing marine debris [51] or interagency efforts on protected species management [52]. The establishment of the monument also further complicated the legal landscape of the area by preserving the existing management responsibilities and preexisting ecosystem protections established by federal and state agencies [28].

The institutional co-trusteeship represents a novel governance arrangement in US MPA management. Governance models for MPAs in the US have been traditionally based on an institutionally fragmented, hierarchical system, where a lead agency is the primary institution engaged in the formulation of policy and management actions with partner agencies. In creating a "co-trusteeship", the proclamation required state and federal co-trustee agencies to break new ground in institutional collaboration for co-management of the protected area [53] and ostensibly gave equal management authority to each of the co-trustee agencies. The establishment of the monument initiated a major management transition, where agencies and stakeholders were required to create new management structures and approaches to support the institutional co-trusteeship, including a Monument Management Board (MMB) that serves as the primary nexus for decision-making and policy formation among the seven partner agencies (Figure 2).

The first major co-trustee initiatives included the creation of a joint permitting process to review proposed activities in the monument, the development of a monument management plan, and the completion of an application

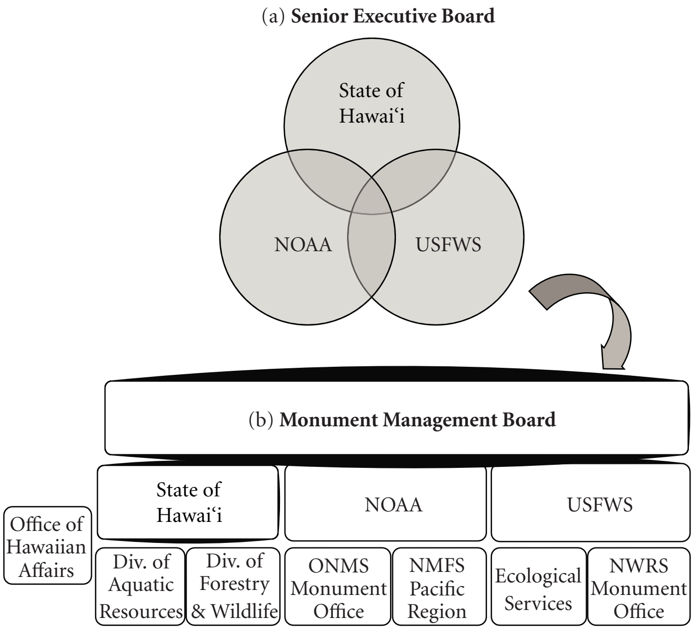

Figure 2: Polycentric governance arrangement for partner agencies that manage the Papahānaumokuākea Marine National Monument. Operational decisions are made at the level of the Monument Management Board (b), which is overseen by a higher-level Senior Executive Board (a) comprised of senior managers from each of the three co-trustee agencies. The Monument Management Board is comprised of members from seven different resource management agencies. Abbreviations are as follows: NOAA: National Oceanic and Atmospheric Administration; USFWS: US Fish and Wildlife Service; ONMS: Office of National Marine Sanctuaries; NMFS: National Marine Fisheries Service; Div.: Division; NWRS = National Wildlife Refuge System (administers the Hawaiian and Pacific Islands NWR Complex, which includes Papahānaumokuākea Marine National Monument).

nominating the area for inscription as a UNESCO world heritage site. Each of these co-trustee initiatives required the agencies to break new ground in formulating policy and decision-making processes, and the monument management plan was particularly illustrative of the challenges that the co-trustee agencies were required to confront. The objective of the monument management plan is to coordinate a comprehensive management regime for cooperative stewardship of the monument. This required both cooperative co-trustee management of areas with joint or adjacent jurisdiction as well as specific agency responsibilities required by institutional policy or statutory mandates. To accomplish this, the monument management plan contains 22 action plans with specific strategies and activities to address six priority management needs.

3. Methods

We conducted in-depth, structured interviews with 23 natural resource managers from March–May 2009. Each interview was conducted in person and lasted 1–1.5 hours. Interviewees consisted of field staff, mid-level managers, lead representatives for agencies or subagencies (e.g., superintendents), and regional-level principals (Tables 1 and 2). Interviewees were from agencies on the Monument Management Board, related working groups, and institutional partnerships involved in management, planning, and research in the NWHI (Figure 2). Interviews followed accepted social science research methods and techniques [54, 55], and the confidentiality of participants' responses was protected. Our interview instrument consisted of a series of questions targeting specific aspects of the multi-agency management structure for the monument; these topical categories included (1) interagency processes and institutional co-trusteeship, (2) barriers and solutions to multiple agency management, (3) learning processes, (4) path dependencies, and (5) power dynamics.

Interviews were analyzed using a grounded theory approach [56, 57], which relies on an inductive analysis process that allows the researcher to develop theory on the research topics addressed while simultaneously grounding the results in empirical observations or data [58–60]. Interviews were audio recorded and professionally transcribed and, together with notes taken during the interviews, responses were coded into conceptual categories. A comparative analysis was performed between the conceptual categories for each series of questions and the descriptive respondent data (i.e., agency affiliation, hierarchical position, and management tenure) to identify potential relationships between respondents' position and experience within their agencies and their perceptions of multiple-agency management. In addition to interviews, we conducted a comprehensive review and synthesis of secondary sources, including published reports, government publications, and policy documents.

Table 1: Summary of interviews by agency division for 23 natural resource managers involved in the management and planning of the Papahānaumokuākea Marine National Monument. Abbreviations are as follows: NOAA: National Oceanic and Atmospheric Administration; USFWS: U.S. Fish and Wildlife Service; NOS: National Ocean Service; NMFS: National Marine Fisheries Service; WPRFMC: Western Pacific Regional Fishery Management Council; Div.: Division.

Institutional Co-Trustee	Agency Division	Interviews
State of Hawai‘i	Div. of Aquatic Resources	4
	Div. of Forest & Wildlife	1
NOAA	NOS Monument	6
	NMFS Pacific Region	4
	WPRFMC	1
USFWS	Pacific Island Refuges	4
	Ecological Services	2
Office of Hawaiian Affairs		1
Total:		*23*

Table 2: Summary of interviews by hierarchical position rank for 23 natural resource managers involved in the management and planning of the Papahānaumokuākea Marine National Monument. The average tenure (years involved in management and planning in the NWHI) of interviewees was 6.98 years (median = 5 years).

Hierarchal level	Interviews
Regional or higher	2
Lead agency representative*	6
Manager	10
Staff & field	5
Total:	*23*

*Representative that acts as a lead for their agency or subagency in the MMB forum (e.g., superintendent).

4. Results

Interviews were conducted with managers representing all of the agencies involved in the planning and management of the monument and with individuals representing different hierarchies of decision-making authority (Tables 1 and 2). Interviews postdated the monument designation by ~2.5 years and generally focused on the period immediately prior to and after monument designation; occasionally respondents discussed longer histories of management and agency involvement in the NWHI for context. Generally, the number of interviews per agency and position hierarchy reflected the institutional capacity (number of dedicated managers) in each agency and at each decision-making level (Tables 1 and 2). Interviewees averaged 6.98 years of experience in managing or studying ecosystems in the NWHI (median = 5 years), with a range from <1 to 30 years of experience among interviewees. Generally, coded responses *were not* associated with agency affiliation, tenure, or hierarchical position. As such, responses were grouped and major trends in responses and conceptual themes are presented below with respect to the primary topics addressed in interviews, including interagency processes, barriers to multiple-agency management, institutional learning, power dynamics and solutions.

4.1. Interagency Processes and Institutional Co-Trusteeship. Respondents provided information on inter-agency processes and relationships between partner agencies through a series of survey questions focused on agency relationships, management roles, dynamics of the Monument Management Board (MMB) (Figure 2), and perceptions of successes and failures of multiple-agency initiatives (Table 3). The principal challenge to the relationship between co-trustee agencies, as identified by 65% of respondents, was in the delineation of roles and responsibilities of each agency (Box 1(a)–(c)). The second and third most commonly identified challenges were the differences between agencies' cultures, personalities, and visions (Box 1(d)) and disagreements about jurisdiction.

When asked about their perceived role in the management of the monument, unsurprisingly the majority of interviewees stated that their role was to fulfill their own agency's objectives; however, interviewees also recognized their role in collaborating with other agencies (Table 3). Respondents also mentioned that the designation increased their jurisdiction, provided their agency with a clearer role in resource management within the monument, and expressed their desire to "do what's best for the monument" and "conserve resources for future generations."

The maturation or evolution of the monument designation process was a recurring theme throughout the interviews, with many of the respondents recognizing the infancy of both the MMB and the planning process in general. When asked to comment on the dynamics of the MMB, respondents felt that the Board lacked sufficient leadership and was further hindered by differences in agency's cultures, personalities, and interpersonal relationships (Box 2(a)–(d)). Comments on leadership and the MMB were primarily focused on turmoil that occurred prior to the formalization of decision-making processes for the MMB and related working groups.

There was considerable agreement among respondents as to the successes and failures of the monument designation process. A total of 57% and 35% of respondents respectively identified the completion of the monument management plan and the UNESCO World Heritage application as successful outcomes of the process, with 17% noting improved

(a) “If you were to put it on a scale of 1 to 10, I’d still put (the) relationship. . .somewhere in the middle: 5, 6?... I can tell you, some of that comes from. . .unequal starting points, both organizationally and statutorily. . . . With the overall. . . theme that we (want to) be coequal. Yet, there’s truth in the fact that we’re not.”

(b) “As soon as we became a monument, people started drawing lines in the sand. . . . It was really interesting. . .because our cultures are so different, across NOAA (National Oceanic and Atmospheric Administration) and (the U.S.) Fish and Wildlife Services in particular, that it began a whole new way of engaging and trying to speak... trying to communicate with different languages.”

(c) “When the monument was first designated, people made a concerted effort to really foster a team environment and I would say that since then it (has) disintegrated, and we’ve gone back to each entity being very territorial.”

(d) “I think that there is kind of the day-to-day staff operation relationship, and then there’s the kind of upper level superintendent type relationship, and I think those are very different. I think that the superintendent type relationship is strained, and then at the staff level, I think my impression is its pretty good.”

Box 1: Co-trustee relations.

Table 3: Inter-agency processes: interviewee responses by conceptual category (a)–(d). Numbers in parentheses indicate number of responses from a total pool of 23 respondents.

(A) Co-trustees relationships and monument designation
Negative perceptions
(1) Challenge delineating roles and responsibilities (i.e., mandates, statutes, and jurisdiction) (15)
(2) Different agency cultures (i.e., personalities, perceptions, visions) (4)
(3) U.S. Fish and Wildlife Service jurisdiction challenged (3)
Positive perceptions
(4) Continued collaboration between agencies (3)
(B) Respondents’ perception of agency role in the management of the monument
(1) Fulfill our agency’s objectives (12)
(2) Collaborate with partners (4)
(3) Clearer roles and delineated responsibilities/ Expanded jurisdictions/resource caretaker (2/2/2)
(C) Dynamics of the Monument Management Board
Negative perceptions
(1) Agency cultures, personalities, and interpersonal relationships/Lack of leadership (8/8)
(2) Unclear roles and responsibilities (6)
Positive perceptions
(3) Management Board is maturing (4)
(D) Inter-agency initiatives: Success stories and failures
Successes
(1) Management plan completed (13)
(2) World Heritage application completed (8)
(3) Joint permitting process/interpersonal relationship improved (4/4)
Failures
(4) Interpersonal relations and unprofessional behavior (6)
(5) Joint permitting process (4)

interpersonal relationships. Fewer numbers of respondents identified failures in the process; however, those of concern were strained interpersonal relations and displays of unprofessional behavior (Table 3). The joint permitting process, which enabled multiple-agency review of proposed activities, was viewed as a success by 17% of respondents, while an equal number of respondents stated that the permitting process still required considerable work and was a “messy” process.

4.2. Barriers to Multiple-Agency Management. A total of 83% of respondents identified institutional cultures and management styles as the primary barrier to successful multiple-agency management (Table 4). Interviewees perceived a lack of understanding and acknowledgement of different approaches to management, differences in terrestrial versus marine management styles, institutional rigidity, and different ways of communication among agencies (Box 3(a)–(g)). The second and third most commonly cited barriers were interpersonal relations (61%) (i.e., lack of trust, unprofessional behavior), and jurisdictional issues and legal authority (43%) (i.e., authoritative rigidity, interpretation of mandates, and unfamiliarity with regulations) (Box 3(f)–(k)).

When asked about persistent disagreements or sources of conflict affecting the process, respondents focused on many of the same concerns that surfaced in the previous question, namely legal and jurisdictional issues (57%) and interpersonal relations (26%); however, they also mentioned disagreements and disparities in funding and resources between agencies (26%). Though we didn not specifically target data on conflict intensity, examples provided by respondents indicated that conflicts exhibited a range of intensities, from inefficient transactions between partners to seriously disruptive interpersonal conflicts that resulted in breakdowns in partner agency relationships. When pressed further about persistent conflicts, respondents commonly commented on strained interpersonal relations and disruptive behavior (Box 3(g) and (h)) and cited the impact that managers’ personalities, leadership and management style can have on interagency collaborations and perceptions of success or failure. Other responses on sources of conflict are related to funding disparities, which mediated the inability

> (a) "We entered this process not knowing each other's agencies all that well. . . . And we rapidly learned that our agencies, even though we operate under some of (the) same laws and regulations that the other (agencies do), we interpret them very differently. So that set up some additional controversy to begin with, I think exacerbated by differences in personalities. . . . It's very difficult to sit through a meeting and be yelled and screamed at, to be very honest. And it has happened many, many, many times."
>
> (b) "There have been really good times when people really rolled up their sleeves and really worked. . .towards a common goal, and there have been times when I've had some of my coworkers. . .qualify some of the later meetings. . .as abusive and. . . a hostile work environment."
>
> (c) "Maybe it's a lot to ask of. . .that young (of) an organization. . .but it needed more leadership at all agency levels, between all the agencies involved. . . . And if we all take a look at the place and are guided by that, we can find ways within our agencies to. . .support what's going on here and to make the best decisions. And instead, it just seems a lot of times to kind of get mired in the more stereotypical government approach of being governed by the regulations as opposed to, you know, what you want to see in that area."
>
> (d) "We had to figure it out from the moment at which the proclamation went into effect with no guidance, and we had to start managing this place as well as write a management plan, develop a world heritage document. . .we had (to) invent the wheel as we are going along."

Box 2: Dynamics of the monument management board.

Table 4: Barriers to multiple-agency management: interviewee responses by conceptual category (e)–(h). Numbers in parentheses indicate number of responses from a total pool of 23 respondents.

(E) Primary barriers to the multiple-agency management of the monument
(1) Institutional culture and management styles (19)
(2) Interpersonal relations (14)
(3) Jurisdictional issues and legal authority (10)
(F) Inter-agency conflicts
(1) Legal and jurisdictional issues (13)
(2) Funding and resources/interpersonal relationships (6/6)
(G) Primary source or root cause of conflict
(1) Jurisdictional issues and legal mandates (12)
(2) Different agency cultures and approaches (11)
(3) Interpersonal relationships (9)
(4) Monument process and design (8)
(H) Institutional cultures and interagency relationships
(1) Approach to management (6)
(2) Disparities in funding and resources/Jurisdictional issues and mandates (2/2)

to fund adequate staff and to source transportation to access the NWHI.

Interviewers asked respondents to comment on their perceptions of the root causes of persistent conflicts, and again interviewees focused on jurisdictional issues and legal mandates, specifically misunderstandings derived from the lack of clear mandates (52%), differences in agency approaches (48%), and interpersonal relationships (39%) (Box 4(a)–(f)). A total of six respondents felt that management approaches were most directly impacted by differences in agency culture. Respondents cited specific differences between agency approaches, which included references to perceived and actual differences in the types of management activities, statutory requirements, and institutional cultures.

Table 5: Institutional learning: interviewee responses by conceptual category (i)–(k). Numbers in parentheses indicate number of responses from a total pool of 23 respondents.

(I) Mechanisms for interagency learning
(1) Interagency meetings (9)
(2) Collaboration (8)
(3) Evolution of process/communication (7/7)
(J) Evidence of learning outcomes
(1) Increased collaboration on documents and processes (11)
(2) Institutional maturation and processes/working relationships improved (7/7)
(3) Sensitivity and problem avoidance (6)
(K) Shifts in approach due to institutional learning
(1) Sensitivity and problem anticipation/evolution and maturation of the process (9/9)
(2) Collaboration and cooperation on management (8)

4.3. Institutional Learning. Interviewees were asked to indicate whether the monument designation process has resulted in co-trustee agencies learning about their partner agencies, to describe how learning was enabled, and provide examples of learning outcomes. Respondents cite four common processes or mechanisms where learning has occurred: interagency meetings (39%), collaborative initiatives (including workshops, retreats, and informal gatherings) (34%), evolution of the management process (30%), and communication (30%) (Table 5). Respondents viewed interagency meetings as opportunities to engage with the larger group, to plan together, and to learn about other agencies and their processes. Five respondents noted that the presence of deadlines served to increase collaboration between agencies, and seven interviewees cited improvements in both formal and informal communication throughout the monument management planning process. The replies of seven respondents spoke to the maturation of the process; specifically how

(a) “. . . the lack of understanding and acknowledgement of other agency’s mandates and other agency’s processes.”

(b) “I think that [the] primary barrier is that approaches on land are very different than approaches in the water and that people who have land holdings really look at the boundaries and the fences and say, “this is ours” and have a much more. . .rigid approach and are less willing to let go of how things have been done previously under that kind of jurisdiction than what happens in the ocean. . .”

(c) “. . .when people get wrapped up in their agency versus the place and look for reasons that their regulations or policies can restrict their abilities to work versus looking at the ways to creatively find ways to actually work together to do it. It’s very very frustrating.”

(d) “These. . ..natural resources are also cultural resources from a Hawaiian epistemology and cosmological point of view. Our history, our eldest ancestor out of darkness is the coral polyp. When you manage from that, and you manage with the 7 generational view, it’s very different to somebody managing with a 15-year management plan mind, even a single generation mindset, a budgetary 3-year cycle or “how long am I gonna be stationed here’ view.”

(e) “I guess, and this sounds weird, but I’d have to say traditional thinking. You know, there’s ways that agencies think. They develop a group think, and I’ve alluded to the fact that unless people are willing to kind of ease up, break out of the old mold and be a bit flexible, this thing can all come off the rails in a hurry.”

(f) “The other is simply personalities. I mean to make this work, it’s tremendously dependent on a set of personalities that can interact well together and trust each other. And we have had personality conflicts.”

(g) “. . .the individual personalities have played the largest role in the limited success and bigger failures of this whole process.”

(h) “They have very strong personalities and I think that that has actually been part of the issue of breakdowns and communication. I think they are all very good at fighting for their piece but have missed the picture that they should be fighting for the monument as a whole and not for their piece of the monument, and I think that has been a real breakdown.”

(i) “I don’t think there should be any barriers between interagency management. . . .people should be able to jointly manage these areas because the resources don’t have lines down them and you know, it’s pretty seamless when you’re out there. So, I just think whatever way your agency does stuff, whatever history you have, whatever beliefs you have, you’ve got a—you have an obligation as a resource manager to sit down at the table with everybody else and just jointly manage it. . . . I don’t understand why there were the problems. . . . The MMB heads are all high-level, highly skilled, highly trained people. They should be able to sit down at a table and figure it out.”

(j) “I think one is just a lack of clarity from the get-go of the jurisdictions. . .of the different agencies involved in this. (The boundaries were) unclear. . .as to who exactly was responsible for what.”

(k) “. . .that law says that all national wildlife refuges are closed to all users until specifically opened to a use. That’s different in Alaska because they have a different law, but for your purposes here in Hawaii, all those refugees were closed until opened, and we never opened the Hawaiian Islands National Wildlife Refuge or the Midway Atoll National Wildlife Refuge to commercial fishing.”

Box 3: Barriers to multiple-agency management.

(a) “There are still some core legal issues that we’re starting to work through that are causing points of conflict between you know, between NOAA (National Oceanic and Atmospheric Administration) and (the U.S.) Fish and Wildlife Service. Its wilderness and what wilderness means. It definitely means something to them and doesn’t mean anything to us.”

(b) “We would have less conflict if we could clearly articulate what our statutory authorities are.”

(c) “(A) lot of it had to do, I think, with the pressure of getting the management plan. We had pressure to get our jobs done, pressure to get the management plan done before the end of the year. We were under a [deadline]. . .in a forced time frame when there is so much confusion. . . emotions were high, stress level was high. . .. You know what, just get the management plan done. We focused on that, got the thing out.”

(d) “One is the interpersonal relationships or the personality conflicts at the ground level... I would say the interpersonal relationships were the number one.”

(e) “I think, we all are competing for limited resources.”

(f) “I still think it’s the corporate difference, the corporate culture difference and jurisdiction. . .that everything stems from those.”

Box 4: Root cause of conflicts.

as time progressed agencies recognized the importance of flexibility and realized the need for institutional change.

Interviewee responses provided evidence of learning, including (1) the collaboration of agencies on formal documents, including the monument management plan and the UNESCO World Heritage application, (2) improvements in working relationships and institutional processes, and (3) an increased attention to problem avoidance, coupled with an improved understanding and sensitivity to partner agencies' positions and objectives. Respondents indicated that evidence for learning was manifested as shifts in management approaches, decision-making processes, and problem solving techniques. Respondents cited a greater sensitivity to agency cultures and problem anticipation, noting that as time progressed issues were addressed up front, agency responses could be anticipated, and there was a heightened awareness to rules and protocols. Responses indicated that through collaboration, agencies gave greater consideration to each other's ideas and approaches, and some recognized the need to formalize the organizational structure of the monument to advance the process and clarify rules and responsibilities.

4.4. Inter-Agency Power Dynamics. Though the proclamation created a co-trusteeship that ostensibly provides each partner agency with equal authority, respondents indicated that power dynamics were unequal between the various agencies responsible for resource management within the NWHI. Respondents cited four instances in which disparities in funds and resources among partner agencies affected the management process, including (1) uneven distribution of power (39%), (2) the precedence ascribed to agency priorities and participation (17%), (3) access to transportation and logistical support (13%), and (4) impacts on working relationships (9%). Respondents perceived an uneven distribution of power and resources across the agencies, remarking that, while some agencies hold monetary power, others retain power in their jurisdiction over land and water resources. For example, the perception noted by several respondents is that NOAA holds increased power over USFWS and the State of Hawai'i in terms of funds, facilities, and staffing; however, the State and USFWS have a history in the NWHI and a jurisdictional presence that affords them a unique level of power and participation in management and planning processes (Box 5(a)–(e)). Respondents perceived discrepancies in funding as affecting the working relationships relationships between resource managers, as well as an agency's ability to participate in research and management projects, and to secure adequate transportation and access to the NWHI. Actualized power was reflected primarily in the extent to which a given agency had resources and how these resources were distributed among partner agencies (e.g., funds for specific initiatives, transportation to the NWHI). Additionally, actualized power was manifested in control over physical access points in the NWHI (e.g., Midway Atoll National Wildlife Refuge) and through legal mandates dictating specific processes (e.g., permitting or planning requirements) that affected the activities of partner agencies.

Table 6: Solutions for multiple-agency management: interviewee responses by conceptual category (L–N). Numbers in parentheses indicate number of responses from a total pool of 23 respondents.

(L) Effective strategies for integrating efforts in multiple-agency management
(1) Adopting formal processes and structures (14)
(2) Collaborative interagency initiatives (10)
(3) Common purpose/Involvement of higher-level management in decision making/Increased familiarity and education about other agencies (4/4/4)
(M) Mechanisms that trigger the development of new strategies and structures
(1) Conflict and disagreement/Recognition of problems and needs (7/7)
(2) Requirement, deadline, or mandate (4)
(3) Involvement of higher-level management (3)
(N) Mechanisms that diffuse new ideas and innovations through interagency organizations and relationships
(1) Formal processes (11)
(2) Informal processes (6)

4.5. Solutions for Multiple-Agency Management. Respondents identified several strategies that have been effective in facilitating multiple-agency management, including adopting formal processes and structures (61%) and interagency collaborative initiatives (43%) (Table 6). Additionally, a total of 17% of respondents recognized the involvement of higher-level management, the identification of a common purpose during planning processes and interagency interactions, and an increased familiarity and understanding of other agencies as effective techniques in the designation process.

The development of new strategies and structures was driven primarily by the recognition of a problem or need, as well as the presence of conflict or disagreement, and secondarily driven by the requirement of a deadline or mandate, or through the involvement of higher-level management. Respondents cite the diffusion of new ideas and innovations primarily by formal processes (i.e., working groups, MMB meetings) but also through informal mechanisms of communication, such as social gatherings, and through relationships between managers at partner agencies.

Throughout the survey respondents provided several suggestions for ways to improve multiple-agency management. When asked to describe broader solutions to co-management, respondents cited the importance of increased collaboration and agency flexibility (30%), the need for greater leadership (13%), and the need to equalize funding and resources across agencies (9%). Additional suggestions that surfaced throughout the survey include the need to clearly define agency roles and responsibilities, increased understanding of legislative mandates, the prioritization of resource allocation, the establishment of a single management body, improvement in interpersonal relationships among agency members, and an effective and streamlined public engagement procedure.

(a) “NOAA [National Oceanic and Atmospheric Administration] has tons of money, USFW (U.S. Fish & Wildlife Service) has less, and the State (of Hawai‘i) has very little, so naturally this effects who can do what and who put more resources into the NWHI management.”

(b) “Suddenly… sanctuaries get seven million dollars…so they’re in charge of you know, they have most of the money to implement things. But ironically, you know, once it did not become a sanctuary and it became a monument, the sanctuary program probably had the least amount of legal jurisdiction in comparison to say, (NOAA) Fisheries or (the U.S.) Fish and Wildlife Service. And so it created an awkward power dynamic, where you know, the person in control of most of the money wasn’t the one who necessarily had a lot of the other authorities.”

(c) “I think the issues of equality or the problems, they’re not equal in my opinion. Fish and Wildlife Service is...not the land owner but they have the land which is power. NOAA is water and has lots of money and resources. That’s power. The state of Hawai‘i, I think 90% of all the activities that occur in the monument are actually in state waters so maybe you could call that power, but they don’t have any staff. They have very little staff, and they have little to no resources especially given the past, you know, year.”

(d) “The power I think that the state has is the community…is the voice of the community much more so than the other agencies, and likewise OHA (Office of Hawaiian Affairs), and so everybody has shared power at different levels. NOAA’s power does not just come from the money either. They’re very visible and effective.”

(e) “When you have money for staff and resources and projects and boats and access, you’re gonna have inequitable power.”

Box 5: Power dynamics.

5. Discussion

The surprise designation of the NWHI as a marine national monument created a major change in the governance arrangement that initiated a management transition among partner agencies from a hierarchical and sectoral model to a polycentric governance system and institutional co-trusteeship. Polycentric institutions have been characterized as nested, quasiautonomous decision-making units that operate at multiple scales and nurture diversity for dynamic responses in the face of change and uncertainty [61]. It has been posited that complex, multilevel governance systems exhibit a diversity of responses and capabilities that contrast. with traditional centralized governance units and thus may possess an element of adaptability that may convey resilience to disturbances or crises (human and natural) [61–63].

In the NWHI, polycentric governance systems were first established through the creation of novel, multi-agency management structures and an agreement among agencies to work toward consensus in decision-making processes [53]. The Monument Management Board (MMB) served as the primary nexus for multiple-agency decision-making and was overseen by a higher-level Senior Executive Board, which was occasionally activated in the case of disagreements at the MMB level (Figure 2). Below the level of the MMB, working groups were formed to address specific management needs and networks of individuals at different agencies with related work descriptions worked collaboratively to facilitate collaborative management (e.g., agency permit coordinators). These polycentric, multi-agency management structures were formulated based on the need to move from a hierarchical, fragmented decision-making process towards more integrated processes, and the establishment of these governance structures required the agencies to break new ground in rule formulation, operating procedures, and protocols for decision-making.

We argue that the monument designation has resulted in some institutional transformations among partner agencies, but not all of these transformations have been adaptive. Transformability has been defined as the capacity to cross thresholds or transcend rigid pathways to provide an opportunity to develop along new trajectories [64]. By adaptive we mean changes in institutions that convey the capacity to adjust responses dynamically to changing external drivers and internal processes (Table 7). Adaptive responses convey advantages in allowing institutions to develop along new trajectories or pathways, whereas transformations are described more simply as abandoning more rigid, path-dependent approaches in favor of increased institutional flexibility. Adaptive responses by partner agencies seem to be limited to few collaborative initiatives and interagency processes, where institutional learning, accrued experience in the co-trusteeship arrangement, and new knowledge have resulted in the adjustment of agency approaches and decision-making systems as a response to both external drivers and internal dynamics. Adaptive responses include specific initiatives such as the joint permitting program, the multi-agency environmental impact review process, and the formalization of protocols governing the MMB, all of which required agencies to break new ground in rule formulation and adopt new decision-making pathways. Institutional learning processes, which we discuss below, appear to have provided the impetus for these adaptive responses. In contrast, institutional transformations have resulted in shifts in institutions toward more flexible approaches and sensitivity to partner agencies and appear to have occurred throughout the transition to co-trusteeship for the NWHI. Institutional transformations were most commonly manifested in institutions’ shifts in their approach to partner agencies, including increased sensitivity and awareness of partner agencies’ mandates, mission, and organizational cultures.

Table 7: Concepts and definitions in ecosystem-based management and institutional resilience.

Concept	Definitions and key criteria
Adaptive management	Managing institutions purposefully formulate policy as an uncontrolled, nonreplicated experiment, monitor the results of the strategy, and iteratively revise their approach in order to adapt to changing social and ecological conditions. *Key criteria*: multiple steps in a prescribed cycle of actions; monitoring results used in evaluation of policy or management actions; purposeful implementation
Organizational transformation	The abandonment of more rigid, path-dependent approaches in favor increased institutional flexibility as a purposeful response or as the result of internal dynamics or external drivers; transformations can result in the capacity of institutions to cross thresholds or transcend rigid pathways to provide an opportunity to develop along new trajectories. *Key criteria*: markers of increased institutional flexibility; Abandonment of previous protocols or procedures in favor of new methods or approaches
Adaptive transformation	Changes in institutions—initiated purposefully or not—that convey the capacity to adjust responses dynamically to changing external drivers and internal processes; adaptive responses convey advantages in allowing institutions to develop along new trajectories or pathways through adjustment of agency approaches and decision-making systems as a response to external drivers or internal dynamics. *Key criteria*: markers of increased institutional flexibility; new decision-making processes or structures adopted; Evidence that changes have conveyed an advantage in terms of institutional responses to internal dynamics or external disturbances

Institutional maturity and accrued experience in the co-trusteeship also appears to be a major determinant in whether responses result in transformations and whether these transformations are adaptive. Our analysis primarily focused on a retrospective view of the periods immediately prior to and after monument designation and thus can be considered a snapshot of an ongoing and dynamic process. The maturation of the co-trusteeship was reflected in the adoption of formal rules and protocols for decision-making processes by partner agencies, and transformations in individual agencies (e.g., shifts in approach toward partners, increased communication and sensitivity toward partners) also appear to evidence an evolving maturation process internal to individual agencies.

Below, our analysis focuses more fully on three specific topical areas germane to the monument designation and management transition. These include our assessment of the barriers to effective institutional co-trusteeship and the solutions employed to surmount these barriers. Next we discuss the role of institutional learning in institutional transformations and conclude with an assessment of the monument as a model for US MPAs.

5.1. Barriers and Solutions to Effective Institutional Co-Trusteeship. Our analysis reveals that the relationships between co-trustee agencies were complicated at the outset by several barriers that presented challenges to the partner agencies. Barriers to effective institutional co-trusteeship have been both formal and informal and were first confronted by managers in the partner agencies during the planning process for the monument, where multiple institutions and stakeholders worked to establish a common vision and goals and collaborate on strategies and interagency initiatives (e.g., the monument management plan).

Formal barriers include differing statutory responsibilities, jurisdictions, and legal regulatory challenges associated with integrating management legislative mandates (*legal regimes*) and decision-making hierarchies employed by the different managing agencies. Informal barriers, in contrast, include differences in agency formulation and implementation of policy, operations, interpretations of responsibilities, management activities, and permitting requirements (*regulatory approach*), and differences in agency philosophy, core ethics, institutional culture, and guiding principles (*management paradigms*).

Partner agencies were primarily able to confront and successfully resolve formal barriers that created contention for issues such as the creation of a joint permitting process, a multi-agency monument management plan, and other initiatives. Respondents viewed the completion of these multi-agency initiatives as evidence of successful collaboration among partner agencies (Table 3), despite citing persistent jurisdictional issues and differing legal mandates as a root cause for conflict (Table 4). These results suggest that interagency collaborations have largely been successful in resolving formal barriers. For example, significant resources were invested by legal teams from each of the partner agencies to agree on a joint permitting process, which resolved many of the outstanding issues among partner agencies on multi-agency review for proposed activities in the monument. This process required significant investment to satisfy the agencies myriad statutory responsibilities while creating a multi-agency review process for proposed activities in the monument. Attorneys from co-trustee agencies worked through jurisdictional and statutory requirements via interagency conference calls and meetings, and agencies worked toward an agreement on a common permit form and review procedure. Other, more informal mechanisms were

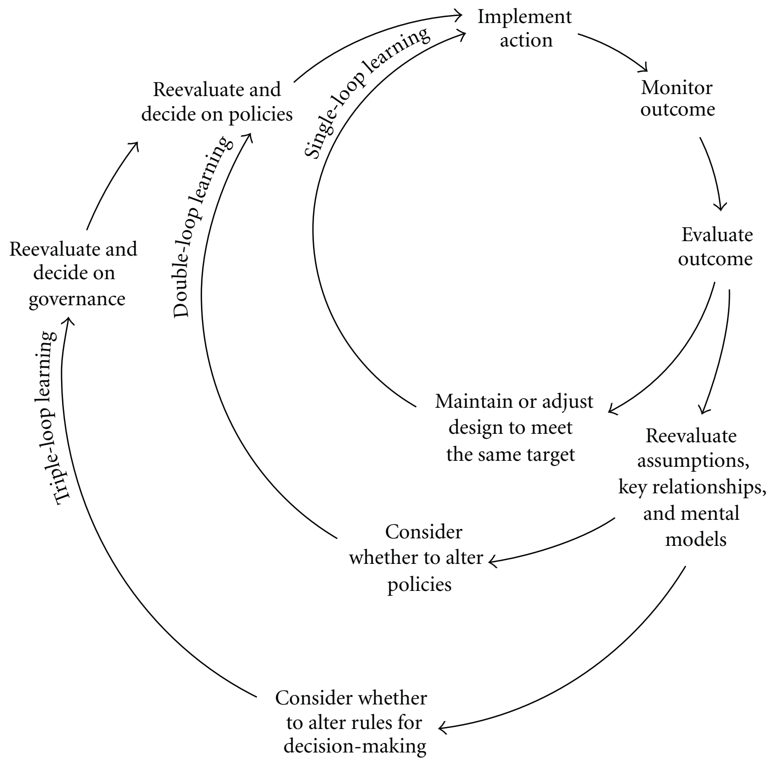

Figure 3: Different pathways and outcomes of institutional learning. Triple-loop learning involves the same re-evaluation of assumptions and models as double-loop learning but considers whether to alter rules for decision-making and fundamental changes in governance systems. Reprinted with permission from Folke et al. (2009:105) [38].

also employed by partner agencies to resolve or skirt formal barriers—for example, managers made a tacit agreement not to use the “j-word” (jurisdiction) in decision-making contexts.

Informal barriers have, however, proved to be more resistant to solutions. These barriers were identified by respondents as including differences in agency culture, interpersonal relationships, and approaches to management (Tables 3 and 4). Agency culture was defined variably by respondents as including the core ethic, management paradigms and approach by the differing co-trustee agencies, as well as the interpersonal relationships and “group think” that develop within institutions (Box 6). Respondents indicated that ideological clashes and interpersonal relationships originated in part due to differences in agency cultures and institutional rigidity, which occasionally caused breakdowns in interagency relationships. Differences in power among partner agencies, particularly in funding disparities also contributed (Boxes 3 and 4). Our results suggest that these informal barriers have been addressed primarily through learning processes and increased trust and social capital among agency managers, which over time caused agencies and managers to abandon more rigid approaches in favor of increased flexibility as they learned more about their partners.

5.2. The Role of Institutional Learning. Institutional learning has been defined as the “detection and correction of error [65]” through the “process of improving actions through better knowledge and understanding” [66]. Institutional learning provides an adaptive mechanism that informs how agencies respond to change, particularly in the face of crisis or surprise [38]. Adaptive institutional learning can take three forms, including (1) “single-loop” learning, in which institutions monitor and evaluate outcomes and maintain existing management approaches, (2) “double-loop” learning, where institutions re-evaluate their management actions or policies based on the recognition that change may be required, and (3) “triple-loop” learning, where institutions go beyond evaluating their approach and consider changes in existing rules for decision-making and governance models to meet management goals and objectives (Figure 3).

In this case study, institutional transformations appear to be the result of institutional learning processes. Adaptive responses were mediated by deeper learning processes, which in some cases caused institutions to alter their decision-making pathways and protocols and develop along new pathways in response to the co-trusteeship governance arrangement. Deeper learning processes include double and triple-loop learning, which can result in major changes in management approach and provide a mechanism by

(1) "Agency culture to me means "what's your core ethic?" "

(2) "By culture I mean. . .just the way agencies operate"

(3) "Culture differences (are) just in terms of how you approach issues"

(4) "A culture is nothing but a series of. . .relationships that manifest themselves. . .collectively, in a group of people. . . .I think you really have to take the time to get to know people."

(5) "What I'm kind of alluding to when I say agency culture (are different interpretations of) definitions. . .uses of these terms"

(6) ". . .you know we have our own culture. We have our own way of doing things. We have our own way of thinking"

Box 6: Respondents' definition of agency culture.

which institutions remain flexible and resilient to changing ecological and social conditions [38, 67–69]. In contrast, transformations can be negated or stymied by institutional path dependencies, or "lock-ins," that institutions develop through time and which constrain future choice sets [70, 71].

For the NWHI, respondents indicated that several mechanisms enabled learning opportunities, including interagency meetings and processes, collaborative initiatives, and formal and informal communications (Table 5). Successful completion of interagency collaborative initiatives (e.g., the monument management plan; UNESCO World Heritage application) was commonly cited as tangible evidence of learning outcomes. Learning outcomes were also manifested as shifts in approaches to interagency collaborations and greater sensitivity and anticipation to partner agencies in the management process (Table 5). Double- and triple-loop learning processes appear to have initiated adaptive transformations in at least three collaborative initiatives, where partner agencies made significant shifts in decision-making processes and developed along new pathways as a result of learning. These initiatives include the decision-making process for the MMB, which underwent formalization in protocols, meeting structure and leadership processes, and the multi-agency environmental impact review process. The joint permitting process for proposed activities in the NWHI was also significant in that it required agencies to formulate new decision-making patterns and processes. Respondents indicated that changes in these processes constituted major challenges to agencies, and changes as a result of these initiatives were beneficial to working relationships and other interagency collaborations (Table 5). These shifts in approach suggest that the institutional co-trusteeship has enabled transformative learning processes (double- or triple-loop learning), but evidence of persistent barriers also points to the interplay between learning processes that facilitate interaction and institutional path dependencies that give rise to conflict and tension.

Lock-ins or path dependencies seem to have structured early interactions among partner agencies in the planning process for the monument and were at least partly responsible for conflicts between partners. Path dependencies were reflected in respondents' descriptions of differences in the legal and statutory responsibilities underpinning their specific agency's role and objectives in the co-trusteeship as well as their approach to management and institutional culture. For example, partner agencies differed significantly in their approach to satisfying requirements of the National Environmental Policy Act, which requires US agencies to engage in an assessment of potential environmental impacts for management activities. Though each of the federal agencies and their divisions were beholden to the same statutory requirements, their approach to satisfying these requirements differed significantly and the process required major investment in collaborative meetings to agree on a common process and approach. As in the joint permitting process, agency attorneys and policy experts collaborated to resolve statutory responsibilities and agreed on a common process that fulfilled each of the co-trustees' requirements. Other path dependencies included differences among partner agencies in the definitions for core terms, differentiating between what constitutes "research" versus "management," and disparities in hierarchies of authority in collaborative decision-making processes. Generally, institutional learning processes served to mitigate conflict associated with path dependencies over time as institutions moved toward more flexible approaches, but experience with the co-trusteeship process and the natural maturation of agencies and the polycentric MMB forum also served to diminish conflict.

5.3. The Institutional Co-Trusteeship Model: Lessons Learned from the NWHI.

Promoting interagency coordination in managing the marine environment has been identified as a major need by two high-level reports on US ocean policy [72, 73], but it is largely unknown whether institutional collaboration leads demonstrably to improved environmental outcomes [74]. Institutional collaboration provides advantages in reconciling sectoral approaches into cohesive EBM approaches, but barriers to effective co-trusteeship may also negate comprehensive management and planning and the establishment of sustainable, adaptive governance structures [75, 76].

Adaptive management, whereby managing institutions formulate policy as an uncontrolled, nonreplicated experiment, monitor the results of the strategy, and iteratively revise their approach in order to adapt to changing social and ecological conditions [68, 77–79] (Table 7), is posited as a major component of EBM [17, 20]. Dietz et al. characterize the adaptive process as akin to a coevolutionary arms race, where a set of rules created for a particular set of social and ecological conditions can erode in the face of dynamic and shifting social, economic, and technological developments [75]. Learning in the adaptive management cycle provides a process by which institutions can retain transformability and remain flexible in the face of change [67]. Double- and triple-loop learning, in particular, may convey adaptability to institutions by providing the impetus for agencies to reevaluate their approach, including rules, regulations, and governance approaches. Alternatively, institutional rigidity and path dependencies can negate adaptive responses and give rise to conflict, entropy, or institutional collapse, which in turn can negatively affect ecosystem integrity and resilience.

Can adaptive management, however, be accomplished through institutional co-trusteeship? The multi-agency governance structure for the NWHI has resulted in increased complexity in management and planning processes, with resultant declines in efficiency. For example, agencies have devoted significant resources to reconciling legal and regulatory regimes, management approaches, and differing goals and objectives. Institutional co-trusteeship has also generated conflicts associated with power dynamics and other disparities, which contributed to inequality in relationships among partner agencies (e.g., funding disparities; control of access). Despite these persistent issues, barriers to successful institutional co-trusteeship have been surmounted by a portfolio of successful approaches—or transition strategies—employed by partner agencies. Formal barriers have been primarily resolved through interagency collaborations on specific rules or legal responsibilities, adopting formal processes and structures for decision-making, and informal agreements among managers to avoid issues of contention and work towards consensus. Informal barriers have been resolved by a number of mechanisms, including institutional learning and maturation in the co-trusteeship, which have strengthened partnerships through time and served to reduce conflict in partner agency interactions.

Our results suggest that adaptive management can be achieved through institutional co-trusteeship but that planning processes for similar multi-agency governance arrangements must seriously consider the formal and informal barriers that may exist between partner agencies prior to crafting governance arrangements. Ideally, formal barriers could be clearly identified via in-depth consultations with partner agencies beforehand (e.g., jurisdictional issues), and mechanisms could be explored to minimize potential sources of conflict or contention (e.g., funding disparities that may drive power dynamics). Interagency consultations on specific initiatives in the NWHI suggests that the existence of formal barriers and their associated path dependencies can often spur transformations in partner institutions toward more flexible approaches that minimize conflict associated with formal barriers. In some cases, deeper learning processes through close collaboration have resulted in adaptive responses from institutions (e.g., joint permitting, environmental impact assessment, MMB formalization).

Our results also suggest that multi-agency governance arrangements will be more adaptable if mechanisms are incorporated to allow for iterative evaluations of the efficacy of the governance arrangement, including the rules that structure working relationships and decision-making processes. Such mechanisms may be effective in maintaining flexibility in the relationships between partners and allow the institutions involved to iteratively recraft the way partners engage if current arrangements are not optimal.

Informal barriers, in contrast, have been more resistant to solutions but may be surmounted through processes that rarely receive much attention. These include (1) establishing common languages, goals, and objectives and a shared identity early in the process, (2) consciously enabling institutional learning processes that increase flexibility and sensitivity to partner agencies, (3) maturation of planning processes and establishment of formalized processes and frameworks for interagency collaboration, and (4) building social capital among managers that is developed through repetitive and reciprocal interactions that build trust. We suggest that identifying specific mechanisms by which these informal processes can be promoted (e.g., retreats, facilitated workshops) may be effective in surmounting informal barriers (e.g., agency cultures and path dependencies) and in fostering a high level of innovation in organizational cultures necessary to address cross-cutting and emerging issues in marine EBM.

Dramatic shifts in ecological or social conditions can give rise to periods of crisis or surprise during which institutions and the connections between them are most open to dramatic transformation [71, 80, 81]. The monument designation for the NWHI was itself a major surprise, and initiated institutional transformations as a novel governance system forced partner agencies to move towards polycentric management. It remains unclear, however, how these institutional transformations have translated into achieving ecological restoration goals or progress towards conservation objectives for the NWHI. The review process for proposed activities in the NWHI has benefited from the joint permitting process, but the primary activities that occur in the monument are still research, monitoring, restoration, species and asset management, and cultural activities that have little ecological impact. Though the partner agencies have successfully navigated the transition to institutional co-trusteeship, more tangible markers of successful management will be measured by how the agencies manage or respond to allochthonous threats such as climate change or marine debris accumulation as well as ecological restoration activities within the monument (e.g., rehabilitation of endangered and depleted species). For example, rapid or abrupt ecological shocks, such as a major coral bleaching event or disease outbreak, may elicit different institutional responses than longer-term and slower ecological changes [61]. Longer-term studies that link investigations of governance systems with specific management actions and ecological data will be necessary to more fully evaluate the efficacy of multi-agency collaboration as a model for US MPAs.

6. Conclusions

Governance systems or the sets of rules (formal and informal) that determine how human systems and institutions interact remain an integral component for the successful management of complex, linked social-ecological systems. Put more simply, the rules that structure human-environment interactions are critical determinants of both social and environmental outcomes [82]. Ocean governance is moving towards increased collaboration, and multiple-agency co-trusteeship is an emergent feature of larger MPAs and seascapes in the Pacific and beyond. Our results suggest that institutional co-trusteeship presents several barriers to effective planning and management and declines in efficiency, but institutional responses and increased maturity in the co-trusteeship have been successfully employed to reduce conflict and facilitate interagency interactions. The monument's multiple-agency governance structure has allowed for a unique examination of how partner agencies have reacted to collaborative governance and institutional co-trusteeship, which remains a central problem and focus in ocean and coastal management [83–85]. As one respondent put it, "We need to break down the barriers [between] county, state and federal. We need to break down the barriers between this department and that department…taxpayers and the general public…have an expectation that government works together." The institutional co-trusteeship created for the NWHI remains a unique model in US marine conservation, and new US marine national monuments and other existing and proposed MPAs in the Pacific have similarly unique governance structures that require institutional collaboration. Understanding the multiscale social processes that influence collaborative governance arrangements in MPAs is critical in determining the successful pathways to EBM.

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Research Article

Effects of Land-Use Change on Characteristics and Dynamics of Watershed Discharges in Babeldaob, Palau, Micronesia

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This study assessed the impacts of differing levels of land development in four watersheds in Palau on river sediment yield and on sedimentation and turbidity. Area corrected sediment yield was strongly related to land development ($r^2 = 0.96$, $P = 0.02$), varying from 9.7 to 216 tons km^{-2} yr^{-1} between the least and most developed watershed. Mean sedimentation rates on reefs ranged from 0.7 to 46 mg cm^{-2} d^{-1}, and mean turbidity ranged from 9 to 139 mg l^{-1}. The higher values exceeded those known to harm corals. Because Palau's watersheds and estuaries are small, river floods were short-lived (typically lasting less than a day) and the estuaries adjusted just as quickly to a number of different estuarine circulation patterns that, in turn, generated a large variability in the export of riverine fine sediment to the reefs. The ultimate fate of the fine sediment deposited on the reefs depended on wind resuspension, local currents, and geomorphology (whether the bay was open or semi-enclosed). Palau's small estuaries were generally not as effective as bigger estuaries in trapping sediments and thus at sheltering the reefs. Therefore, greater efforts are needed to control and mitigate land activities that contribute to the increase in sediment yield.

1. Introduction

Coral reef ecosystems include some of the most diverse biological communities on earth, and like other ecosystems, are being lost due to anthropogenic disturbance. Approximately 20% of the world's coral reefs are already severely degraded, with another 24% under imminent risk and 26% expected to be lost within the next several decades [1]. Documented losses include taxonomic diversity, genetic diversity, elements of ecosystem structure and function, resilience to disturbance and ecosystem services. The major human-induced stressors affecting coral reefs include exploitation of resources (including overharvesting of herbivorous fishes that control algal populations), global climate change responsible for mass-bleaching events and ocean acidification, and land-based sources of pollution tied to increased levels of erosion and sedimentation from the modification of adjacent watersheds.

Sedimentation of coastal environments is a major issue worldwide, with most of the increase attributed to land clearing for agriculture and other activities that disturb the land surface [2]. A worldwide analysis of high sediment areas shows that coral reefs are less likely to be found near areas with naturally high terrestrial runoff [3]. For those areas that do have coral reefs, 22% of them face medium to high threats from increased sedimentation [4].

Numerous studies have documented the effects of sedimentation on local coral reefs at the community level [5, 6]. Declining coral cover [7–12], low coral density [11], low biodiversity [7–9, 12, 13], and reduced coral recruitment [11, 14–16] have been found on reefs exposed to sediment stress. Sedimentation combined with overfishing can hinder the

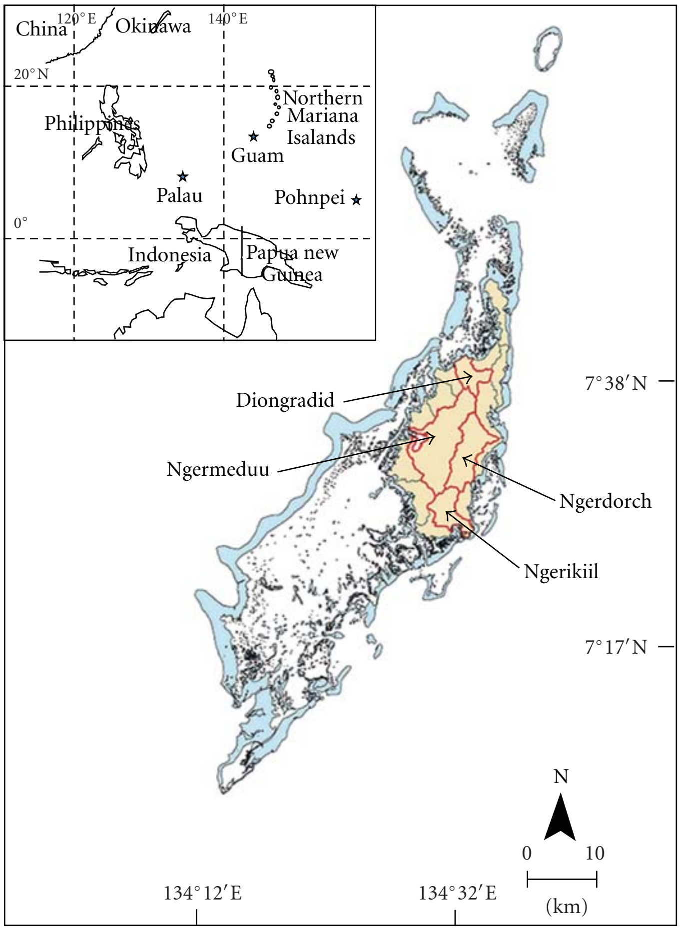


Figure 1: Map of region and Palau showing the four watersheds studied. Beige color indicate Babeldaob land area, blue indicates the reef area and the red lines mark the boundaries of the four watersheds studied.

recovery of coral reefs damaged by bleaching [17]. Fabricius et al. [18] documented species-specific mortality of coral reef organisms exposed to high sedimentation, and predicted that repeated sedimentation will lead to lower cover and diversity on reefs.

Recent studies have demonstrated that increases in sediment discharges from watersheds associated with poor land-use practices can impact reefs over 100 km from shore, and that ecosystem-based management efforts that integrate sustainable activities on land with maintaining the quality of coastal waters and benthic habitat conditions are critically needed if coral reefs are to persist [19]. Land-sea connections are well recognized within Pacific Island communities, and several of these cultures reflect this understanding through land ownership practices that incorporate the “ridge to reef” concept and the integration of sustainable activities and responsibilities. Many Pacific Island cultures maintain reef tenure systems, where village ownership extends from “ridge to reef”, with a clear understanding that upstream activities will impact downstream ecosystems including mangroves, seagrasses and coral reefs. These cultures demonstrate recognition of key elements of ecosystem-based management and even marine spatial planning that segregates incompatible activities through traditional restrictions on certain practices, the prohibition of harvesting particular species, and keeping certain areas closed or accessible only during limited periods to avoid harvesting during spawning events.

Micronesia is a region in the western Pacific made up of many small islands and island states, including Palau (Figure 1). While coral reefs in Micronesia are generally healthy and in good condition [20], most face threats from increasing sedimentation due to their close proximity to land, and the increasing activities and development within adjacent watersheds. Several studies in Micronesia have shown that an increase in sedimentation had severe consequences for the adjacent coral reefs [13, 19, 21–24]. These studies focused on single watersheds on Micronesian islands that have been degraded by human activities. What is lacking is the analysis and quantification of how varying levels of development in the different watersheds with similar soil types and rainfall affect adjacent coral reefs, and in turn, how these findings may be used to promote ecologically sustainable development in island states that have few other natural resources on which to rely.

Our study area is the island of Babeldaob in the Palau archipelago. Babeldaob has experienced major landscape

Table 1: Summary of physical parameters and sediment rates at the four watershed study sites.

Watershed	Size (km^2)	*Non forested area (km^2)	# of earthmoving permits (2000–2007)	Mean rainfall (mm $month^{-1}$)	River Flow Q ($m^3 s^{-1}$)	Sediment Flux (kg s^{-1})	Sediment Yield (tons $km^{-2} yr^{-1}$)	**Sedimentation rate (mg $cm^{-2} d^{-1}$)	Mean SSC on reef (mg l^{-1})	Peak SSC on reef (mg l^{-1})
Diongradid	20.6	1.3	20	231	5.7	0.03	49.2	1.1	9	636
Ngermeduu	86.3	9.1	55	292	18.4	0.59 (0.19)***	215.7	4.6	139	1,123
Ngerdorch	47.4	7.8	15	235	3.8	0.01	9.7	1.8	2	24
Ngerikiil	28.5	2.8	168	312	7.2	0.42	462.4	4.1	38	943

*Mike Aurelio, David Idip, Jr. and Tarita Holm provided the data on nonforested area. The data were digitized from Quick Bird satellite image of Babeldaob. It was digitized as a shapefile using Arc view. Later the data was converted into arcinfo coverage.

**Data are from the first reef station with the highest sedimentation rate closest to the river mouth.

***Number in parenthesis indicates the sediment flux of one river. This number was multiplied by 3 to get total sediment flux for this watershed. This was done because only one of the three rivers that drain into Ngermeduu Bay was gauged and we assumed that all three rivers have about the same sediment flux, since their catchment areas and degree of development were similar.

modifications over time, including extensive terracing and population growth, resulting in development and the overharvesting of resources [25]. The reefs in our study sites were not in pristine condition at the start of our study in the year 2006 because they had suffered from numerous anthropogenic and natural disturbances including an extensive bleaching event in 1998 [26, 27]. There is concern that today's rapid rate of development and extensive land clearing may lead to further degradation and eventual demise of reefs adjacent to Babeldaob.

To support and inform local land management initiatives, the aim of this study was to assess the impact of differing levels of development in the watersheds on sedimentation and health of adjacent coral reefs. In particular, this study provides answers to the following questions: (1) how can differences in land use and land development be quantified? (2) what is the explicit relationship between land development in the four watersheds and their river sediment fluxes? (3) what is the relationship between the river sediment fluxes in the four watersheds and the rates of sedimentation on coral reefs, based on local sediment dynamics? This paper also explains how the data from this and previous studies are being used by communities to guide development through activities that bridge science to management and policy in a culturally appropriate manner.

2. Materials and Methods

2.1. Study Sites. The volcanic Babeldaob Island in Palau (Figures 1 and 2) was our study area. It is the largest island in the Palau archipelago, with a total land area of 409 km^2. It is dominated by highly weathered and highly erodible tropical soils, some of which occur on steep slopes. The island is drained by numerous streams and rivers that flow either directly onto the fringing reefs surrounding the island or into the bays before flowing to the reefs. The most developed watersheds are on the southern part of the island, while farther north, the watersheds are less affected by human activities. Between the fringing reef and the barrier reef, patch reefs occur at varying distances from the mouths of the rivers. Four watersheds were selected for this study. Two of the watersheds (Ngerdorch and Ngerikiil) are located on the east coast, and the other two watersheds (Diongradid and Ngermeduu) are on the west coast. The soils in our study sites are volcanic in origin [28]. The degree of development varies among the different watersheds. Earth moving permits in the period from 2000 to 2007 were used to indicate the level of development in each of the four watersheds, as summarized in Table 1. The Ngerikiil watershed was the most developed watershed followed by Ngermeduu and Diongradid. Ngerdorch was the least developed, having the least amount of earth moving permits issued for activities in this watershed.

2.1.1. Diongradid Watershed and Bay. The Diongradid watershed, with an area of 20.6 km^2, is the smallest of the four watersheds in this study. Unpaved roads are an issue here as well as in the other three watersheds. There are also abandoned bauxite mining sites from the 1900s that still have little vegetation cover. Ninety-four percent of the area is forested while 6% is impacted by human development (Table 1). The Diongradid watershed drains into Diongradid Bay (Figure 2).

2.1.2. Ngermeduu Watershed and Bay. The Ngermeduu watershed is the biggest watershed in Babeldaob with an area of 86.3 km^2, containing several big farms and many unpaved roads. Eighty-nine percent of the Ngermeduu watershed is forested, while 11% of the area is nonforested (Table 1). Our study focused on the Ngermeskang River, one of the three rivers of the Ngermeduu watershed. These rivers drain into Ngermeduu Bay, which is an area of high marine biodiversity, with well-developed reefs near its mouth (Figure 2).

2.1.3. Ngerdorch Watershed and Bay. The Ngerdorch watershed has an area of 47.4 km^2(Figure 2). While Ngerdorch does not have the large-scale development found in Ngerikiil, there are unpaved roads and minor housing projects in the watershed. The watershed area is 84% forested, while 16% is not covered by forest (Table 1).

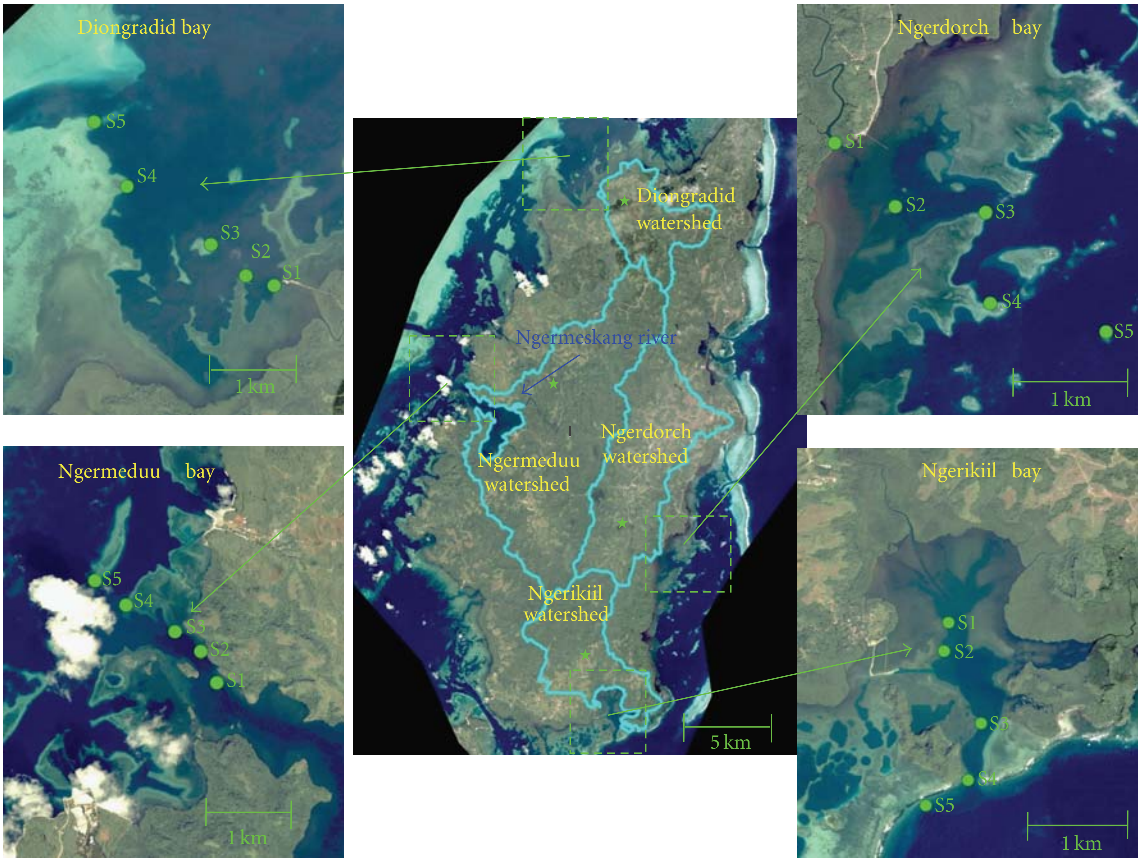


Figure 2: Aerial photograph of Babeldaob showing the four watersheds and a close-up of their adjacent bays with stations (S) marked. Stars indicate locations of level loggers along the river in each watershed.

2.1.4. Ngerikiil Watershed and Bay. The Ngerikiil watershed has an area of 28.5 km^2. It is the closest watershed to Koror, the main city in Palau, and is thus subject to the largest development pressure (Figure 2). Ninety percent of the area is vegetated, while 10% is heavily impacted by human development including many unpaved roads, urbanization, commercial and artisanal farms, and various land clearing activities (Table 1). The watershed is located in Airai State, bordered by Koror State, the commercial center for Palau.

The watershed delineations were provided by Palau Automated Land and Resource Information System. The data was digitized from USGS topographic maps. It was digitized as a shapefile following the contours of the USGS Topo map, using ArcView, and converted into coverage data using Arcinfo. The original line definition for the watershed shapes were created by the USDA Natural Resource Conservation Service along with official watershed identification numbers (codes). The Natural Resource Conservation Service delineates watershed boundaries based on United States federal guidelines [29]. The topography of Babeldaob, with little flatlands, allow for easy delineation of the watershed boundaries. Each watershed drains into a single bay, and any flows from adjacent watersheds would be very minor compared to those coming directly from the rivers in the watershed studied.

2.2. Rainfall. Daily rainfall data were collected using HOBO (Onset Computer Corporation, Massachusetts, USA) Weather Station Rain Gauges at the four watershed sites from April 2005 to August 2007.

2.3. River Sediment Flux. Water level loggers (Solinst Levelogger model 3001, Solinist Canada Ltd., Ontario, Canada) were placed in the rivers draining the four watersheds from December 2005 to February 2007 (Ngermeduu data are only available up to May 2006). The water level loggers recorded the water level every 10 minutes. For each of these four rivers, we measured water currents over the entire depth of the river cross-sectional area. Measurement were conducted at ten stages of discharge that ranged from very low flow to flood conditions. We thus obtained a rating curve to convert water level data into river discharge data. Similarly, a sediment-rating curve was obtained by measuring the suspended sediment discharge and relating it to flow and water level. Using both generated rating curves, we calculated the water flow and sediment discharge in each river at 10 minutes intervals throughout the study period.

2.4. Oceanographic Moorings. Oceanographic moorings were deployed at the four bays draining the watershed study sites (Figure 2). Within each of the bay, five reef stations were established along a perceived discharge gradient from the mouth of the rivers to offshore. YSI (YSI incorporated, Yellow Springs, Ohio) self-logging CTD-cum nephelometers were used to measure coastal turbidity (quantified as suspended solid concentration, SSC), temperature, and salinity. The YSI loggers were placed about 0.3 m above the bottom of the reef at a depth of 3 m. The YSI instruments had wipers that cleaned the sensors every 10 minutes and the data were logged every 10 minutes. A bottom-mounted Sontek (YSI Environmental Company, San Diego, California) ADP logger was used to measure currents every second and these readings were averaged over one minute at 10 minutes intervals. Data from the current meter could be rotated to show currents moving in different directions.

Data were collected over consecutive time periods from each of the four watersheds. At Diongradid Bay (Figure 2), SSC was measured at stations 1, 2, 4 and 5, salinity at stations 1 and 2, and currents at station 2, from June-July 2005. At Ngermeduu Bay, the SSC loggers were deployed at stations 1–4, salinity loggers at stations 1–3, and currents were measured at station 1, from December 2005 to January 2006. At Ngerdorch, the SSC and salinity loggers were deployed at stations 1–3, salinity only was recorded at station 4, and currents at station 1, from December 2006 to January 2007. For Ngerikiil Bay, SSC and salinity were measured at stations 1, 2, 3 and 4 and currents at station 4, while only salinity was recorded at station 5, from January through February 2007. The data were recorded at 10 minutes intervals.

2.5. CTD Casts. Vertical profiles of salinity, temperature and SSC were taken at each of the four sites. During flood events, and for 6–8 days afterwards, casts were made along transects moving from inshore to offshore at stations 1 through 5. The number of days during which vertical profiles were taken was based on how long it took the freshwater plume to clear the area. A YSI (YSI incorporated, Yellow Springs, Ohio) multiparameter probe attached to a YSI 650 Multiparameter Display System with a long field cable was used from a small boat to profile the sites at different depths to record salinity, temperature and SSC.

2.6. Sediment Traps. At each of the five reef stations, duplicate bottom-mounted sediment traps with 5.1 cm diameter openings were deployed. The traps were collected and replaced every month for one year. Sediment samples collected from the traps were dried, weighed to the nearest 0.1 mg using an A&D (A&D Company Limited, Tokyo, Japan) analytical semimicro balance (GR-120) to obtain total sedimentation rates (mg DW $\text{cm}^{-2}\,\text{d}^{-1}$), reweighed after treatment with 10% hydrochloric acid to remove carbonate to obtain the carbonate fraction, and then burned at 600°C for 2 hours to remove organic matter, to obtain the organic matter fraction. The remaining weight was used to estimate terrestrial (inorganic noncarbonate) sediments. The volcanic soils of the watersheds in Babeldaob contain insignificant amount of calcium carbonate [28].

2.7. Statistical Analyses. Because rainfall data did not meet the assumptions of normality, a Kruskal-Wallis analysis was used to test the differences in rainfall among the four watershed sites. A Kolmogorov-Smirnov Test was used to test the differences between sedimentation rates in watershed sites in Palau and Pohnpei. Linear regression models were used to determine the relationships between sediment yield and earth moving permits, and between the ranked locations of the stations and reef sedimentation rates. Statistical analyses were conducted with the statistical software, Statistica (StatSoft, Oklahoma, USA).

3. Results

3.1. Rainfall. There were no significant differences in rainfall among the four watersheds ($P = 0.69$, Kruskal-Wallis). The daily mean rainfall averaged 10 mm $\text{day}^{-1} \pm 0.8$ (SE) and the daily maximum was 148 mm day^{-1}. The monthly mean for the study period was 272 mm $\text{month}^{-1} \pm 27$ and the monthly maximum was 531 mm month^{-1}.

3.2. River Sediment Flux. All rivers showed episodic high flows (i.e., short-lived floods). The Diongradid River averaged sediment flux was 32.2 $\text{g}\,\text{s}^{-1} \pm 0.05$ (1014 tons yr^{-1}; Table 1). The Ngermeskang River had an average sediment flux of 196.8 $\text{g}\,\text{s}^{-1} \pm 2.5$ (6205 tons yr^{-1}). The Ngermeskang River is one of the three rivers that drain into Ngermeduu Bay; if all three rivers have about the same sediment flux (their catchment areas and degree of development are similar), the combined sediment flux from the Ngermeduu watershed would be about 590.3 $\text{g}\,\text{s}^{-1}$ (18615 tons yr^{-1}). The Ngerdorch River had the lowest average sediment flux among the gauged rivers at 14.6 $\text{g}\,\text{s}^{-1} \pm 0.02$ (460 tons yr^{-1}), while the Ngerikiil River had the highest average sediment flux at 417.9 $\text{g}\,\text{s}^{-1} \pm 0.59$ (13178 tons yr^{-1}). In terms of area-corrected sediment yield (sediment flux divided by watershed size), Ngerikiil had the highest and Ngerdorch had the lowest among the four watersheds (462.4 versus 9.7 tons $\text{km}^{-2}\,\text{yr}^{-1}$; Table 1). There was a strong positive relationship between the number of earth moving permits across the four watersheds and area-corrected sediment yield ($R^2 = 0.96$, $P = 0.02$). There were no significant relationships between the number of earth moving permits and sediment flux in the river ($r^2 = 0.007$, $P = 0.9$), coastal turbidity ($r^2 = 0.03$, $P = 0.8$), and sedimentation rate at the stations ($r^2 = 0.6$, $P = 0.2$).

Ngerikiil watershed is the most developed and had the highest average river sediment flux, while it had lower SSC than Ngermeduu and Ngerdorch and lower sedimentation rates than Ngedorch (Table 1). Ngermeduu watershed has the biggest nonforested area and had the highest coastal turbidity, while its sediment flux in the river was lower than in Ngerikiil, and its reef sedimentation rate was lower than Ngerdorch and Ngerikiil. Diongradid was the least developed and had the smallest nonforested area. It also had the lowest sediment flux in the river, the lowest coastal turbidity and the lowest reef sedimentation rate compared to the rest of the watersheds. The results show that the measure "nonforested area" (which includes areas with substantial vegetation cover that produce less sediment than areas under construction) is insufficient to predict coastal turbidity and reef sedimentation rates.

3.3. Tides and Currents. The tides were similar at the four sites, and were semidiurnal with a conspicuous diurnal inequality. The tidal range was about 2 m during spring tides and 1 m during neap tides at the four reef sites.

The currents at Diongradid (station 3) did not show strong spring-neap fluctuations and were variable, similar to those at Ngerdorch. Both the currents moving in the southeasterly-northwesterly directions from land toward the ocean, and a longshore current in the southwesterly-northeastly direction fluctuated around 0.06 m s^{-1}.

The currents at Ngermeduu Bay (station 1) were strongly tidal, semidiurnal with a strong spring-neap tidal fluctuation. There are two entrances to Ngermeduu Bay (Figures 1 and 2); the narrower but deeper northwest entrance and the shallower but wider southwest entrance. Flood tidal currents through the northwest channel peaked at 0.17 m s^{-1} during spring tides and 0.08 m s^{-1} during neap tides. Flood tidal currents through the southwest channel were larger, peaking at 0.30 m s^{-1} during spring tides and 0.13 m s^{-1} during neap tides. The outflowing current was similar for both channels, peaking at 0.2 m s^{-1}.

The currents at Ngerdorch Bay (station 1) flowed predominately toward the east and south, and were not strictly tidal, nor did they show strong spring-neap tide fluctuations. The freshwater plumes coming out of the estuary as well as the predominant winds from the northeast had strong influences on the tides, especially near the ocean surface. The maximum near-surface currents moving out of the estuary toward the east reached 0.1 m s^{-1}, while the incoming current peaked at 0.07 m s^{-1}. There was also a north-south current near the surface with the current going north peaking at 0.08 m s^{-1}, while the southern current peaked at 0.06 m s^{-1}.

The currents at Ngerikiil Bay (station 4) were mainly semidiurnal tidal, with strong spring-neap tide fluctuations. The outflowing current peaked at 0.5 m s^{-1} while the inflowing current reached 0.7 m s^{-1}. Station 4 was the narrow channel leading into the bay so the currents were faster there than inside the bay. There was a pronounced vertical shear in currents moving in and out of the channel with larger currents near the surface than the bottom of the channel due to friction slowing the water closest to the bottom. Inshore from station 4, during river floods, the freshwater plumes flowed over the bay as a near surface outflow. This effect extended to site 4 only during large river floods. Closer to the mouth of the bay, the freshwater inflow was more apparent at neap tides than at spring tides when strong currents favored vertical mixing. During flood events around neap tides, the surface currents took longer than the bottom currents to turn from an outgoing tide to incoming tide, therefore, the surface and bottom currents were out of phase. This difference between phases of the surface and bottom currents was not observed during spring tides.

3.4. Suspended Solid Concentration (SSC) as a Measure of Coastal Turbidity. At Diongradid, SSC at station 1 peaked at 636 mg l^{-1} and averaged 9 mg l^{-1} ± 0.4 (Figure 3(a)). At stations 2 and 5, the SSC maximum only reached 34 mg l^{-1} and 15 mg l^{-1}, respectively. Station 5 was exposed to strong winds and waves, hence many of the SSC spikes were due to sediment resuspension rather than floods.

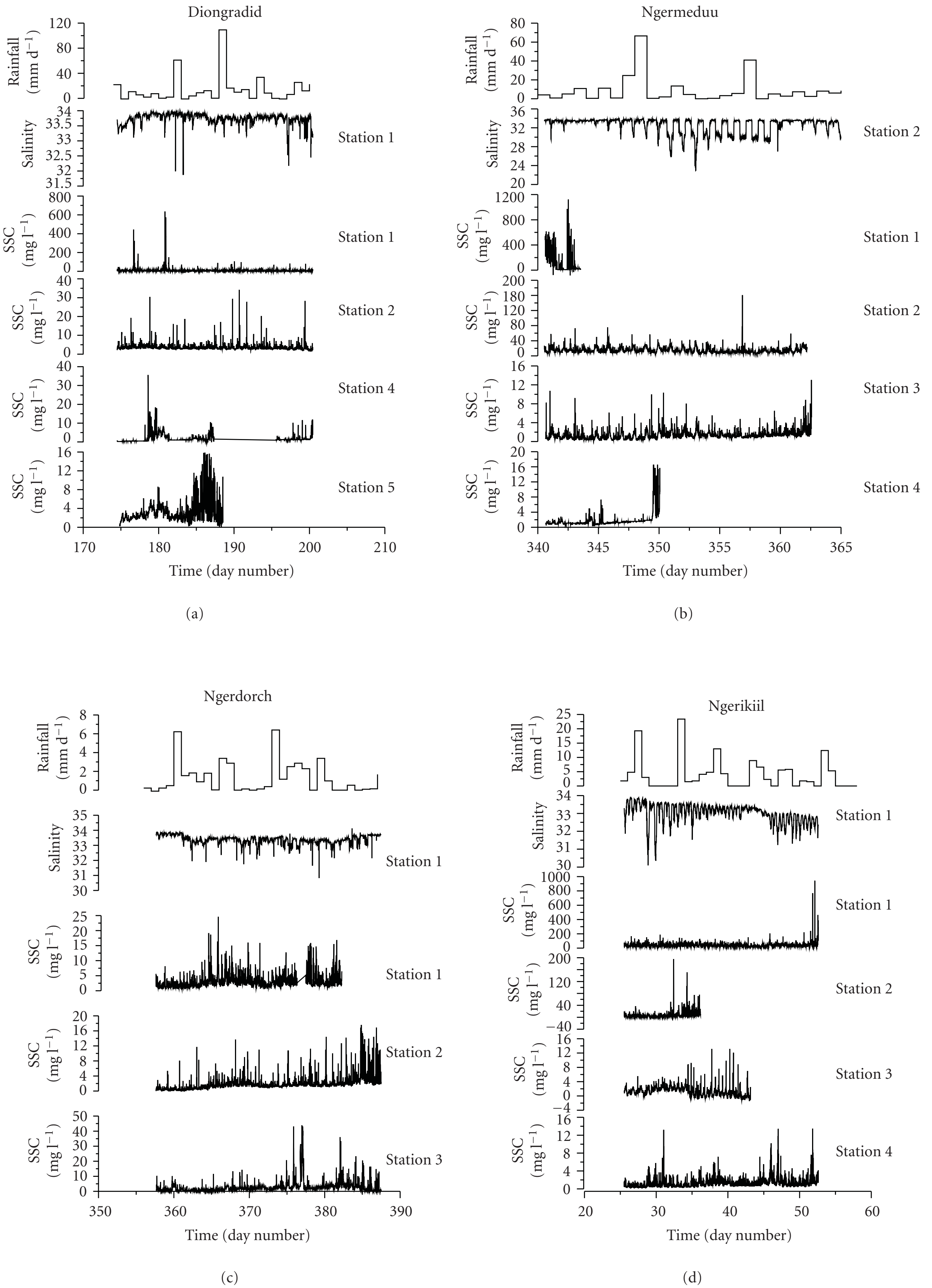
At Ngermeduu, station 1 had the highest SSC of all the sites, with maximum values exceeding 1000 mg l^{-1}, and high turbidity also outside of flood events at 20–40 mg l^{-1} (Figure 3(b)). At station 2, maximum SSC reached 160 mg l^{-1} with the average SSC at 14 mg l^{-1} ± 0.1. Station 3 and 4 had maximum SSC values at 13 and 16 mg l^{-1} respectively, and both stations had SSCs of less than 3 mg l^{-1} outside of flood events.

At Ngerdorch, SSC was highest at station 1, exceeding 1,000 mg l^{-1} (Figure 3(c)). Outside of flood events, station 1 also had high turbidity ranging from 40–60 mg l^{-1}. At station 2, turbidity was much lower, with a maximum of 24 mg l^{-1} during flood events and 0–3 mg l^{-1} outside of flood events. At station 3, the maximum SSC was 43 mg l^{-1}, with spikes both from flood events and resuspension due to strong winds in these open waters.

At Ngerikiil, SSC was highly variable depending on the sites and tidal cycle. At station 1, SSC averaged 38 mg l^{-1} ± 0.5 while the maximum exceeded 900 mg l^{-1} (Figure 3(d)). SSC decreased from station 2 to station 4 (means: 6.4 versus 1.1 mg l^{-1}, maxima 195 versus 13.4 mg l^{-1}). During a falling tide, the SSC was higher than during a rising tide, with spikes in SSC occurring during low tides. The high SSC spikes resulted from river runoff, as evidenced by the drop in salinity during the rise in SSC.

3.5. CTD Casts. At Diongradid, there was inflow of turbid water with high SSC at station 1 on 3 July 2006 (Figure 4). On the next day, the plume, as indicated by lower salinity, was still present but the suspended sediments had disappeared. Unlike observations made at the other sites, the sediments at Diongradid rapidly settled to the bottom and were not resuspended. On 5-6 July, the plume decreased in size. On 7 July, there was a smaller flood than the one on the 3 July. The flood brought in new sediments that dropped out of suspension as the plume moved seaward.

At Ngermeduu, a river plume was evidenced by the upward slope of the temperature and salinity contour lines on 15 December 2005 (Figure 5). The plume upstream was touching the bottom; and on reaching deeper water it lifted off the bottom (lift-off point). The SSC contours followed the same pattern. SSC values were small (10 mg l^{-1}) underneath the plume in offshore waters. A turbidity maximum existed at the plume lift-off point. The next day, temperature showed minimal stratification, suggesting strong tidal mixing. Salinity had increased but the plume was still active since the isohalines were sloping upward offshore. The SSC contour lines also sloped upward offshore. The SSC values were smaller than those of the previous day; therefore the peak of the sediment flux had passed. On 17 December, the 3rd day of the river plume, cold oceanic water was moving in under the plume. The isohalines were horizontal, indicating that the lift-off point had moved landward into the bay. The sediments were dropping out of the plume but they



(a)

(b)

(c)

(d)

Figure 3: Time-series plot of rainfall, salinity and SSC at (a) Diongradid bay, (b) Ngermeduu bay, (c) Ngerdorch bay, (d) Ngerikiil bay.

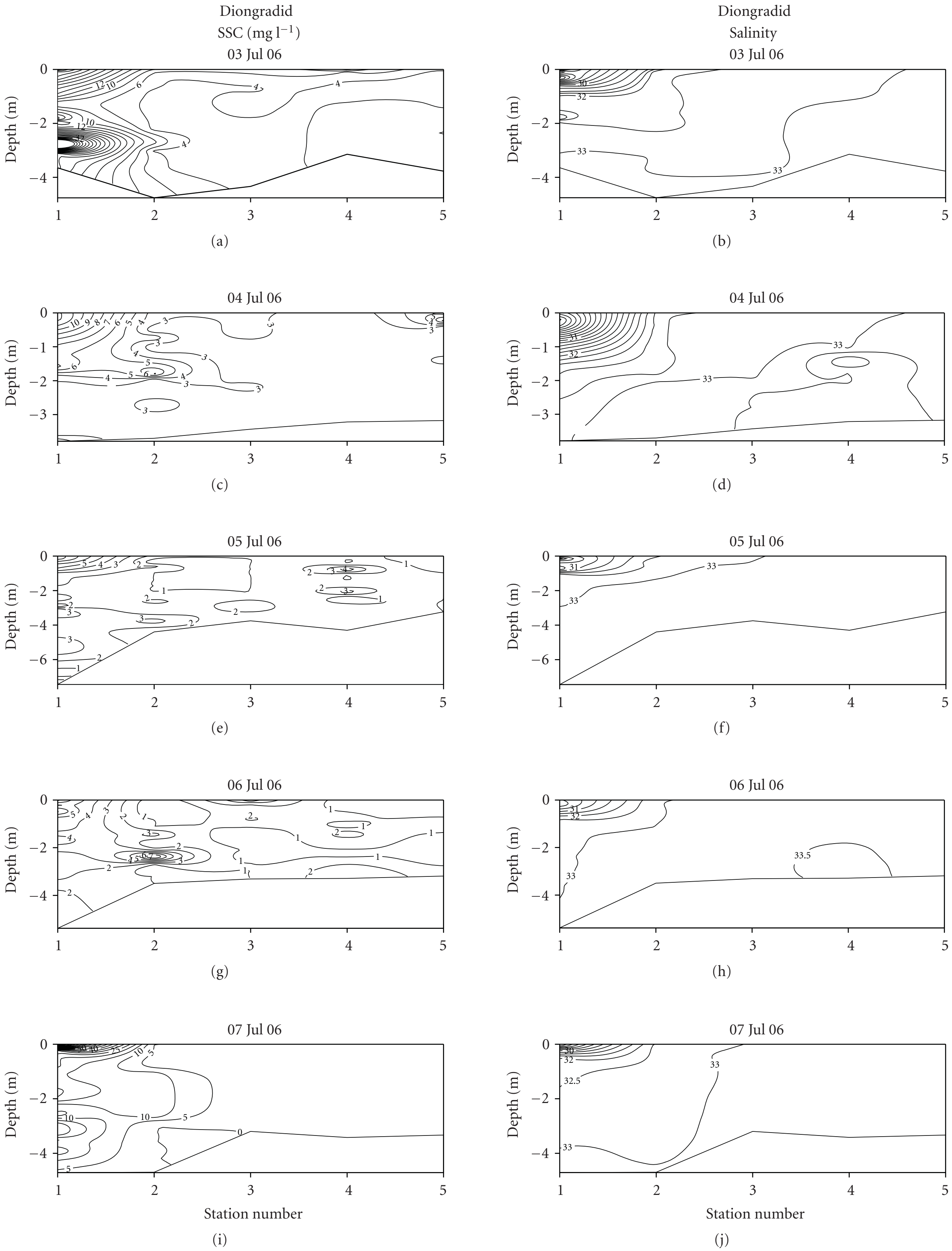
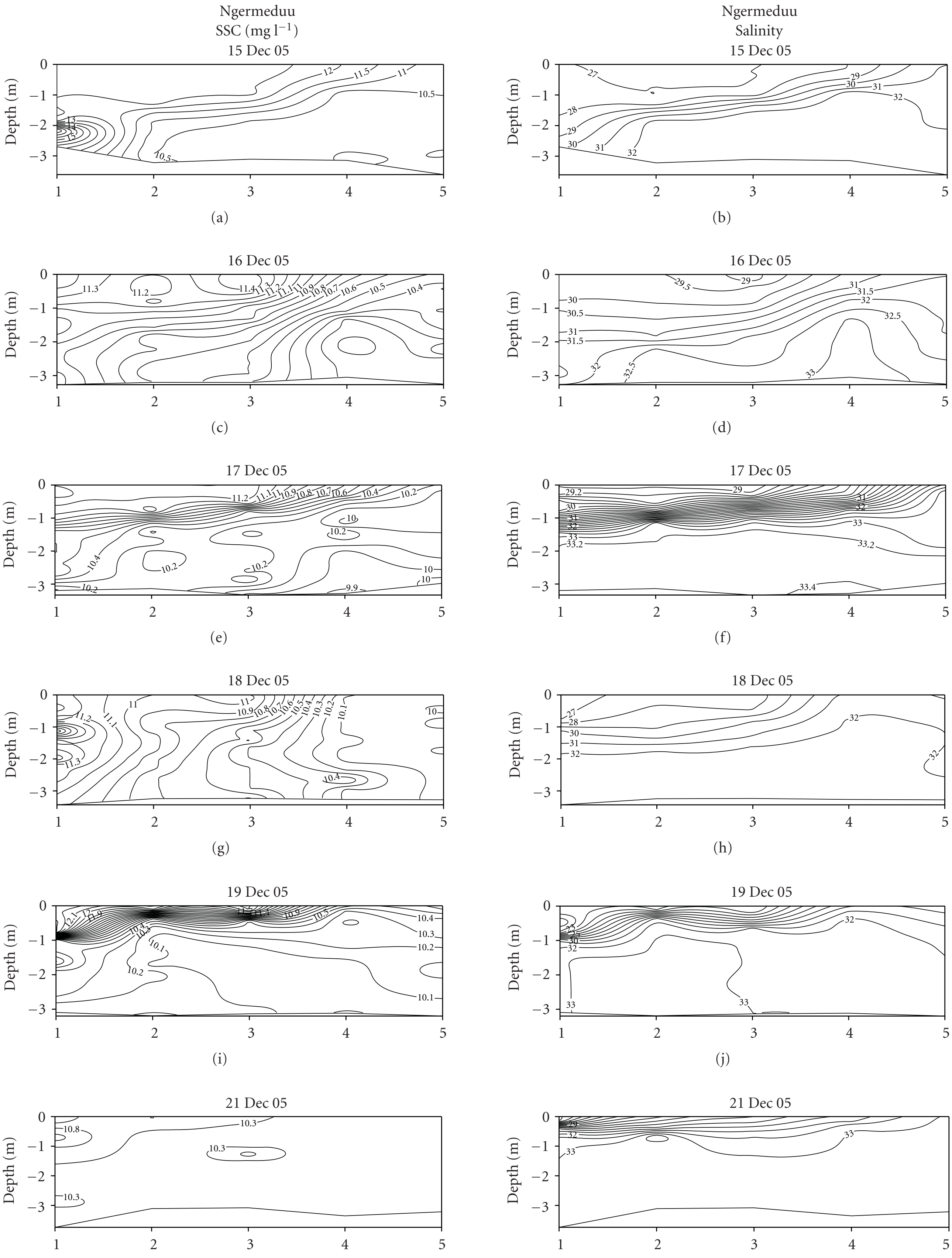


Figure 4: Snapshots at daily intervals of the two-dimensional distribution along the channel of salinity and SSC at Diongradid from CTD casts. The bottom line indicates the sea floor.



(a) (b)

(c) (d)

(e) (f)

(g) (h)

(i) (j)

(k) (l)

Figure 5: Continued.

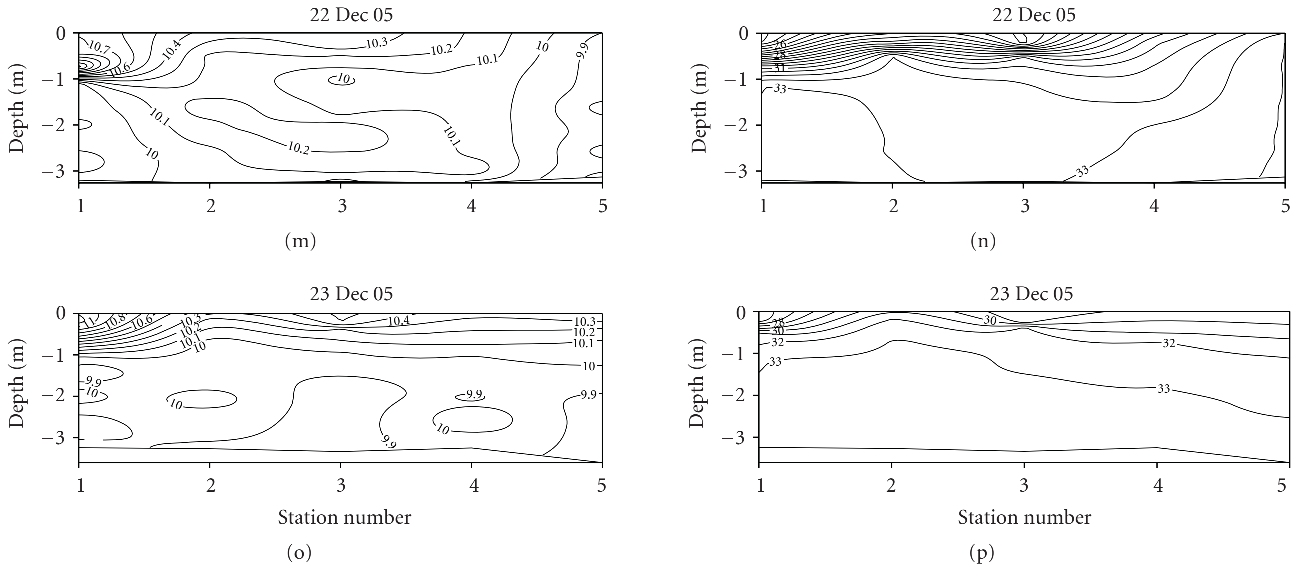


Figure 5: Snapshots at daily intervals of the two-dimensional distribution along the channel of salinity and SSC at Ngermeduu from CTD casts. The bottom line indicates the sea floor.

were being advected back toward the river mouth by the bottom intrusion of seawater, as indicated by the SSC profile (Figure 5). On the 4th day, the system had recovered. On 19 December, the river flooded again but the flood was smaller since the plume lift-off point was located upstream from station 1. From 20–23 December, the surface plume remained but the sediments had largely dropped out.

At Ngerdorch, there was an inflow of cooler, turbid river water at station 1, which was situated right next to the mangroves, on 9 January 2007 (Figure 6). The highest SSC values (280 mg/l) were recorded at this site. The freshwater plume barely reached site 2 since the fine sediments had already settled out of the plume. The system recovered slowly at station 1, as evidenced by the increase in salinity while the SSC remained high until 18 January. Farther offshore, seawater moved in while SSC decreased. On 19 January, river inflow increased slightly and a new river plume formed. From 21–23 January, there was another flood and a new plume formed. The plume remained on the surface while sediments dropped out.

At Ngerikiil, after a flood event, there was an abnormal temperature stratification due to the intrusion of cooler water as a river plume on 29 January 2007 (Figure 7). The SSC was largest ($182\,\mathrm{mg\,l^{-1}}$) at the plume lift-off point during the river flood. One day later, after the peak of the flood had subsided, the abnormal temperature stratification remained and the freshwater plume was still present, but was less sharply delineated. Sediments were dropping out of suspension as the plume was moving out of the bay so by the time the plume passed station 3, most of the sediments had dropped out. By the third day, the temperature stratification was negligible, the salinity plume was passively floating on top of ambient water, as evidenced by the nearly horizontal salinity contours, indicating negligible river inflow. Sediments were settling out throughout the bay. On the fourth day, water temperature was well mixed throughout, the plume was passive, and SSC was low throughout the bay. Sediment was accumulating at the bottom near the plume lift-off point, forming a nepheloid layer. By the 5th day, the temperature anomaly no longer existed. The SSC was more uniform with depth, indicating that tidal mixing and turbulence predominated. By the 7th day, the plume had disappeared and SSC was low throughout the bay; thus at that stage the system had recovered from the flood. For Ngerikiil Bay, the recovery stage for SSC depended on the tidal range. Spring tides resuspended the mud causing the SSC lines to become more vertical, while neap tides did not resuspend the mud as much causing the SSC lines to become horizontal.

3.6. Sedimentation. Terrestrial sedimentation rate was highest at station 1 in all bays except for Ngermeduu, where rates were highest at station 2 (Table 2). There was a general gradient of decreasing terrestrial sedimentation from station 1 to station 5 in all bays. Terrestrial sedimentation rate was related to the ranked locations of the stations, decreasing by $0.9\,\mathrm{mg\,cm^{-2}\,day^{-1}}$, ($-0.9 \pm 0.1$ SE, $r^2 = 0.1$, $P < 0.001$) from one station to the next moving offshore.

4. Discussion

In Palau, construction activities that involve movement of soil require an Earth Moving Permit. These permits were used to quantify development in each watershed. Among the three measures, river sediment yield, reef sedimentation rate, and reef turbidity, the river sediment yield increased strongly with increasing numbers of earth moving permits ($R^2 = 0.96$, Table 1). These sediments are directly discharged onto the reefs where they undergo deposition (measured as sedimentation rates) or (re) suspension (measured as turbidity). Our study quantified how sedimentation and coastal turbidity depended in complex fashions not only

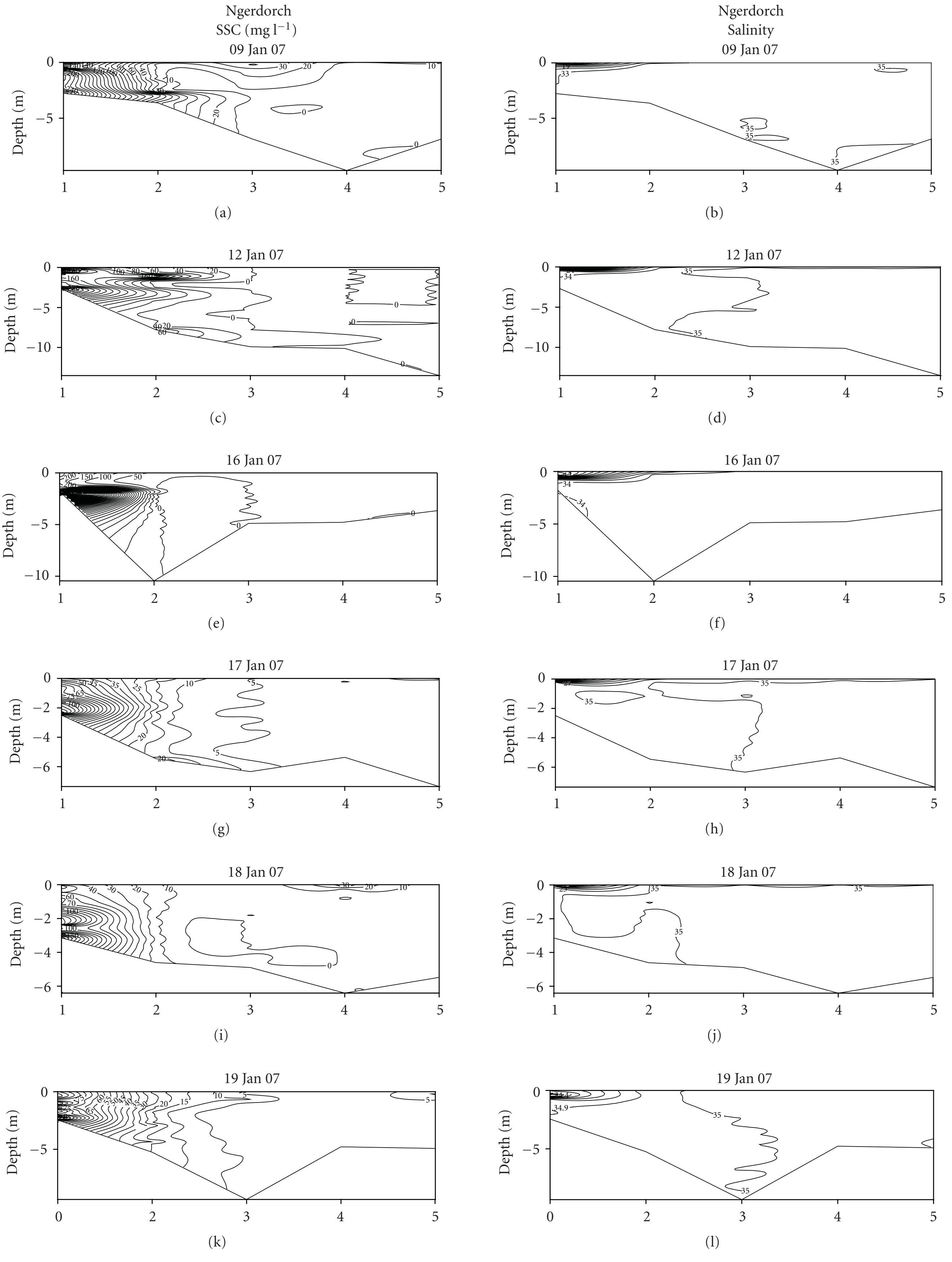
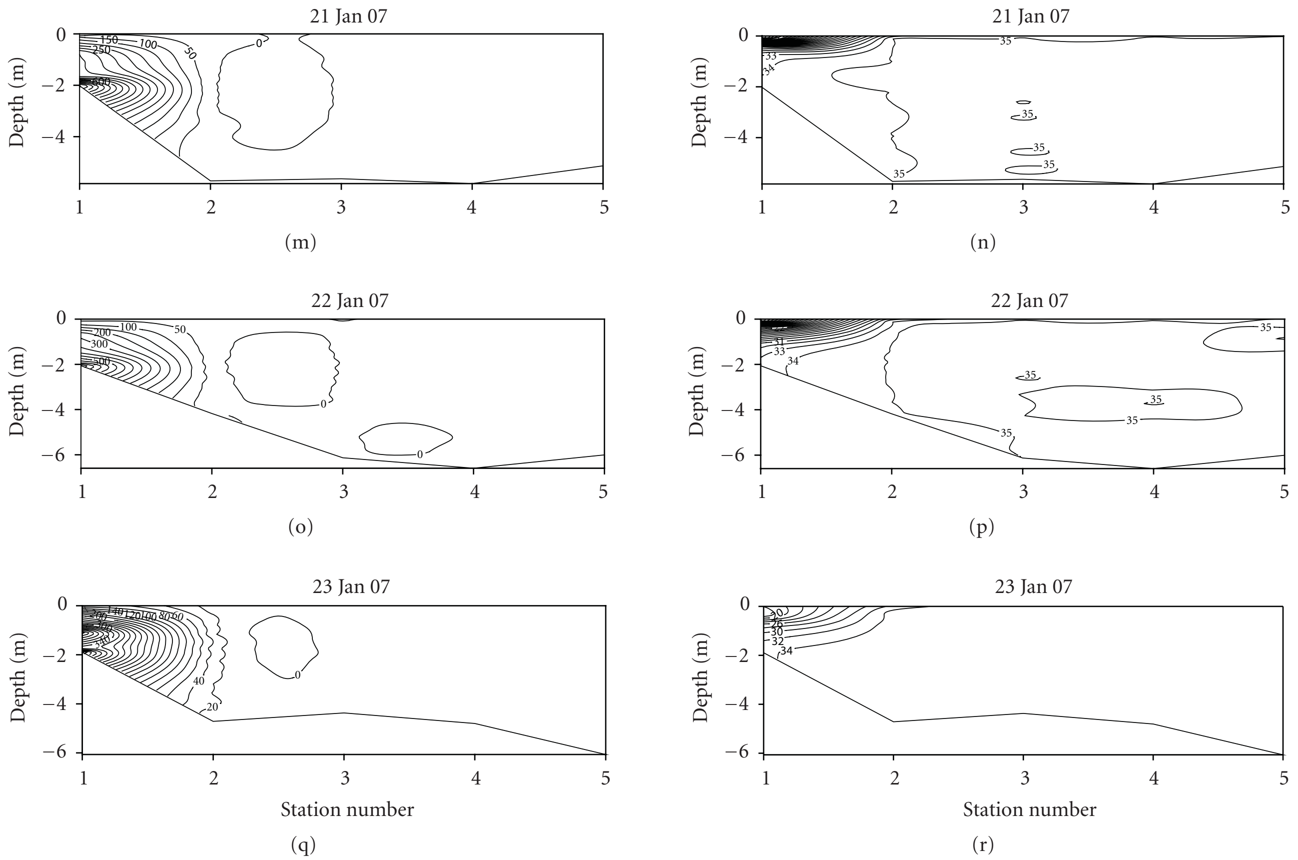


Figure 6: Continued.



(m) (n)

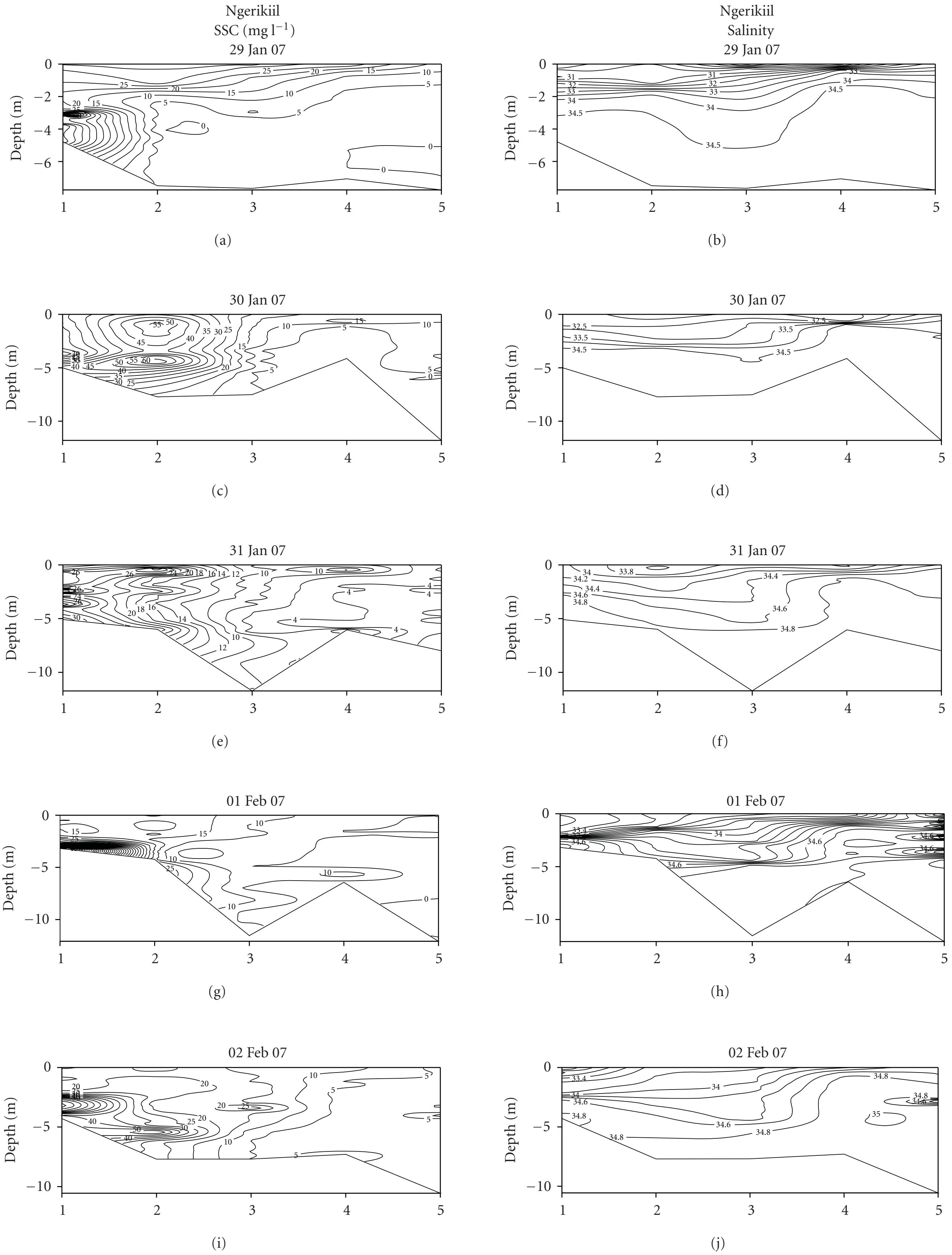
(o) (p)

(q) (r)

Figure 6: Snapshots at daily intervals of the two-dimensional distribution along the channel of salinity and SSC at Ngerdorch from CTD casts. The bottom line indicates the sea floor.

Table 2: Terrestrial, organic, and carbonate sediments recorded in sediment traps at the different stations at the four reef sites. Numbers shown are mean sedimentation rates in mg cm^{-2} d^{-1} ± SE.

Bay site	Station	Sample size (n)	Terrestrial sediments	Organic sediments	Carbonate sediments	Total sediments
Diongradid	1	22	1.05 ± 0.24	0.47 ± 0.11	0.66 ± 0.10	2.18 ± 0.42
Diongradid	2	22	0.12 ± 0.01	0.09 ± 0.01	0.57 ± 0.13	0.77 ± 0.51
Diongradid	3	22	0.15 ± 0.05	0.09 ± 0.02	0.87 ± 0.14	1.11 ± 0.14
Diongradid	4	22	0.12 ± 0.04	0.07 ± 0.01	0.62 ± 0.06	0.82 ± 0.07
Diongradid	5	22	0.25 ± 0.10	0.18 ± 0.07	1.92 ± 0.24	2.35 ± 0.35
Ngermeduu	1	18	3.21 ± 0.47	1.20 ± 0.12	1.36 ± 0.36	5.77 ± 0.91
Ngermeduu	2	18	4.62 ± 0.66	2.65 ± 0.45	3.13 ± 0.92	10.09 ± 1.53
Ngermeduu	3	18	2.14 ± 0.15	1.12 ± 0.11	2.57 ± 0.38	6.84 ± 1.12
Ngermeduu	4	18	0.48 ± 0.08	0.29 ± 0.04	1.31 ± 0.13	2.07 ± 0.24
Ngermeduu	5	18	0.41 ± 0.06	0.18 ± 0.02	1.78 ± 0.19	2.36 ± 0.26
Ngerdorch	1	14	29.95 ± 1.26	9.49 ± 0.47	6.32 ± 0.36	45.76 ± 2.10
Ngerdorch	2	14	1.76 ± 0.39	0.57 ± 0.12	1.27 ± 0.15	3.47 ± 0.57
Ngerdorch	3	14	0.54 ± 0.10	0.21 ± 0.04	2.00 ± 0.36	2.70 ± 0.45
Ngerdorch	4	14	0.65 ± 0.09	0.20 ± 0.03	3.40 ± 0.47	4.17 ± 0.57
Ngerdorch	5	14	0.40 ± 0.07	0.20 ± 0.03	4.77 ± 0.71	5.32 ± 0.80
Ngerikiil	1	14	4.08 ± 0.37	1.51 ± 0.13	1.75 ± 0.16	7.24 ± 0.55
Ngerikiil	2	14	0.85 ± 0.11	0.31 ± 0.04	0.98 ± 0.44	2.05 ± 0.44
Ngerikiil	3	14	1.08 ± 0.09	0.81 ± 0.14	5.73 ± 1.37	7.59 ± 1.53
Ngerikiil	4	14	0.88 ± 0.16	0.47 ± 0.07	6.80 ± 1.14	8.11 ± 1.31
Ngerikiil	5	14	0.30 ± 0.06	0.39 ± 0.08	10.68 ± 3.01	11.7 ± 3.7



Ngerikiil
SSC (mg l^{-1})
29 Jan 07

Ngerikiil
Salinity
29 Jan 07

30 Jan 07

31 Jan 07

01 Feb 07

02 Feb 07

(a) (b) (c) (d) (e) (f) (g) (h) (i) (j)

Figure 7: Continued.

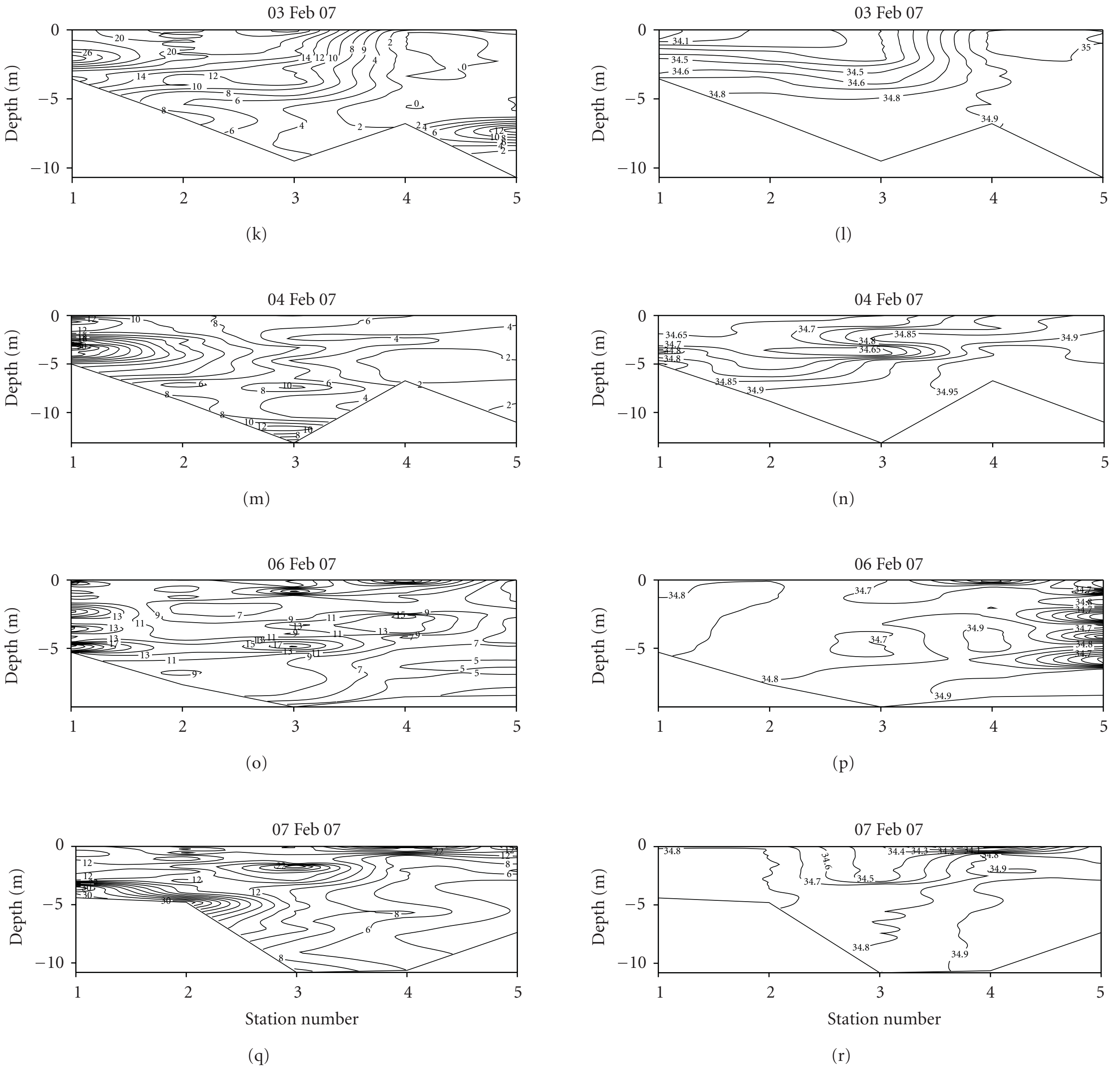


Figure 7: Snapshots at daily intervals of the two-dimensional distribution along the channel of salinity and SSC at Ngerikiil from CTD casts. The bottom line indicates the sea floor.

on river sediment yields but also on factors that control the ultimate flushing or retention of this mud on the reefs, namely winds, currents and the geomorphology (i.e., whether the areas constituted open or semi-enclosed bays). For example, at Diongradid Bay, the sedimentation rate and water turbidity exceeded levels considered harmful to corals [5, 30] because sediments were constantly being resuspended by the winds and currents, and were not exported away. Generally, total rates of sedimentation were similar to rates of terrestrial sediment patterns (Table 2). Differences were only found at stations with strong winds and waves that caused resuspension. For example, in Ngerikiil, Ngerdorch and Diongradid, station 5 had higher total but smaller terrestrial sediment loads than the inner stations.

Sediment dynamics varied for each reef station based on currents and tidal turbulence. In Ngerikiil, Ngerdorch and Ngermeduu, the river plume formed a jet and a jet lift-off point during the early stage of a flood (Figure 8). At that point, the plume lifts off the bottom as it moves seaward, while oceanic waters move in landward under the plume. As sediment particles dropped out of the plume into intruding oceanic waters, they were advected towards the plume lift-off point, where they were mixed upward by the intense turbulence at the plume lift-off point [30]. Spring tides

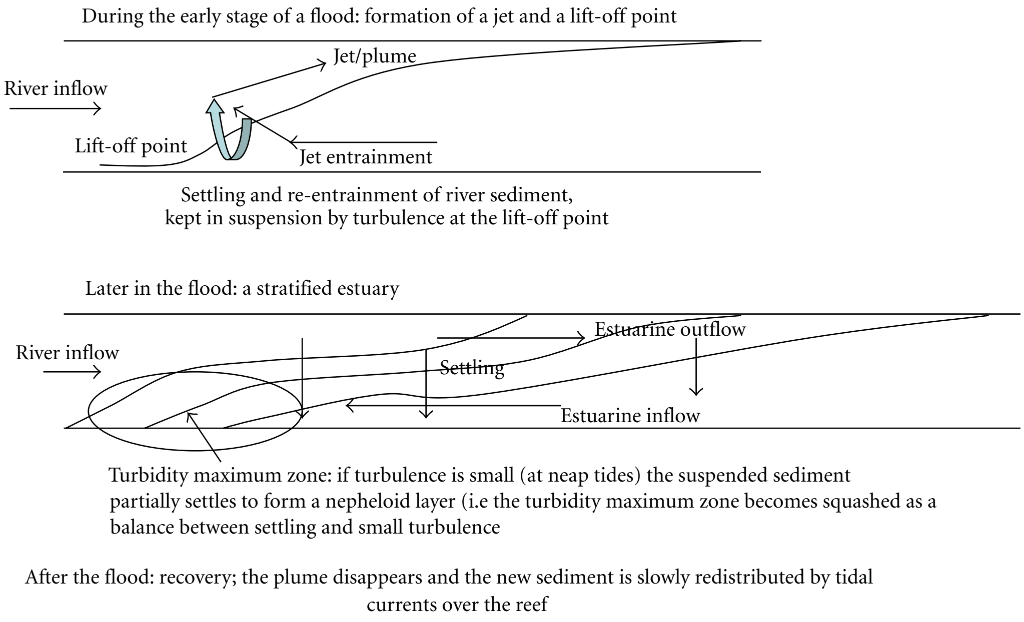


Figure 8: Diagram showing the jet formation and lift-off during the early and later stages of a flood.

also resuspended the sediment (Figure 8). During neap tides when the turbulence was smallest, the suspended sediment partially settled to form a nepheloid layer (Figure 8). In Ngerdorch and Ngermeduu, the turbulence was high so sediment was readily resuspended into the water column, while in Ngerikiil, it was only suspended to mid-depth because of the smaller tidal turbulence. During the later stages of the floods, the systems recovered, the plume disappeared and new sediments were slowly redistributed by tidal currents. In contrast to the other three sites, sediments were not resuspended at Diongradid, and once sediments dropped out of the plume, they settled to the bottom where they remained.

The data show a large variability in Palau's small estuaries in the dynamics and fate of the riverine fine sediment. All the classical types of estuarine water circulation were encountered in Palau, including well mixed, partially stratified, and salt-wedge [31]. The small estuaries of Palau switched from one type to another in a day or a few days at most, as a result of the rapid changes in freshwater discharge from the small catchments. As a result, Palau's small estuaries in general are not effectively shielding the reef from riverine sediment. The results are different from well-studied, large estuaries, where the time scales are longer (weeks to months) and much of the riverine sediment is trapped in the estuaries [32]. The important lesson learned in Palau is that small estuaries are much less effective in trapping sediment than larger estuaries.

Sedimentation had previously been recorded at Ngerdorch in 2003, when the mean total sedimentation rate at station 2 was $8.8 \pm 3.6\,\mathrm{mg\,cm^{-2}\,day^{-1}}$ [22] compared with $3.4 \pm 0.8\,\mathrm{mg\,cm^{-2}\,days^{-1}}$ in this study in 2006. The mean sedimentation rate had decreased by 52%, probably due to decreased erosion after completion and paving of the road around Babeldaob in 2004.

Pohnpei is another wet, high island in Micronesia. The sedimentation rates on coral reefs adjacent to the four Palau watersheds in this study (Table 2) were smaller than those reported for the Enipein watershed in Pohnpei, Federated States of Micronesia [23]. In Enipein, the mean sedimentation rate over the reef was 37.7 ± 1.1 (SE) $\mathrm{mg\,cm^{-2}\,day^{-1}}$ [23], 10–20 times higher than values from this study (Table 1). The sedimentation rates at each of the four sites in Palau were significantly lower than those from Enipein (Kolmogorov-Smirnov Tests, $P < 0.005$). The sedimentation rates in impacted reefal areas off the Enipein River are lethal to corals and other reef organisms, while those in Palau may be sublethal for some species [5, 29] but lethal to the more sensitive taxa [18].

Guam is yet another wet, high island in Micronesia. Data for shallow reefal waters off the La Sa Fua watershed show the sedimentation rate peak at $30\,\mathrm{mg\,cm^{-2}\,day^{-1}}$ [24]. Such high sedimentation rates are harmful to most corals [6, 25]. The Guam receiving waters and reef are frequently flushed of fine sediment by typhoon-driven swell waves, so that there might be some potential for coral cover to regenerate somewhat on clean substrate after a typhoon, at least until the next flood deposits riverine sediment again. Nevertheless, as a result of the very high sedimentation rate immediately following river floods, coral cover is minimal [33]. In Palau however, the sediment remains largely trapped in the bay and the degradation within the bay is longer-term or permanent, with no chance for the coral to recover, unless the sediment is removed through active remediation measures.

5. Conclusion

The results of this study show that land-based development activities have a direct impact on the amount of sediment that goes into rivers and eventually ends up on coral reefs. The amount of sediments being released into the rivers and reefs on Babeldaob Island, Palau, depended on the degree of development within adjacent watersheds. While different reef areas had different geomorphology and hydrodynamic regimes that affected the flow of sediments on the reef, the biggest factor contributing to sedimentation on the reef was from development on land. Once sediments reached the reef, geomorphology and hydrodynamic properties determined the fate of sediments. Previous studies have demonstrated the numerous negative impacts of sediments on coral reef resources [6]. Thus, the fate of reefs around Babeldaob ultimately will depend on the type and number of development activities within the watersheds.

The clear and quantifiable relationships between land-use activities and coral reef ecosystem structure and function are being used to support ecosystem-based management activities. Interestingly, scientifically documented problems associated with the overharvest of key fish guilds were addressed in Palau by re-implementation of traditional "bul" or closures made possible by passing the Marine Protection Act of 1994. Since then, similar efforts guided by the use of our data and traditional Pacific Island practices are being applied to land-use activities to address negative impacts of sedimentation on coral reefs. Following a study in the Ngerikill Watershed, the Ngerikiil community placed a moratorium on clearing coastal mangroves [19]. Having learned the lessons of severe coral reef degradation in Ngerikiil Bay through the lack of land-use management and realizing that this degradation may be permanent in the absence of practical remediation measures, the Ngerikiil Bay community leaders are actively developing a master plan that includes zoning and land-use management. In addition, EBM partners in Palau, including the Babeldaob Watershed Alliance, are communicating these lessons through public meetings with communities in the other less-affected watersheds. These efforts with communities affected by the watersheds in this study are leading to better planning activities including state and national legislation requiring watershed management plans, the use of best management practices, and the restriction of unsustainable activities in specific sites. While ecosystem-based management, Marine Protected Areas and marine spatial planning are often presented as relatively new, western concepts, Palau and other Pacific Islands have been using these for generations, and it was largely due to outside influences, that sustainable practices were either lost or ignored. The inclusion of indigenous researchers has facilitated the bridging of the science to policy development and implementation to better management of human activities responsible for the decline of ecosystems of cultural, economic and ecological value.

Coral reefs are important to the people of Palau economically, culturally and ecologically; they provide food resources, materials for construction, areas for recreation and support a world renowned diving industry. Tourism is a very important industry in Palau with 80% of visitors who come to Palau doing so because of Palau's coral reefs [34]. For the people of Palau to continue to enjoy the benefits of productive and healthy coral reefs, efforts must focus on controlling land activities that increase sediments going into the rivers and onto the reefs.

Acknowledgments

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Review Article

Marine Resource Management in the Hawaiian Archipelago: The Traditional Hawaiian System in Relation to the Western Approach

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Over a period of many centuries the Polynesians who inhabited Hawai'i developed a carefully regulated and sustainable "*ahupua'a*" management system that integrated watershed, freshwater and nearshore marine resources based on the fundamental linkages between all ecosystems from the mountain tops to the sea. This traditional scheme employed adaptive management practices keyed to subtle changes in natural resources. Sophisticated social controls on resource utilization were an important component of the system. Over the past two centuries a "Western system" gradually replaced much of the traditional Hawaiian system. There are major differences between the two systems in the areas of management practices, management focus, knowledge base, dissemination of information, resource monitoring, legal authority, access rights, stewardship and enforcement. However, there is a recent shift toward incorporating elements of the traditional scheme using methods and terminology acceptable and appropriate to present day realities. This trend is exemplified by the management plan for the newly formed Papahānaumokuākea Marine National Monument in the Northwestern Hawaiian Islands. This is one of the largest protected areas in the world and is being managed with a focus on Native Hawaiian cultural values in relation to conservation, ecological, historical, scientific, and educational resource protection.

1. Introduction

For the past century Hawai'i has been dominated by a "Western" model of marine environmental management. Recently, however, there has been a renewed interest in the traditional management practices of ancient Hawaiians. Throughout Hawai'i, a growing cultural, sociological, and scientific movement is working to investigate and revive some of these traditional management tools and to integrate them with modern scientific methodology. The native islanders had devised and implemented every basic form of what are now considered modern marine fisheries conservation measures centuries ago, long before the need for marine conservation was even recognized in Western nations [1]. Traditional restrictions on fishing in Hawai'i were achieved by the use of closed seasons, closed areas, size restrictions, gear restrictions, and restricted entry. Additional social, cultural, and spiritual controls strengthened the conservation ethic under the old system. Ancient Hawaiians used a holistic approach that we might now recognize and strive for as integrated coastal management. Bridging the gap between traditional management and Western science represents a challenge to researchers, government agencies, resource managers, cultural practitioners and organizations, and to the people of Hawai'i. This paper was undertaken in order to define, describe, and clarify primary differences and similarities between the traditional and Western systems in various areas such as management practices, management focus, knowledge base, dissemination of information, resource monitoring, legal authority, access rights, stewardship, and enforcement methods. Finally, we summarize evidence that a synthesis of the two management systems is slowly occurring throughout the Hawaiian Archipelago.

2. Description of the Traditional System

Elements of the traditional Hawaiian management system for managing nearshore resources are known from several sources. The primary historical literature translated to date contains written descriptions of various practices and customs used in ancient times. The most important accounts were written between 1830 and 1870 as reported by Kamakau [2–4], Iʻi [5], and Malo [6]. Additional information on marine resource usage is contained in works by Beckely [7], Kahāʻulelio [8], Cobb [9], Handy [10], Titcomb [11], Kawaharada [12] and E. S. C. Handy & E. G. Handy [13]. Recent ethnographic studies include K. Maly and O. Maly [14, 15], Peterson and Orr [16] and Glazier [17]. Thousands of additional primary source documents and newspaper articles written in the 100 year old Hawaiian language remain to be translated and studied and will one day reveal more than is known today. An oral tradition also persists, especially in the more isolated areas of the Hawaiian Islands.

Certain traditional Hawaiian words are used in this discussion because of nuances in meaning that do not translate into the English language. These Hawaiian terms are increasingly used within the State of Hawaiʻi and within the U. S. Government in reference to various management practices. For example, the Hawaiian word *pono* does not have a suitable direct English language meaning and refers to actions that are "appropriate, correct, and deemed necessary by traditional standards in the Hawaiian culture". Therefore this word was included in the regulations that established the Northwestern Hawaiian Islands Marine National Monument as published in the Federal Register [18]. Likewise the native Hawaiian name *Papahānaumokuākea* was subsequently chosen for the monument in keeping with the intent to manage the area using traditional values. This name has deep spiritual and cultural meaning (http://papahanaumokuakea.gov/about/name.html/) that is relevant to past and present management practices in that region of the archipelago.

2.1. Tenure and Management Concepts. The predominant traditional system in the eight high islands of the Main Hawaiian Islands (MHIs) was based on the *ahupuaʻa*, which is a unit of land that extends from the mountains to the sea and generally includes one or more complete watershed(s) and all nearshore marine resources [19, 20]. Each *ahupuaʻa* contained a broad cross section of island resources and was managed within a complex social system associated with each area. The general belief is that each *ahupuaʻa* met the needs of the local population with an excess for tribute and trade. At present the traditional cultural, economic, and social structure of the *ahupuaʻa* are no longer in general use although the land boundaries continue to be informally recognized in the State of Hawaiʻi. However, a resurgence of interest in traditional Hawaiian resource management during the last decade has led to wide use of the term *ahupuaʻa* in reference to integrated coastal management based on individual watersheds and their offshore waters.

The modern concept of the *ahupuaʻa* may not be totally accurate compared to what it meant to the ancient Hawaiians. The *ahupuaʻa* can be viewed as a unit for production of goods. Maintaining ecological integrity led to sustainable production of foods and other material which could be offered in *hoʻokupu*. Pukui and Elbert [21] define *hoʻokupu* as tribute, tax, or ceremonial gift given as a sign of honor and respect. An alter (*aha*) was located at the edge of each *ahupuaʻa* with a likeness of a pig's head (*puaʻa*), and it was here that tribute to the ruling chief was deposited each year during the *makahiki* as the long god circled the island [13, 22]. However, the smaller strips within the *ahupuaʻa*, the *ʻili*, represented the true basic unit of land division to which the local people retained fidelity over long periods of time. The various *ahupuaʻa* were redistributed to secondary chiefs after every major power shuffle on an island, so that frequently the *aliʻi* (chiefly caste) that ruled an *ahupuaʻa* did not actually come from that *ahupuaʻa*, or even from the island on which it was located [2]. There were times when *aliʻi* from Maui controlled many of the *ahupuaʻa* on Oʻahu [13]. By contrast, the *ʻili* were inhabited by the same extended families, or *ʻohana*, for many generations. Just as with our modern concept of the *ahupuaʻa*, the *ʻili* required a cross-section of available resources—they generally incorporated a piece of the mountain, a piece of the valley, and a piece of the shoreline. If this condition could not be accommodated in a single narrow mountain-to-shore strip (*ʻili paʻa*), then an *ʻili* could be set up as a series of two or three disconnected units (*ʻili lele*) that provided the necessary components; in some cases these separate pieces comprising a single *ʻili* could be in separate *ahupua'a*. Thus a family's traditional near shore gathering grounds might be some distance from their upland fields (or even at the mouth of another valley).

Prior to Western contact all land and ocean resources were held in trust by the *aliʻi* (chiefs) with harvest rights overseen by a *konohiki* (an expert resource manager for each area) who was responsible for the coordinated stewardship of all extractive natural resources. Although the *konohiki* was originally considered to be merely a manager of the *ahupuaʻa*, the term eventually came to mean landlord/chief of the *ahupuaʻa* [23]. The *hoaʻāina* (native inhabitants) had rights to the resources for subsistence and tribute. The *konohiki* was advised by *kūpuna*, who were elders acknowledged for their knowledge and wisdom. The *poʻo lawaiʻa* (master fishermen who held and transmitted knowledge) also consulted with the *konohiki* on matters concerning management of marine resources.

Knowledge was developed over centuries and handed down from generation to generation. Decisions were based on detailed information on the local area and a keen understanding of natural cycles. Transmission of knowledge occurred through an oral tradition and by direct teaching and experience. One of the primary management tools was the *kapu* which was a decree that imposed restrictions on extraction of resources at certain times and places. The term *hoʻomalu* is found in announcements by *konohiki* when reserving fish for themselves as was articulated in the laws of 1839-40. Certain marine resources (e.g., turtles, octopus, dolphins, and jacks), were also *kapu* for women and those not of the *aliʻi* caste. Violation of *kapu* was often punishable by death [24]. Enforcement often was immediate and severe.

2.2. Spiritual and Cultural Values. Deeply ingrained traditional sociospiritual aspects of the culture provided a further safeguard against overexploitation. The *kānaka maoli* (native Hawaiians) demonstrated a deep spiritual connection with nature that was expressed through offerings and prayers that were an integral part of the fishing effort. *Koʻa* (fishing shrines) were built along the coast. Help from ocean creatures was sought for success in the fishing effort. Sharks, turtles, and various fishes served as *ʻaumākua* (family guardians). *ʻOli* (chants) and the *hula* (dance) were important parts of the Hawaiian oral transmission of information concerning the importance of the sea. For example, the predominant Hawaiian creation chant, the *Kumulipo* [25], describes the first creation of life following the male and female as the coral polyp, which in turn gave rise to subsequent organisms.

> *Hānau ka ʻuku koʻakoʻa, hānau kāna, he ʻakoʻakoʻa, puka.* (Born was the coral polyp, born was the coral, came forth.)

Cultural values and concepts were also shared and practiced through *ʻōlelo noʻeau* (proverbs). Many of these traditional sayings [26] refer to the lifeline of the native people:

> *Mālama i ke kai, a mālama ke kai iā ʻoe!* (Take care of the ocean and the ocean will care for you.) [15].

The term *kuleana* refers to specific responsibilities that accompanied the privilege of sharing in the resource. *Kuleana* also means "interest" as in having a shared interest in some entity. The Hawaiian concept of *kōkua* requires sharing of resources with those in need, and the responsibility of all resource users to maintain the systems that produced those resources [27]. *Mālama* is the practice of caring for the land.

2.3. Management Practices. In ancient Hawaiʻi, the art of fishing was passed along family lines. Fishermen were of a special lineage and trained for years as an apprentice. During this time they were taught to observe subtle and major changes in the condition of the marine resources. They were educated in the life cycle, diet, daily, and seasonal feeding habits, preferred habitat, and growth conditions. They obtained knowledge of the appropriate season, time of month, time of day, and method for harvesting of the many species of fishes, invertebrates, and seaweeds. Harvest management was not based on quota, but on identifying the specific times and places that fishing could occur so that it would not disrupt the basic habits of important food resources nor deplete fish stocks. Until training was complete, young fishermen were only allowed to observe the process and hold the catch. Fishing activities were often regulated by the moon calendar [28] which emphasized repetitive biological and ecological processes (e.g., fish spawning, aggregation, and feeding habits). Social and cultural controls assured compliance of a strictly imposed code of conduct. Behavior of the fishermen before, during and after fishing was controlled. The belief was held that resources were limited and there was a social obligation to exercise self-restraint in resource exploitation. The ancient Hawaiians viewed themselves as an integral part of nature [12, 14, 15, 19, 22].

2.4. Transmission of Knowledge. Based on centuries of trial and error and astute observation, Hawaiians incorporated their understanding of the oceans into self-sustaining management practices. Hawaiians possessed a complex understanding of the life histories of fishes. Perceptive observations led to a keen familiarity of physical (e.g., weather patterns, currents, tides, wind, waves), biological (e.g., spawning seasons, recruitment, and growth), and ecological (e.g., foraging patterns, behavior, and habitat) factors that influence fisheries. In these areas the traditional knowledge of Hawaiian fishermen may have surpassed what is known by modern marine biologists [29, 30]. Knowledgeable *kūpuna* also consulted with *poʻo lawaiʻa* (master fisherman) who had intimate awareness of the status of various populations of reef organisms. When populations declined to low levels, a *kapu* (forbidden practice) was placed on extraction to allow the resource to recover [14, 15]. Knowledge and management practices were place specific, and kept secret. Kamakau reported that Hawaiian fishermen would paddle out of sight before pulling up their catches so that no one would know exactly where the fish were taken: "In this way those who had secret fishing grounds kept their locations from becoming common knowledge" [3]. Families and communities found especially fertile areas above seamounts, information of which they passed on orally to their offspring but tried to keep secret from others [31].

2.5. Effectiveness of Traditional Management System. Historical accounts from the nineteenth century attest to the abundance of the marine resources of precontact Hawaiʻi and the sustainability of the fisheries [15]. This would also be true for the coastal pelagic and open ocean species given their widespread distribution and abundance and the limitations in the harvesting technologies of the day. For nearly a millennium, Hawaiʻi's fishers and gatherers helped to sustain a native population, which according to some accounts reached between 500,000 and 1 million [19], but more likely was in the range of 150,000 to 250,000 [32–35]. The current population of the State of Hawaiʻi is 1.3 million, but it is estimated that over 90% of the food and seafood consumed by the population come from outside of Hawaiʻi. It is difficult to know with certainty the status of inshore and coral reef associated resources during the precontact period and whether the supply decreased as the Hawaiian population grew. Evidence from archaeological excavation suggests that nearshore marine resources in Hawaiʻi and the Pacific were susceptible to human overuse [36–38]. Early overexploitation of marine food sources in Oceania might have led to increased dependency on more reliable and predictable terrestrial food resources [39]. The widespread construction and operation of fishponds [40–44] supplied the *aliʻi* and others with fresh fish during times when the reef resources were under *kapu* and during times when severe weather prevented fishing. Also, such ponds augmented or replaced wild caught stocks, as is the case for modern analog aquaculture and stock enhancement programs. The placing of permanent or temporary *kapu* on various species and life stages of marine life [6] was motivated by various economic, cultural, and spiritual factors, but certainly the maintenance of fishery stocks was an important motivation. During post-contact times there are accounts of periodic famine [13] and reports of a "deficiency of fish" [36] suggesting that resources were sensitive to overexploitation at that time if not managed properly.

2.6. Breakdown of the Traditional System. The breakdown of the traditional marine management system was precipitated by major cultural changes following Western contact. The abolishment of the traditional kapu system in 1819 by Kamehameha II (Liholiho) and Kaʻahamanu was one of the most significant and transformative events in Hawaiian history [45, 46] that set the stage for further changes. The Hawaiian Kingdom attempted to resist colonialism and adapt to the changing global political environment through modification of traditional structure using Hawaiianized Euro-American practices to suit their own needs [47]. For example, the mapping of the lands was largely conducted by the *aliʻi* and other Hawaiian nationals as a means for the Hawaiian State to secure national lands in the face of colonial pressures [48]. A key element in the breakdown was the redirection of the activities and energies of the *hoaʻāina* (native tenants) to produce products for trade in order to acquire foreign goods for the *aliʻi* and their *konohiki* [10]. Contemporary writers and the historian Kuykendall [49] considered this redirection as one of the prime causes of famine, sickness, and depopulation of the Hawaiian Kingdom prior to 1829 [10].

Subsequent changes in land tenure led to a further erosion of the *ahupuaʻa* as a social unit. The *Māhele ʻĀina,* (division of the land) in 1848 was followed by the *Kuleana Act* in 1850, which established fee simple ownership in which land could now be sold to parties with no historical interest in sustaining the *ahupuaʻa* as a whole. This transfer of land created large plantations. Importation of workers resulted in a rapid ethnicity shift. Hawaiian communities were diluted, eroding traditional management. Foreigners brought new technology and unfamiliar concepts of resource exploitation, replacing centuries old sustainable management practices.

Although the *ahupuaʻa* concept of management began to break down on land, elements of the system still persisted in the marine environment. In laws published between 1839 and 1859, King Kamehameha III codified fishing rights and divided the fishing grounds amongst the people of Hawaiʻi. The King granted fishing rights within the reef (or to one mile offshore in those areas without a reef) to the *konohiki* and the tenants of the *ahupuaʻa* (known as the *hoaʻāina*). The *konohiki* could *kapu* a single species of fish for his exclusive use or after consultation with the tenants prohibit fishing during certain months of the year [23]. During the 1848 land division, the Land Commission received over 1,000 claims for ocean resources. These fisheries records also document the testimonies of the *aliʻi* and *konohiki* that were awarded *ahupuaʻa*. Public notice was issued concerning the *iʻa hoʻomalu* (*kapu* or protected fishes). A plethora of information about Hawaiian fisheries and traditional practices were recorded in 1874 when the Commission of Boundaries was established to ascertain the location of each of the *ahupuaʻa* that had been awarded in the *Māhele ʻĀina.*

Following the overthrow of the Hawaiian kingdom and annexation to the United States in 1898, fisheries management was delegated to various government agencies. As was the case with colonial powers throughout much of Oceania traditional fishing rights were systematically extinguished in the name of the discredited "freedom of the seas" concept and because such customs prevented newcomers from expropriating the islanders' resources [1]. Ocean tenure practices based on regulation of fisheries through control of fishing rights were replaced by unlimited entry, often referred to as the "tragedy of the commons," leading to eventual resource depletion through overharvesting. The traditional system based on cooperation for the good of the community was slowly replaced by commercial forces and competition to benefit the individual. The subsistence-based, locally governed economy was converted to a cash-based economy controlled by remote global market demand. As time progressed, technology provided refrigeration and more efficient fishing gear, further accelerating the shift from subsistence to profit-based economies. A dramatic decline in Hawaiian fisheries stocks and fishery production occurred during the period of commercialization of fisheries [15]. The spiritual connection to the ocean slowly deteriorated, along with the concepts of *kuleana*, *kōkua*, and *mālama* (responsibility, sharing, and caring) with the increasing disconnect between neighbors. The social pressure to support the traditional system was reduced as fisheries management switched from within the local community to a more remote and poorly enforced organizational scheme. The Hawaiian Organic Act of 1900, passed a year after Hawaiʻi's annexation as a United States Territory, further limited most *konohiki* fishing rights through condemnation of *ahupuaʻa* fisheries. [50]. The 1900 law repealed earlier laws conferring these exclusive rights and opened the fisheries of the Territorial waters to all citizens of the United States. Specifically excluded were fisheries which were already vested and filed with the circuit court within two years, but even these fisheries could be condemned for public use upon payment of just compensation. As recently as the 1940's several of these *konohiki* fisheries were still extant [15]. The Organic Act and subsequent state court decisions effectively eliminated *konohiki* and *hoaʻāina* fishing rights, but more recent federal courts have taken a broader view and continue to recognize them as a legal form of property ownership [23]. The breakdown of *mālama* coupled with the loss of traditional guidance from *kūpuna* (knowledgeable elders in the community) further removed social controls on fishing and hastened the decline of traditional near-shore fisheries resources. The dismantling of this system undermined native Hawaiian lifestyles, values, and culture.

Between 1898 and 1905 detailed reports on the condition of the fisheries and management recommendations based on commercial values of catch were prepared by the U. S. Fish Commission. These data [51] provide an important baseline that has been used to document an 80% reduction in coastal fish catch (Figure 1) between 1900 (1,655,000 kg) and 1986 (285,000 kg).

2.7. Management of Offshore Waters. A different management scheme existed in offshore waters beyond the boundaries of the traditional *ahupuaʻa* of the MHI. Native Hawaiians located and utilized offshore fishing grounds above banks and seamounts that were located far from the coastline of the MHI [2–4, 52–56] extending into the NWHI. At that time all inhabitants were free to fish on the high seas so long as they respected specific restrictions set by the ruling class and observed cultural and religious taboos. Locations of deep sea fisheries were the proprietary knowledge of individual fishermen [3, 31], not the communal property of the *ahupuaʻa*. These management policies were eventually codified into written law by King Kamehameha III.

Deep water snappers in Hawaiʻi are only found in localized areas (known as a *koʻa*) that are characterized by proper depth range, presence of rock outcrops and other conditions that are favorable to the fish. These locations were the guarded knowledge of single families [4], and as such were probably more closely associated with the *ʻili* to which the families were bound. Bottom fishing was not linked to the spawning cycle as was the case for inshore species due to unpredictability of offshore weather conditions which could limit access [8]. Bottom fishing continued through the summer, a season of fine weather, but also the season in which most of the deep water species were spawning. Given the simple technology in use at that time (e.g., *olonā* hand lines that were woven from native plant fibers, hooks made of bone or shell, and dugout canoes), this arrangement appears to have had no major impact on fish stocks.

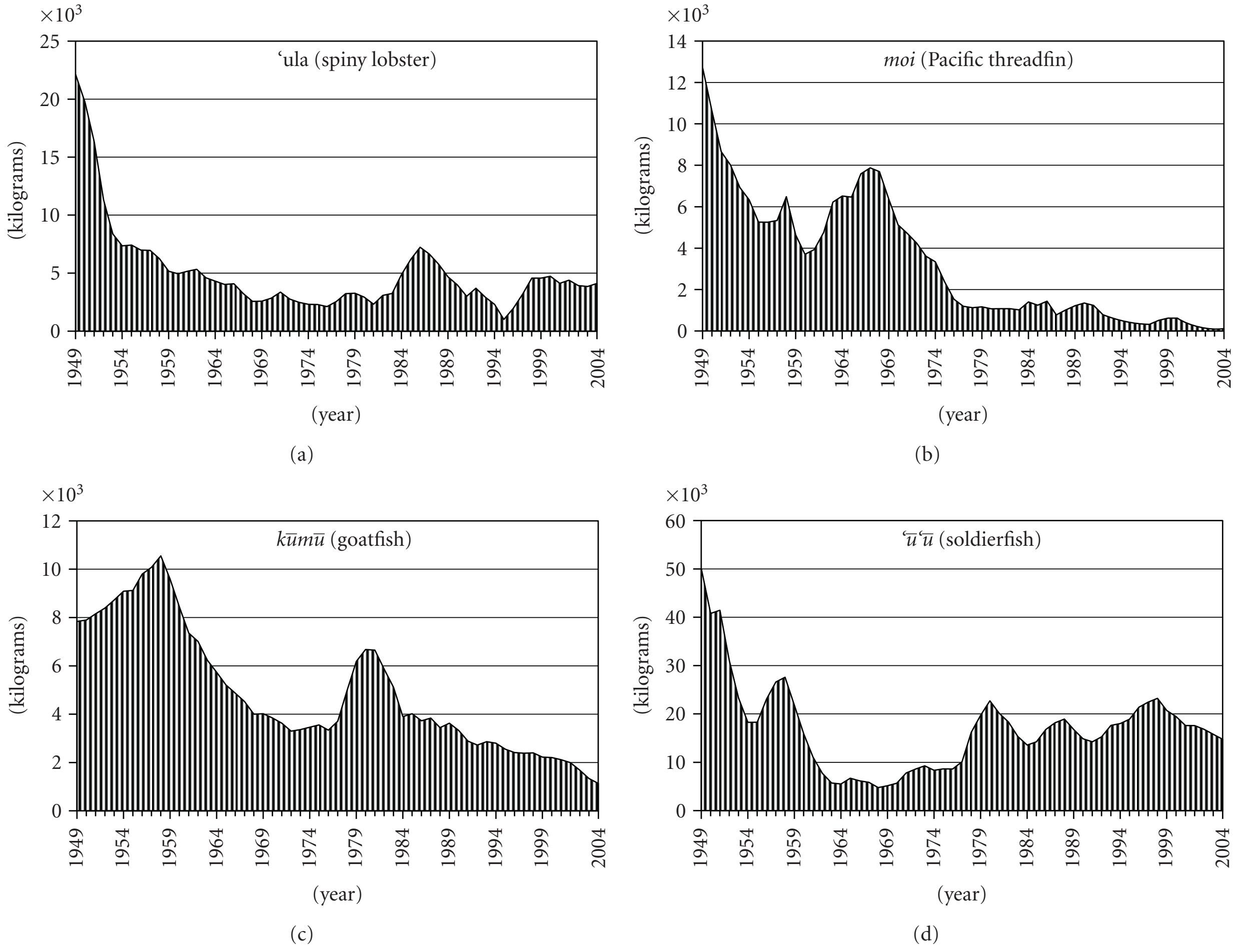
3. Description of the Contemporary System

The existing Western-based management system must deal with social and economic conditions that did not exist in ancient times. Major changes in land use and alterations of stream and near-shore environments have occurred almost everywhere. Waste disposal, invasive species, major shoreline construction, and other major environmental changes are presently occuring at a rapid rate. Hawaiʻi has experienced massive immigration of various cultural groups, fundamental changes in government, and advances in technology that have changed fishing practices and essentially eliminated past harvesting limitations of depth, distance, weather conditions, and darkness. Multiple interest groups vie for recognition and major shifts have occurred in societal perceptions. Conflicts arise with mandated protection for endangered species, difficulties with enforcement transpire, and national and global influences combine to create an environment that can be counterproductive to sustainability.

3.1. Structure and Functioning of Contemporary Management System. Under the present Western scheme, management responsibility of the marine environment is split between numerous agencies. The Hawaiʻi State Department of Land and Natural Resources (DLNR) administers all marine resources within 3 miles of land through the activities of various divisions. The DLNR Division of Aquatic Resources (DAR) is the primary agency responsible for management of living marine resources throughout the archipelago within 3 miles of land, with the exception of waters around the island of Kahoʻolawe which are administered by the Kahoolawe Island Reserve Commission (KIRC). The DLNR Office of Conservation and Coastal Lands (OCCL) is responsible for overseeing approximately 2 million acres of private and public submerged lands that lie within the State Land Use Conservation District and for beach and marine lands out to the seaward extent of the State's jurisdiction. The DLNR has overlapping responsibility with other state and federal agencies. The U. S. Federal Government manages waters from 3 to 200 miles offshore (the U. S. Exclusive Economic Zone). The recently created Papahānaumokuākea Marine National Monument encompasses 137,792 square miles of U. S. waters, including over 4,500 square miles of relatively undisturbed coral reef habitat and is administered jointly by the U. S. National Oceanic and Atmospheric Administration (NOAA), the State of Hawaiʻi and the U. S. Fish and Wildlife Service. The U. S. Environmental Protection Agency (EPA) and Hawaiʻi State Department of Health are responsible for enforcing laws on water quality. Additional management responsibility in certain areas falls to the U. S. Army Corps, National Park Service, and the U. S. Coast Guard. Certain marine areas are under partial military jurisdiction. In addition there are numerous agencies involved in the regulation of activities affecting watersheds and streams that have an impact on marine resources.

In the MHI the DAR utilizes several management tools including full or partial closure of a reef area as a marine protected area (MPA), rotational and seasonal closures, restrictions on fishing gear or methods, size and bag limits, and rules preventing the take of certain species. Identifying and addressing a resource problem is a protracted process that requires surveys and scientific studies to establish the cause of decline, as well as the "buy in" of various user groups and interested parties through public meetings. Fishermen blame pollution and introduction of alien species for reductions in fish stocks and demand unequivocal evidence that overfishing is the cause of decline. Often the proper course of corrective action is unclear or controversial, and the problem is studied or debated for years. The "trigger" for management action is ill-defined and, based on available data, must often involve a devastating decline in the resource before action can be initiated.

Once there is sufficient scientific data to identify a problem and the appropriate course of corrective action, the DAR has two alternative procedures for establishing new



(a)

(b)

(c)

(d)

Figure 1: Main Hawaiian Islands commercial marine landings 1949–2005 for the *ʻula* or spiny lobster (*Panulirus* spp.), *moi* or Pacific threadfin (*Polydactylus sexfilis*), *kūmū* or goatfish (*Parupeneus porphyreus*) and *ʻūʻū* or soldierfish (*Myripristis* spp.). Data presented as 3 yr. moving average. Source: Division of Aquatic Resources unpublished data.

rules and regulations. The first method is to propose and draft a bill as an element in the Governor's legislative package that is developed internally each year from September to December. The bill is introduced when the legislature convenes in January. No public hearing is required for this process, but the legislature typically holds several public committee meetings. A legislative bill must be passed by both houses and be signed by the Governor to become law. The process takes approximately six months following the time that the bill is introduced and is effective immediately after being signed into law. It is up to the individual fisherman to know which bill passed and which laws are in effect. New laws may be published in the newspapers but this is not mandatory. The Hawaiʻi Revised Statutes which contains such laws can be accessed by the public and is updated annually, as is the rulebook published by the DAR. Those with a personal agenda often prefer the legislative process because bills can be introduced by any legislator on their behalf. Furthermore, all activity and discussion on a bill occurs in Honolulu, the seat of the Legislature. Time and travel constraints effectively reduce the opportunity for input from people living on the neighboring islands, particularly in remote areas. If a bill is not passed during a legislative session it can be introduced again in a later session, so a persistent minority of the population can potentially change regulations, given enough time.

The second means of establishing new regulations is the Administrative Rules Process which involves a series of public meetings and public testimonies. This process generally takes from one to five years to implement a new rule. DAR prefers this approach because it addresses concerns of all stakeholders and incorporates the public's point of view. Simple matters such as modification of zones within an MPA can take a year while more complex and controversial issues that have a great impact (such as gill net ban or establishment of fishery management areas) can take over five years. The process generally leads to compromise on all sides. Once the laws or administrative rules are enacted they can subsequently be repealed, amended or new rules can be initiated.

3.2. Effectiveness of the Contemporary Management System. Even though a much smaller proportion of the population presently fishes or consumes local fish products relative to ancient times, marine resources have steadily declined over time coincident with the shift away from the traditional Hawaiian management system [14, 15, 51]. Early in the 20th century Jordan and Everman [57] noted that the fisheries of Honolulu were falling rapidly due to localized overfishing. Titcomb [11] relates that in 1923 one Hawaiian wrote to the Hawaiian newspaper *Ka Nūpepa Kuokoa* inquiring "why there was so much fish in the days of our ancestors and so little in our time…?" Responding to concerns over the high cost of fish in the markets in the 1920's, Hercules Kelly, Territorial Fish and Game Commissioner noted that wasteful methods, destructive fishing techniques, pollution, and overfishing had reduced the abundance of fish in Hawaiʻi's waters [27]. In 1927 it was reported that the fish fauna of Hawaiian reefs was much less abundant than several decades earlier and many common species were now rare [58]. Declining marine resources were acknowledged again by resource managers in the 1950's when they reported that desirable food and game fishes were "on a declining trend and have deteriorated to such an extent that the need for sound conservation measures is urgent" [59].

In Hawaiʻi only commercial fishers are required to file catch reports. Catch reports for several key species over the past 60 years are shown in Figure 1. Since the termination of ocean tenure practices and the associated controls on fisheries, the harvest of many species has decreased [51]. The largest declines in reported catch occurred in the first two decades after World War II. Commercial catch in more recent decades has remained relatively stable [60] albeit at a much lower level than in the preceding decades. Comparison of fish abundances in the MHI to those of the relatively unexploited Northwestern Hawaiian Islands (NWHI) also points to abnormally low levels of fish stocks near the populated islands [61].

Catch data are not available for recreational and subsistence fisheries. However, reconstruction of the noncommercial catch for both inshore and bottom fishes indicates that total landings in this sector are approximately three times that of the commercial sector. The commercial catch underwent a 70% decline from 5,641,000 kg 1950 to 1,868,200 kg in 2002 [62]. Fishermen and other ocean users are well aware of declining reef resources. Surveys of both commercial and noncommercial fishers [63, 64] have clearly documented this perception. In the 1998 survey 57% of respondents felt inshore fishing was now poor to terrible. Overfishing is most often cited as the prime cause of resource depletion [64, 65].

In contrast to the technological limitations in ancient times, modern fishing technology has depleted bottom fish stocks throughout the MHI and even in remote areas of the NWHI [65]. The National Marine Fisheries Service (NMFS) determined that overfishing was occurring on the bottom fish multispecies complex around the Hawaii Archipelago, with the primary problem being excess fishing effort. NMFS requested the Western Pacific Regional Fishery Management Council to take appropriate action to end the overfishing. An interim seasonal closure was placed in effect from May 15, 2007 to October 1, 2007, and the fishery has been managed by an annual total allowable catch since 2007.

4. Comparisons between the "Traditional" and "Western" Systems

Available information from various sources consistently identifies the same dominant features of the traditional management method versus the current Western management scheme. Both systems were developed in an attempt to ensure protection and sustainability of marine resources. However, tabulation of the dominant characteristics graphically shows fundamental differences in nearly every important respect (Table 1). There are positive and negative aspects of each system, so the comparison is intended as an objective means of sorting out the differences without a bias towards either the traditional system or the Western system. Each major aspect of the management comparison of Table 1 is discussed in more detail as follows.

The Western system of management is based on federal, state, and local laws and regulations implemented by various agencies or departments, which is a reality that hampers effective management. In contrast, the traditional system was based on the authority of the ruling *aliʻi*. The central feature of the traditional system was that reef tenure as well as land tenure was in the hands of the residents of the watershed (*hoaʻaina*) and under the rule of a single authority (*aliʻi*) and his manager the *konohiki*. When fishing regulations were formalized in law, the *aliʻi* were required to consult with the *hoaʻaina* before closing the fishery which suggests that the local community traditionally had input into the process. Nevertheless sources generally acknowledge that the traditional system was highly autocratic and has features that would not be acceptable in a democracy.

Under the traditional system local inshore marine resources were held in common with equal access to all people living within the boundaries of the *ahupuaʻa*, but with certain management restrictions. Inhabitants of the *ahupuaʻa* in consultation with *aliʻi* limited access to others, but outsiders could gain access by permission from chiefs and local villagers. This aspect of the traditional system provided another means of limiting the impact of humans on the resource. In the Western system, access is unrestricted, so any person from any district can fish in other districts, so a given area can be heavily exploited by the entire population with no control of outsiders.

Under the Western system, trained professionals in multiple government agencies are the managers with responsibilities defined by law. They generally have responsibility for very large areas and cannot possibly be knowledgeable about local conditions and local resources. In contrast, under the traditional system a very knowledgeable *konohiki* (district manager) was appointed by *aliʻi* to manage a very specific geographic area for a specific community of people. Stewardship was supported by an individual sense of *kuleana* or responsibility for the local resource.

Under the Western system enforcement of any rules that are in place is generally weak and inconsistent due to concern for "due process" and rules of evidence. The positive social outcome is that rights of individuals are respected, but there is a negative impact on natural resources. In contrast the traditional system was based on the absolute authority in

Table 1: Comparisons between major aspects of “Traditional Hawaiian” and “Western” management systems in Hawai‘i for inshore reef fisheries.

Management component	Western management system	Traditional Hawaiian management system
(1) Authority	Federal, state, and local laws and regulations implemented by various agencies or departments.	*Ali‘i* (chiefs)
(2) Access rights	Reef held in common, equal access to all.	Inhabitants of the ahupua‘a (district) in consultation with *Ali‘i*. Limited access by permission from chiefs and local villagers.
(3) Managers-stewardship	Trained professionals in multiple government agencies with responsibilities defined by law.	*Konohiki* (district manager) appointed by *Ali‘i.*
(4) Enforcement	Generally weak and inconsistent due to concern for “due process” and rules of evidence.	Authority in the hands of *Ali‘i*. Punishment is immediate and can be severe. Conservation ethic reinforced by ingrained cultural rules of social behavior and spiritual principles.
(5) Management focus	Commercial as well as recreational fishery, economic development, conservation, endangered species, environmental protection, sustainability, and maintain biodiversity.	Limit take to only what is needed by inhabitants to insure sustainable yield. Focus entirely on plants and animals used for food, medicine, selling and trade.
(6) Management theory	Established western science of management (e.g., Catch Per Unit Effort)—Accepted theory and practice subject to revision with new information.	Traditional management practices that were developed and applied locally over many generations of trial, experimentation, study, application and observation.
(7) Knowledge base	Published reports, records, data bases, documents, objective measurements and observations, and quantitative analyses of data.	Oral transmission with restricted access to information—knowledge generally kept within family lineage.
(8) Primary fishery management tools	“Regulated inefficiency” to reduce harvest. Restrictions on gear type, number of fishing days, and marine protected areas.	Intermittent complete reef closures of reefs as indicated with *Kapu* (forbidden take) of certain species at certain times.
(9) Fishery management target	Generally single species. Increasing focus on ecosystems.	Generally entire reef ecosystem with species specific *kapu* at certain times.
(10) Resource monitoring	Infrequent quantitative surveys of environmental parameters and stocks, direct underwater observations. Perception of “insufficient data” required for decisive management actions.	Continuous daily interaction with reef resources, perception that accurate knowledge of resource is held by the local master fishermen (*po‘o lawai‘a*), elders (*kūpuna*), and *hoa‘āina* of that place.

the hands of *ali‘i*. Punishment was immediate and could be severe [24]. This conservation ethic was reinforced by ingrained cultural rules of social behavior and spiritual principles.

Western management focus has been heavily driven by perceived gain from economic development, although tempered by concern for conservation, endangered species, environmental protection, and sustainability. In the traditional system commercial exploitation was unknown. Only what was needed was taken from the reef, which was considered to be a storehouse for food. These actions protected the resources from over-exploitation. The management focus was entirely on plants and animals used for food, medicine, selling, and trade, with the view that all elements of the *ahupua‘a* were interrelated.

An established, science-based Western management scheme (e.g., Catch Per Unit Effort) drives the Western system of management. Decisions and regulations are based on accepted theory and practice subject to revision with new information, which is a positive feature of the system. Traditional management embraced practices that were developed and applied locally over many generations. These regulations were seen to be practical as evidenced by centuries of trial, experimentation, study, application, and observation. This system functioned well so long as there were no major social changes.

The knowledge base of the Western system consists of published reports, records, data bases, documents, objective measurements and observations, and quantitative analyses of data. Information is exchanged freely and major effort is expended at making all information available. Shared databases, frequent meetings, networking, and outreach are key aspects of the Western system. In stark contrast, oral transmission with restricted access to information was the norm in the traditional system. In general, marine resource knowledge was kept within a family lineage [3, 31].

In the past the primary fishery management tool in the Western system has been called “regulated inefficiency” to reduce harvest. Restrictions were placed on gear type and closed seasons for certain species. The Western model previously was focused on single species fisheries. In recent years there has been an enormous effort underway to use MPAs, including no-take reserves for all species, to augment regulations. This recent effort is reminiscent of the traditional system which maintained fishery stocks through closures of reefs that allowed the ecosystem to recover as a whole.

The traditional system also placed a *kapu* (forbidden take) on certain species, generally based on spawning cycles.

There is a strong contrast between the two systems in the area of resource monitoring. The Western system must depend on infrequent quantitative surveys of environmental parameters and assessment of stocks. There is always a perception of "insufficient data" required for decisive management actions. The traditional system operated at the other end of the spectrum with continuous daily interaction between the managers, fishermen, and the reef resources. Practitioners of the traditional system had the perception that accurate knowledge of resource is held by the local master fishermen (*poʻo lawaiʻa*), elders (*kūpuna*), and commoners (*hoaʻāina* of that place), and had confidence in difficult management decisions such as reef closures.

5. Evidence of Increasing Synthesis

Over two centuries that have passed since first penetration of westerners into Hawai'i, traditional ways of managing fisheries have been replaced with Western and scientific methods at the formal level. However, traditionally informed ways still exist and continue to be exercised in the everyday practices of individual fishermen and their families. A great deal of information still exists in the oral tradition and written documentation. The past thirty-five years have witnessed a renewed interest in traditional ancient Hawaiian culture and practices. Voyages by the *Hōkūleʻa*, which was the first replica of a traditional double-hulled canoe, have been instrumental in this renaissance. Throughout Hawaiʻi there has been a resurgence in the study and practice of the Hawaiian language, ancient chants, hula, and other aspects of the Hawaiian culture. With this shift has come a reevaluation of traditional marine resource management [28, 66] and the previously unquestioned superiority of contemporary management regimes.

There is a growing awareness that traditional management of marine resources contained features that even today may be more effective than the Western management schemes that replaced them. Initial descriptions of the traditional versus Western systems suggest that the two systems are diametric opposites in almost every category (Table 1), yet we are beginning to observe the beginnings of a synthesis of the two systems that incorporates their best features. During the past decade the Western system of management in Hawaiʻi has adopted many aspects of the traditional system that it replaced, albeit using modern terminology and following practices acceptable in our contemporary democratic society. Perhaps the rapidly increasing human population and resulting resource depletion in Hawaiʻi is creating an environmental crisis similar to that which led to development of management in ancient times. The major features of this renaissance are as follows.

5.1. Ecosystem-Based Management (EBM). The emerging Western practice of EBM integrates ecological, social, and economic aspects in reference to humans as a major component of the ecosystem. This approach is philosophically the same as that of the traditional management scheme. EBM is concerned with the sustainability of human as well as ecological systems, which is a key feature of the traditional system. The EBM approach incorporates adaptive management in order to deal with uncertainties due to changes in the natural environment and changes caused by humans. This aspect is analogous to what is known of the traditional method. Tissot et al. [67] note that there has been progress toward key elements of ecosystem-based management (EBM) in Hawaiʻi, including a network of MPAs and community-based co-management. Progress has been slow and driven mainly by increased awareness of the risks facing coral reef ecosystems, which has led to new legislation as well as emergence of increasing local engagement in fishery issues. Key elements of EBM in Hawaiʻi include enhanced coordination among multiple agencies, establishment of place-based and community-based, co-management, and acquisition of data on both the ecology of the nearshore system and the role of human impacts for use in management decisions.

5.2. Integrated Coastal Management. The integrated coastal management concept is in many ways a modern variation of the ancient *ahupuaʻa* system, but lacking some of the cultural and spiritual dimensions of the traditional approach. Nevertheless, there is a growing appreciation among managers and within local communities of the whole-system approach to resource management. This approach includes an integration of the watershed, streams, and coastal regions. Recognition of the impact of land-derived materials on nearshore areas is a central theme in today's ecological science that is analogous to the traditional understanding of the native Hawaiian people. A statewide plan has been formulated by a consortium of the Federal and State management agencies, the Hawaiʻi Local Action Strategy [68]. Other contemporary examples include the Hanalei Watershed Hui (http://www.hanaleiwatershedhui.org/), East Maui Watershed Partnership (http://eastmauiwatershed.org/), and the Waiʻānae Sustainable Communities Plan (http://www.honoluludpp.org/Planning/Waianae/Waianae5yr/Waianae.pdf).

5.3. Education and Outreach. Contemporary managers recognize that the social and spiritual values of the individual are vital in the promotion of a sustainable environment. This was a key feature of the traditional system of management. Today there is increasing emphasis on the importance of public outreach and education. Standards-based curriculum development by the State of Hawaiʻi's Department of Education currently includes the teaching of traditional Hawaiian values and cultural practices. Integrated, interdisciplinary studies based on ancient Hawaiian concepts include "Project *Ahupuaʻa*" which stresses sustainability. The project's motto "*Mālama I Ka ʻAina*" refers to taking individual responsibility for stewardship of our natural resources (Hawaiʻi Department of Education http://www.k12.hi.us/~ahupuaa). Traditional values such as love of nature, preservation of the environment, recycling, proper disposal of waste, exercising voluntary restraint on catch, and so forth, are widely promoted by all natural resource management agencies. Most granting agencies require an education and outreach component for every project that receives funding. Thus, the key traditional social concepts of *mālama, kōkua,* and *kuleana* are being instilled in the younger generation as part of contemporary Western management practice as a means of achieving sustainability.

A program called "Navigating Change," is an education and outreach partnership created in 2001 among NOAA, FWS, the State of Hawaiʻi, the Polynesian Voyaging Society, Bishop Museum, and many other groups [69]. The program includes classroom curricula and multimedia materials and utilizes native Hawaiian voyaging traditions and cultural values to engage students and the public in learning about and caring for the NWHI as well as the MHI. As part of the project, voyages have been undertaken by the traditional Hawaiian double-hulled voyaging canoe *Hōkūleʻa*, to and through the NWHI as well as the associated educational outreach efforts for the voyages.

5.4. Community-Based Management. Community-based fisheries management schemes that involve fishermen and other ocean users in decisions and give them responsibility for care of resources have been most effective in fairly remote communities with a high level of subsistence activity and limited outside intrusion. The community-based management of the *Hui Mālama o Moʻomomi* on Molokaʻi incorporated knowledge from expert fishermen and marine scientists to implement conservation measures that would provide sustainable yields [28, 66]. The concept of *mālama* was employed to restore community stewardship, coupled with a science-based resource monitoring program. In addition, it applied the seasonal changes from the Hawaiian moon calendar to plan fishing activity. This holistic approach to the natural rhythms of the ocean, based on centuries of experience, revolve around the shifting tidal patterns and other environmental cues. Its success however has been challenged by both internal and external difficulties.

A more common model is that of local community organizations which voluntarily take on responsibilities for many aspects of resource management and community planning. For example, the Hanalei Watershed Hui (http://www.hanaleiwatershedhui.org/) on Kauaʻi is directly involved in identifying environmental problems in the marine, freshwater, and terrestrial environments and has undertaken corrective action. The West Hawaiʻi Fisheries Council (WHFC) on the Island of Hawaiʻi is an example of a volunteer community advisory group encompassing a large geographic area (147 miles of coastline) with a diverse population. Formed in 1998, the stated mission of the WHFC includes goals such as "to effectively manage fishery activities to ensure sustainability, enhance nearshore resources, and minimize conflicts of use in the area". The Council has successfully addressed several contentious issues such as aquarium fish collecting and gill netting and has been instrumental in developing and recommending management actions [70, 71]. Government agencies are also promoting the "grass roots" approach through other volunteer programs such as "adopt a stream" beach cleanups and "*makai* watch", an ocean awareness program similar to urban neighborhood watch programs.

The development of community-based co-management and an MPA network along the western Kohala-Kona coast of the island of Hawaiʻi provides an excellent model for development of EBM through an incremental approach [67]. There are major challenges to scaling up the West Hawaiʻi model to other islands within the state due to the limited extent of community involvement as well as legislative and administrative support of community-based co-management and MPAs. Furthermore the complexity of conflicts is much greater on more populated islands with diverse stakeholders.

The Executive Order that designated the NWHI Coral Reef Ecosystem Reserve in 2000 required that native Hawaiians, among others, provide advice regarding management and ensuring the continuance of native Hawaiian practices [69]. This mandate is being carried out through partnerships with native Hawaiian organizations and institutions aimed at identifying and integrating native Hawaiian traditional knowledge and management concepts into management actions.

5.5. Enforcement. Enforcement of management regulations under the traditional system was immediate and severe. Violation of certain *kapu* could mean instant death [24], although less severe penalties could be invoked. Under the traditional system, the importance of obeying environmental management restrictions was clearly understood. The present social system in Hawaiʻi is based on individual legal rights and due process. No one is advocating a return to some of the more extreme traditional practices, but there is growing support for more consistent enforcement of existing rules. An essential and fundamental premise of all fisheries management whether contemporary or traditional is that pertinent rules and regulations must be enforceable and effectively enforced. In Hawaiʻi, public concern over the lack of effective enforcement of fishing and marine resource laws is widespread and frequently voiced and reflected in surveys of both recreational [64, 72] and commercial fishers [63]. The Division of Conservation and Resources Enforcement (DOCARE) is the state's primary agency for enforcement of natural resource regulations. Organized initially in 1925 within the Division of Fish and Game, it was established as a separate division within the Department of Land and Natural Resources (DLNR) in 1978. In 1981 Act 226 of the Hawaiʻi State Legislature expanded DOCARE's traditional duty of enforcing only laws, rules, and regulations relating to the preservation and conservation of natural resources to enforcing all state laws and county ordinances on all state lands, beaches, shore waters, and county parks. As a result, the proportion of citations (including arrests) issued for natural resource violations decreased markedly and is presently among the lowest of all U. S. coastal states. To further hinder enforcement, Hawaiʻi DOCARE officers are prohibited from inspecting the bags, containers, or vehicles of noncommercial fishermen unless there is "probable cause" that a violation has in fact taken place. Preemptory inspections to determine compliance with regulations governing seasonal closures, bag and size limits, and so forth are thus prohibited. Ongoing enforcement trends and inspection limitations undermine the effectiveness of existing and future marine resource regulations. Major structural impediments remain to be resolved for enforcement to be truly effective.

There is a growing movement on the part of government to enhance enforcement by taking such steps as increasing the number of officers, entering into a joint enforcement agreement with NOAA/NMFS, placing interns with a legal background into the management agency and implementing rules permitting administrative handling of resource violations rather than through criminal procedures. An example of the positive shift toward stricter enforcement of environmental regulation in Hawaiʻi is provided by the unprecedented action taken by the government and the community in response to illegal grading that caused a 2001 mudslide which damaged Pilaʻa reef on the island of Kauaʻi. The cost to the landowner for not complying with environmental laws exceeds $12 million, which includes state fines of $4 million, county fines of $3,075, state criminal penalties of $0.5 million, and $8 million in remediation costs as a result of settlement of a federal Clean Water Act lawsuit brought by Kauaʻi community groups [73]. The settlement is believed to be the largest storm-water settlement in the country for violations at a single site by a single landowner and a major precedent for future enforcement action. As evidenced by these actions, the Western management system in Hawaiʻi has the same ability as the traditional system to bring about severe penalties for the breaking of a modern *kapu* if there is a will to enforce regulations.

5.6. Adaptive Management. Adaptive management is an iterative process of decision-making with the aim to reducing uncertainty over time through monitoring the response of the system to management actions. Using this approach, decision-making simultaneously maximizes one or more resource objectives and, either passively or actively, accrues information needed to improve future management. The ancient Hawaiians intuitively devised and operated such a system. The ponderous legal process currently used in Hawaiʻi for adopting and changing natural resource laws and regulations needs to be modified into a more responsive adaptive system. Some initial steps have been taken in this direction. One such example is the 2005 rule for harvesting sea urchins in a formerly closed Marine Life Conservation District (MLCD) in West Hawaiʻi. Based on input from urchin harvesters and the community, the West Hawaiʻi Fisheries Council developed a proposal which permits noncommercial harvesting from June 1 to October 1. Significantly, a moratorium on harvesting can be quickly implemented by the Board of Land and Natural Resources (BLNR) if conditions warrant it (e.g., overharvesting). In many respects this adaptive management parallels the traditional system.

Another example is an effort on the island of Kahoʻolawe, which is one of the main eight Hawaiian Islands but is unpopulated due to its former use as a military target range. In 1993 the Hawaiʻi State Legislature created the Kahoʻolawe Island Reserve consisting of the island itself and the submerged lands and waters extending two miles from its shore. A Kahoʻolawe Island Reserve Commission (KIRC) was also created to manage the reserve while it is held in trust pending establishment and recognition of a native Hawaiian sovereign entity. Recently the island was returned to the Hawaiian people. The KIRC is in the process of instituting traditional Hawaiian management practices based on effective adaptive management. With the input of *kūpuna* (elders, keepers of wisdom), the Commission initiated the first state regulations that allow for the use of the traditional Hawaiian system of closing access to a resource by *kapu*. *Kapu* provides for flexible and responsive management of natural and cultural resources within the Kahoʻolawe Island Reserve. The ability to provide for *kapu* closures protects any resources under pressure from overextraction. In addition, different practices of resource use, for instance traditional extraction methods versus modern methods will be allowed in designated areas, providing an opportunity to evaluate the impact of different resource extraction practices and methods on resource stocks. Thus far the *kapu* system has not met with a high degree of compliance. Fortunately, the remoteness and difficult accessibility limit the number of poachers in the Kahoʻolawe reserve. Management has joined with researchers that work together with *kūpuna* to assess the status of resources, supplementing traditional techniques and values with quantitative scientific methods. Further, measures are being taken to increase enforcement and instill a greater conservation ethic on the part of the public using Hawaiian ethical principles described previously.

There is a long-standing awareness on the part of the DAR that effective management requires intimate contact with the resource. Although final authority is still centralized in the DAR, a process of involving local communities in decisions is in effect involving public meetings and participation of stakeholders in the decision process. There is an overall trend of decentralization of management with local authority on each island. Biologists assigned to the various islands and districts are intimately involved in field work and with those people using the resource. Often this includes working closely with local organizations who are taking increasing responsibility for stewardship of natural resources. There is a general awareness that managers are more effective when they get away from the desk and meetings and spend more time in the field.

Unfortunately in some areas of the state, adaptive management is hampered by various legal and bureaucratic restrictions as previously described. Nevertheless there is continuing interest in the possibility of constructing laws and regulations that describe trigger mechanisms that will immediately lead to a management action such as closure to fishing in areas that are depleted to a dangerous level.

5.7. Limited Entry, Granted Authority to Fish, and Fishing Licenses. A number of mechanisms existed under the traditional system that restricted fishing access. A family lineage existed among the *poʻo lawaiʻa* (master fishermen who held and transmitted knowledge), which limited entry into fishing activity. Permission to extract resources was generally limited to those people living within the district, and under certain circumstances they were expected to share their catch with the management authority. Some analogies can be drawn with the Western system which has similar tools available for use. Freshwater fishers in Hawai‘i are required to purchase a fishing license, but noncommercial salt water fishers are not. Commercial fishers are required to purchase a commercial marine license for a nominal fee ($50) and are required to file monthly catch reports. Movement to a paid marine noncommercial fishing license with funds going to management of the resource would be a step closer to the traditional system which was based on the concept of *kuleana* which emphasized the responsibilities that accompanied the privilege of sharing in the resource. A recent survey of *kūpuna* and *kama‘āina* with extensive experience in fishing and marine resources recommended the establishment of just such a license to support fishery management [15].

5.8. Fishing Closures. The Western system of management continues to utilize regulations governing closures during spawning of certain species as well as size limits and gear restrictions. These regulations are occasionally updated and posted on the DAR website (http://hawaii.gov/dlnr/dar/regulations.html). In ancient times the bottom fishery was not closed during the spawning season because the primitive technology of the time did not deplete the resource. A paradox is that current management practice has placed a “*kapu*” or total closure on bottom fish during the spawning season because modern fishing technology has depleted stocks throughout Hawai‘i. In this case the Western management approach mirrors the ancient traditional practice in dealing with a depleted resource.

In addition to the *kapu* placed on the catching and consumption of specific resource species, traditional Hawaiian practices also involved the closing of entire reef areas for varying lengths of time. Although there are relatively few details known of the workings of these closures, they appear to be directly related to allowing resources time to recover from heavy harvesting or fishing pressures. The traditional system of closing (*kapu*) and reopening reef areas either as short-term or seasonal closures seemingly holds more appeal to fishers than long-term or permanent closures. Closure during the spawning season of a particular species is generally accepted. Seasonal closures by themselves are unlikely to be effective in protecting fish stocks [74]. A rotational closure system of alternate periods of open and closed fishing has been in place at the Waikīkī-Diamond Head Shoreline Fishery Management Area (FMA) on O‘ahu for 28 years. The results of this rotational closure have not been favorable. While fish biomass increased during the closure periods, these increases were insufficient to compensate for declines during open periods. The net effect was that between 1978 and 2002, total fish biomass in the FMA declined by about two-thirds and large food fishes (>40 cm) virtually disappeared from the area [75].

In the practice of Hawaiian resource management, permanent closures did exist for certain species as restrictions and prohibitions related to gender or social status. In addition, technological limitations of those times created numerous natural “permanently closed refuges” in the form of areas where harvesting was difficult or impossible. The modern development of boat engines, depth finders, GPS units, diving gear, underwater lights, and other modern fishing gear in conjunction with the emergence of a market economy have greatly changed the nature of fishing and the ability of fishers to impact the resource. Such natural marine refuges no longer exist due to modern technological ability to extract fish and other resources.

The Western management system in Hawai‘i has attempted to achieve the same result as the traditional *kapu* method through a variety of management strategies (e.g., size and bag limits, seasonal closures, gear restrictions, etc.) and a system of MPAs. The underlying concept of MPAs is that closed areas provide a refuge where fish can multiply in number, live long and reach optimal reproductive size. The protected areas serve as a source of renewal for fished areas through spillover and larval dispersal. In the MHI a total of only 0.4% of all coral reefs have complete no-take MPA status [76, 77]. The closed areas include a few small MPAs, military security restricted areas and the Kaho‘olawe Island Reserve which constitutes the bulk of such closures. An additional 5.7% of the reefs have restrictions on one or more types of gear or fishing activity (e.g., no gill netting, no aquarium collecting, etc.). Recent evaluations of some of Hawai‘i’s MPAs have shown that they can be very effective in terms of increasing fish biomass within MPAs [76] and abundance and fishery yield outside [78].

5.9. Creation of the Papahānaumokuākea Marine National Monument. On June 15, 2006 President George W. Bush signed a proclamation that created the Papahānaumokuākea Marine National Monument. This area encompasses 137,792 square miles of USA waters, including over 4,500 square miles of relatively undisturbed coral reef habitat. This is the largest protected area under the U. S. jurisdiction and one of the largest no-take MPAs in the world (http://www.hawaiireef.noaa.gov/). It also represents an immense step forward in bringing traditional practices into contemporary marine environmental management. Preservation along with education and outreach centered on the traditional Hawaiian spiritual and cultural values are major themes in the management of this Marine National Monument [69]. The Monument’s management plan is focused on engaging the Native Hawaiian community in active and meaningful involvement in the management process. There is an emphasis on increasing the understanding and appreciation of Native Hawaiian histories and cultural practices related to Papahānaumokuākea Marine National Monument. There is a major effort to cultivate an informed, involved constituency that supports and enhances conservation of the natural, cultural, and historic resources [69]. This program is engaging the Native Hawaiian community in active and meaningful involvement in management through its cultural working group comprised of Native Hawaiian practitioners, scholars, teachers, *kupuna*, fishermen, and community members. The Monument also sponsors multi- and interdisciplinary research projects that bring scientists and cultural practitioners and fishermen together to conduct research that is relevant to both groups, synthesizing approaches to knowledge acquisition, data, and ultimately developing an understanding of the natural environment.

In partnership with the University of Hawai‘i at Hilo, the Monument is training students to develop research projects that require the study of both marine science and primary traditional Hawaiian source material. A central management goal is to cultivate an ocean ecosystem stewardship ethic founded on traditional Hawaiian principles, contribute to the nation’s science and cultural literacy, and create a new generation of conservation leaders through formal environmental education.

6. Discussion

This paper presents a paradox in that two systems that are seemingly incompatible are presently showing the beginnings of integration that potentially involves the best features of each system. The emerging concepts that are readily recognized as features of the traditional system include adaptive management, integrated coastal management, community-based management, strong enforcement of regulations, ecosystem-based approach, fishing closures, and limited entry. Strong and shared cultural, social and spiritual values and a conservation ethic are the goals of the growing education/outreach program that will foster sustainability of resources in a manner found in the traditional method. Concepts of *pono* and *kuleana* are valuable tools for sustaining the environment. The strong and direct linkage between management, monitoring, enforcement and those utilizing the resource characterizes the traditional Hawaiian system and is a goal of the Western system.

The Western system that has gradually replaced the traditional system is centralized, often cumbersome, overly complicated and has many elements that could shut out community and “neighbor island” participation. In this area we can learn much from the ways of ancient Hawai‘i. It is now clear that some of the limitations and inefficiencies of the Western management system stem from the absence of the linkages found in the traditional system. Western managers are responsible for large areas and frequently have little direct contact with the resource except through data supplied by occasional surveys, catch statistics, environmental impact statements, and so forth. Management authority often is fragmented between many agencies and enforcement is widely regarded as weak and ineffective. Those using the resource in common are not given any responsibility for stewardship and are often only concerned with exploiting the resource to their private advantage at the expense of the resource. Decision-making is largely “top-down” in the Western management system. However, these decisions are increasingly influenced by the public through active participation in the political process, and by a growing environmental awareness that is manifesting itself by increasing community action in local areas. Thus, the Western management system has the ability to receive input from the community and can be responsive to social and environmental change. The major strength of the traditional system was the ability to be place-specific and sensitive to local issues as well as its ability to deal with any transgression with immediate action by local experts (*kupuna*). A major strength of the contemporary Western system is its ability to adapt to changing social, political, and economic conditions, and to threats presented by pollutants, shoreline construction, invasive species, human pathogens, and so forth that were not components of the original ecosystem. Further, the Western system has the potential to adapt regulations to deal with the major advances in fishing technology (high power boats, GPS, sonar fish finders, power winches, inexpensive monofilament gill nets, self-contained breathing apparatus, etc.) that have eliminated many of the controls that prevented overexploitation in ancient times. Anthropogenic impacts have steadily increased with the increase in human population and technological development to the point where global climate change is now a serious concern. Western management practices must be open to incorporate approaches that have been proved successful in the past.

Perhaps the best evidence of the growing synthesis of Western and traditional management is being provided by the Papahānaumokuākea Marine National Monument mission statement:

“Carry out seamless integrated management to ensure ecological integrity and achieve strong, long-term protection and perpetuation of NWHI ecosystems, Native Hawaiian culture, and heritage resources for current and future generations.” [69].

Delegates to the United Nations Educational, Scientific and Cultural Organization’s (UNESCO) 34th World Heritage Convention in July 2010, inscribed Papahānaumokuākea Marine National Monument as one of only 26 mixed (natural and cultural) World Heritage Sites in the World and the first mixed World Heritage Site in the nation. This action recognizes Papahānaumokuākea’s globally significant natural attributes that incorporate its living, indigenous, cultural connections to the sea and underscores the fact that for many indigenous peoples, nature and culture are one.

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Research Article

Socioecological Approaches for Combining Ecosystem-Based and Customary Management in Oceania

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This paper summarizes various integrated methodological approaches for studying Customary Management for the purpose of designing hybrid CM-Ecosystem-Based Management (EBM) systems in Oceania. Using marine conservation in the Western Solomon Islands as an example, the paper illustrates various interdisciplinary human ecological methods that can assist in designing hybrid conservation programs. The study of human-environmental interactions from a socio-ecological perspective allows us to discern people's understanding of their immediate environment, differential forms of local resource governance and use (e.g., sea tenure and foraging strategies), and existing conflicts between various stakeholders, among other social and ecological factors. More generally, the paper shows how coupled studies of natural and social processes can foster management regimes that are more adaptive and effective and that move toward holistic, ecosystem-based marine conservation in the Pacific Island region.

1. Introduction

Today, ecosystem-based management (EBM) is emerging as a leading approach for fisheries and coastal zone management around the world [1–3]. Essentially, EBM is the management of a particular ecosystem's structure, function, and processes to sustain and foster ecosystem services for human society, and, therefore, it focuses on the interconnectedness of ecological, social, and economic parameters for developing place-based management plans of an ecosystem [4]. For all its potential, however, EBM has been hardly ever implemented successfully because numerous problems can arise from competing interests among stakeholders, undeveloped or inappropriate governance structures, poor science, or lack of political will [5, 6]. Government-sponsored EBM plans tend to focus on protecting biodiversity and ecosystem function, which, while they are important for sustaining and fostering ecological services [7, 8], are not a major concern in many Pacific Island nations. Furthermore, local governments and stakeholders are not too receptive to government-sanctioned schemes that disregard local governance institutions and practices [9], particularly members of customary management systems that are still prevalent in many parts of Oceania.

Customary governance and management (CM) systems are cultural and historical practices designed to regulate the use of, access to, and transfer of resources locally, and they are informed by indigenous ecological knowledge and embedded in customary land- and sea-tenure institutions [10, page 202]. It is important to note that CM system are not designed for conserving marine or terrestrial resources but, rather, for controlling access to and use of natural resources. In addition community-based management regimes designed around CM are often vulnerable to internal community dynamics, and, therefore, biological and social success in resource management is always conditional and susceptible to failure. In the case of the Pacific Islands, simply, given the lack of government resources for coastal management (e.g., policing, monitoring), there is no viable alternative to comanagement or community-based management.

In places where forms of customary management already exist and are functional, the question becomes as follows. Why should EBM be implemented? The answer is that while the origins of EBM and customary management are different—one being created from scientific managerialism and the other from adaptive socio-ecological and historical processes—their conceptual and operational principles intersect in many ways, which creates an opportunity for their cross-fertilization. The objective, therefore, is to work with existing frameworks and not to replace them, although this creates a new series of challenges, problems, and opportunities for the hybridization of EBM with local governance and management frameworks. To achieve this in the Pacific Islands, we need to study various socio-ecological dimensions of human-environmental relationships that characterize customary management systems in the region, and this necessitates the use of interdisciplinary natural and social science methods. Researches, however, rarely spell out the actual approaches and methods used in their socio-ecological research and how such hybridization between forms of management is even possible.

In this paper, using marine conservation as an example, I summarize various integrated methodological approaches for studying CM for the purpose of designing hybrid CM-EBM systems in Oceania. I draw from my own scientific and applied work in the New Georgia Group in the Western Solomon Islands to illustrate various interdisciplinary human ecological methods that can assist in designing hybrid conservation programs. The study of human-environmental interactions from a socio-ecological perspective allows us to discern people's understanding of their immediate environment, differential forms of local resource governance and use (e.g., sea tenure and foraging strategies), and existing conflicts between various stakeholders, among other social and ecological factors. The paper also discusses how hybrid management systems can result in comprehensive conservation and management programs that while not always successful socially and biologically are better tailored to the local context. Practically speaking, such hybrid programs that operate at local scales [11, 12] are likely to be more successful than top-down, state-sponsored EBM plans, particularly in regions like Oceania in which local stakeholders retain a large measure of control over their natural resources.

2. Socio-Ecological Approaches for Designing Hybrid EBM and CM Systems

Most of the approaches illustrated in this paper were originally utilized to understand various dimensions of human-environmental relationships in the Solomon Islands, and the research involved over one hundred months of cumulative fieldwork by the author and his team members between 1992 and 2010. These human-ecological studies used a combination of qualitative and quantitative methods (a mix of ethnographic, geographic, economic, and marine science research methods) to delineate the dynamics of common property institutions and various facets of indigenous ecological knowledge and associated resource exploitation strategies. The research results were used to design a marine protected area (MPA) network in the Western Solomon Islands—MPAs being a primary tool of EBM—that now extends to cover more than six thousand hectares of diverse marine habitats in more than 32 MPAs (see [13]). The outlined approaches are fundamental to understanding human-environmental interactions, and, therefore, they are key to the development of hybrid EBM and CM programs for safeguarding marine biodiversity and ecological function in a culturally and socioeconomically compressive fashion. For this to happen, however, there are several components of CM that need to be disentangled and studied independently. Indeed there are also a number of components in EBM that need disentangling, but these are not presented in this paper.

2.1. Studying Customary Sea Tenure. Marine territoriality in Oceania, or customary sea tenure (CST), is a situation in which particular users have exclusive rights over resources and the ability to exclude nonmembers from accessing and using them. Tenure rights are distinguished through a number of sociocultural rules based on birth (primary rights), marriage and residence (secondary rights), and the direct transfer of rights by traditional authorities (usufruct rights) [14]. Indigenous entitlements allow users access to a benefit stream while excluding nonmembers. Research on Oceania's customary sea tenure includes cases from Polynesia (e.g., [15]), Micronesia (e.g., [16]), and Melanesia (e.g., [17]). Rights to sea space are not only characterized by control of geographical areas but can also entail rights to specific habitats, technologies, and species or a combination of these. Research has shown that these indigenous institutions are diverse and dynamic and that they have emerged from the amalgamation of traditional and imported practices [18]. Furthermore, these systems are more widespread than people actually recognize in the Asia-Pacific region, as recent research shows that these not only survive in Oceania but also across Southeast Asia [19]. Key to this discussion is that exclusive rights allow stakeholders to potentially institute access and use restrictions, fishing gear restrictions, minimum size and catch limits, and to protect breeding aggregations and establish temporal or permanent marine closures—strategies that are at the core of EBM. Next, I illustrate research that is important to understanding CST prior to the hybridization with other management strategies.

2.1.1. Sea Tenure: EthnoHistory, Genealogical Demography, and Settlement Patterns. Studies have found that the institutional strength of marine tenure is related to a number of socioeconomic factors, including marine resource dependency, distance to markets, and settlement patterns among others [20, 21]; factors that are often shaped by internal and external historical processes. History, therefore, matters when designing conservation programs that incorporate local governance institutions into management plans such as community-based management or EBM. For example, in the Roviana and Vonavona Lagoons, Western Solomons, a major basis for current governance differences between local communities lies in the history of regional patterns of settlement and demographic processes, as well as the way these interplay with the political economy to shape current territorial right claims and counterclaims. This kind of institutional variation, which can also be found in other areas of the region such as Papua New Guinea and Vanuatu [21, 22], raises a number of important questions. Do differences in governance and management practices exist among local communities? And what effects do historical demographic, economic, and political changes have on the organizational structure and managerial outcomes of common property regimes today? Researchers can use a combination of ethnohistorical, genealogical demographic, and microeconomic methods to answer these questions.

An initial step in ethnohistorical research is to determine the research population through a household census (either attained from government sources or independently by the researcher), followed by the design of a probability or nonprobability sampling strategy, which depends on the scope and nature of the research. A household questionnaire can be initially conducted across randomly selected households at each targeted village. Variables that can be included in the questionnaire include basic census data as well as questions on labour history, household income, household expenditures, rough estimates of task and time allocation to productive activities, commonly exploited commercial marine resources, asset ownership, and a series of other important issues that place the research population into a socioeconomic context. For an understanding of tenure regimes and their historical context, open and semistructured interviews can be conducted with household heads to explore in-depth, kinship, tribal history, marine territoriality, and particularly people's current perceptions of resource use and access rules and their actual behaviour within each tribal territory (i.e., tenure regime). For more in-depth ethnohistorical research, household heads interviewed during the census and questionnaires can be asked to identify key informants (or a snowball sample). Once identified, these informants can be interviewed with in-depth, open-ended, semistructured and structured interviews on regional oral history. Researchers can then cross-reference the oral history with existing archaeological and historical records to better understand the historical processes that have impinged upon current territorial configurations.

In the Western Solomon Islands, for instance, this information was important for designing hybrid management programs in the region because the household questionnaires and the oral history interviews provided (1) a qualitative review of historical settlement patterns and the identification of different forms of sea tenure in the region and (2) a quantitative measure of the geographical distribution of households having members with tribal affiliations to the major estates of the region. A simple chi-square, which was employed to analyze the distribution of households with at least one member belonging to the major estates, showed that the observed association between contemporary villages and existing tribal affiliations is significantly nonrandom. The results illustrated how peoples' asymmetric regional settlement patterns in the recent past have influenced their current capacity to institute cooperation and enforcement mechanisms communally today. Clearly, such an understanding is crucial when combining strategies such as CM and EBM for managing marine resources.

Studies in Papua New Guinea have shown the utility of reconstructing patterns of population increases over a period of one century using genealogical information [23]. Historical demographic processes have significant impacts on the social institutions that embed indigenous common property regimes such as CST. While there are a number of sophisticated approaches for reconstructing demographic trajectories, there are simple methods that can be used in nonliterate societies or where government data are missing (which is common in many areas of Melanesia) to gauge population trends over the last one hundred years. First, one needs to collect recent demographic data on general regional trends such as fertility, mortality, and population growth from the government (when data are available) and through a census (embedded in the household questionnaire) to gauge the possible effects of demographic changes on resource-management strategies. Simple methods like family mapping and spatial patterns of settlement can be used to further fine-tune information on population trends within an identified CST system in the region.

Family mapping is used to identify main family trees for sampling within selected villages of each sea-tenure territory, starting with the parents of the older living members of a community [24]. Once the main lineages have been identified, members of each family are asked to identify all children born (dead and alive) to each person in each generation beginning with the parents of the older living generation. Because older people find it hard to remember accurate dates, significant historical markers can be used to help people's memory, including WWII (1940s), the coming of development projects such as logging (1960s–1980s), and the new millennium (2000s). Next, informants can be asked to identify all old and new settlements established over the informant‘s life span to determine changes in spatial settlement patterns for villages within each territorial estate. Old people who have resided at a settlement for 75 years or more are asked to identify new settlements across three points in their lifetime (youth, maturity, old age). To allow for variation in settlement size, informants are asked to rank settlements according to a rough estimate of population size (e.g., single family, extended family, village, and so forth). Afterward, the average distance between settlements at the three temporal points are measured and plotted in a set of aerial photographs. Naturally, all this information can be georectified and imported into a GIS according to the estimated year of establishment to furnish coarse measures of population density change patterns over the last century. For example, in our Western Solomons research, these two approaches have allowed us to identify population trends within each sea-tenure regime and to extrapolate the possible effects of population growth on the spatial distribution of stakeholders, and consequently on their territorial strategies.

2.1.2. Sea Tenure: Socioeconomic Transformations and Coping Strategies. Data on demographic and spatial settlement pattern changes need to be combined with current economic activities and changing consumer demands to identify the institutional responses of each regional sea-tenure regime to current socioeconomic changes. Does an open-access common emerge from the breakdown of local institutions caused by transforming consumer demands, the market economy, and population growth? In the Western Solomons research, the economic behaviour of lagoon dwellers was investigated to determine the vulnerability and/or stability of indigenous sea-tenure institutions to changing consumer demands and to the encroachment of the market economy. For instance, in the Western Solomon program I recorded existing economic and livelihood differences between villages across sampling years 1994–1995, 1998–2003, and 2009 to explain the relationship between economic inequality and control of marine resources in the region. Various methods, including income and expenditure analysis, time-allocation studies, food diaries, and structured interviews, were used to understand people's livelihoods and food security and to measure their responses to changing economic conditions. These results, in turn, allowed for the design of MPAs that were sensitive to local coping strategies.

Understanding income and expenditure patterns is important for establishing each household‘s participation in the market economy. There are a number of methods to record this information, but for attaining a larger sample size, a diary method is best suited. A first step is to improve the survey instrument by conducting a pilot study, so that when applied, the survey schedule can be easily comprehended and completed by the selected members of each sampled household. For example, in the Solomon Islands research, I sampled households in targeted villages that had been identified by censuses conducted in 1994 and 2001. I selected members of randomly selected households (at least 50% of households across 15 villages) to keep a record of all economic activities for a week. The income schedule included questions ranging from day of transaction and goods sold to the member selling the product and the contribution to income by each gender. The expenditure schedules were formulated in a similar fashion. Several cycles were conducted to allow for a representative sample within the framework of seasonal variation in economic activities, particularly those concerned with marine resource exploitation. Data were compared across sampling years to examine recent developments and identify any economic and institutional changes associated with sea-tenure regimes. Understanding household income and expenditure and coping strategies is important because, as shown by Evans et al. [25] in Eastern Indonesia, a drop in market price for cash crops can negatively affect household well-being and, in turn, engagement in customary management strategies [10].

Showing how people use time is important for understanding the ways in which households meet their subsistence and economic needs. Time-allocation studies centre on people's use of time and their various productive modes. Analyzing time budgets provides a measure of daily activities in an objectively generated way, without having to rely on vague descriptions of behaviour gathered through interviewing alone. General trends in time allocation to productive activities can be extrapolated from household questionnaires, albeit more accurate methods of observation can be used. The spot check method, for instance, consists of randomly selecting times and dates to visit households and to record household members' activities as soon as they are observed [26]. Activities of absent members are recorded by asking present individuals. Then, the proportion of observations for each behaviour is calculated by dividing the number of observations for any given activities by the total number of spot check observations (for all activities). In the Western Solomons case, familiarity with local modes of production in the region allowed for informed coding of the activity categories. Randomness and generality were maintained by sampling behaviours throughout the year by local research assistants. These measurements helped to (1) discern regional differences in the use of time for income-productive activities in comparison with subsistence ones, (2) examine seasonal interregional shifting patterns of resource use, and most importantly, (3) examine time-use differentiation across the identified sea–tenure regimes and its relation to changing consumer demands and fishery commercial activities. Note that time allocation studies can be complicated and time consuming, and alternative methods such as ordinal ranking of productive activities can be used (e.g., [27]).

Finally, researchers can use interviewing and food diary methods to examine issues of household food security in different target communities. Structured interviews for understanding food security can complement other methods detailed in this paper by exploring (1) the number of meals prepared daily, (2) dietary diversity, (3) incidence of food shortage, (4) coping strategies for insufficient food, and (5) perceptions of food security and adequacy. In the Western Solomons research, I collected these data using a Likert-scale questionnaire design. In addition, food diaries were used to quantify actual household food intake. A member of the household was asked to keep a record for a week of all meals and food per meal consumed by each member. Data (food diaries and kitchen forms) were compared in order to determine if differences existed between sampling years and villages and to measure whether different resource management strategies within each sea-tenure regime had an impact on levels of household food security. In sum, demographic, spatial, economic, and nutritional data (among other potential data sets) can be analysed using a number of different approaches. For instance, Pollnac et al. [28] developed a number of MPAs success measures, which were analysed in relation to a number of independent variables categorized as contextual or project intervention factors, and then they used stepwise multiple regression to determine the most important predictors of success (e.g., levels of participation, decision making, and local population size, and so forth).

2.1.3. Sea Tenure: Institutional Cognition and Governance.

When designing any kind of management program in Oceania, researchers and policy makers need to understand people's differences and similarities in territorial cognition, their cultural attitudes regarding interloping, good governance, resource conflicts (as a proxy for enforcement of access), and why people may or may not cooperate to protect their natural resources. That is, identifying how people understand their territorial rights (i.e., what is claimed, or property rights) and how this translates into an effective activation of those rights—that is, actual behaviour—through the control of participating members and exclusion of interlopers is crucial for understanding current management choices. Various methods can be used to understand these processes, including cultural consensus analysis, structured interviewing, and the use of experimental economic (e.g., public goods games) to provide information about group cohesion, conflict, and likelihood of cooperative behaviour. The aim is to understand the mental processes (i.e., cultural consensus) that inform, among other things, people's current governance and management decisions in local communities, so that successful resource management can be achieved.

Cognitive anthropological techniques are used to investigate the extent of shared knowledge among human communities or to understand the underlying assumptions that inform people's decisions [29]. Cultural consensus analysis, for instance, can be used to develop a cultural model utilized by people under different territorial regimes. Such methods can help to assess whether differences exist among people in their cultural perceptions regarding property rights and management strategies. In the Western Solomons, standard ethnographic methods of participant observation and informant interviews were paired with cognitive anthropological methods that included agreement questionnaires, free lists, and pile sorts [30]. Free listing generated lists of words pertaining to property rights that helped us to identify underlying ideas and notions about sea tenure. In the pile-sorting exercise, informants were given a set of cards inscribed with words in English and Roviana (which were formulated from the free-listing exercise), and they were asked to divide the cards into piles consisting of the most similar concepts. Final groupings were expected to reflect implicit classification elements for a specific cultural domain.

In the data analysis, we converted the survey results into an agree/disagree format and conducted a consensus analysis [30]. The results showed that informants, regardless of age, sex, education, and so forth, were using a single cognized model to answer the survey questions regarding sea tenure. However, cluster analysis of the pile sort data using nonmetric, multidimensional scaling (MDS) revealed that meaningful divergence in cognition existed between communities regarding population size, interloping, and overfishing. These differences, in turn, corresponded with people's notions of positive or negative capacity within each identified sea-tenure regime to manage marine resources (Aswani and Herman, unpublished data; [31]). Gelcich et al. [32] have also utilized an MDS technique to examine stakeholder perceptions following the establishment of comanagement regimes in coastal Chilean communities that already had informal CM systems. Simply put, this kind of information is fundamental for designing management (e.g., hybrid EBM-CM) regimes that account for inter- and intracommunity differences in institutional and environmental cognition.

Understanding community conflicts is fundamental for designing natural resource management. For instance, researchers need to identify whether or not conflicts over natural resources exist in a given area. Researchers can use simple ethnographic methods such as interview schedules and household questionnaires to understand conflicts between participants and between neighbouring communities. The questions can address conflicts among each estate's stakeholders, changes in use and access rules, modifications of boundary delineations, local mechanisms used to enforce management decisions, monitoring capabilities, traditional and legislative conflict-resolution mechanisms, and poaching incidence for each area (carried out by inclusive members or neighbouring groups). The interviews and questionnaires can also inquire about changes in the number of incidences of illegal fishing practices (as measured by fines levied, fishers caught, etc.).

Finally, grasping cooperative behaviour between stakeholders living in a given region is important for designing successful conservation programs. For example, what are the individual-level variables (e.g., age, sex, education, and ethnicity) and group-level variables (e.g., governance institutions, and group coercive action) that lead to cooperative behaviour for managing natural resources? Does ethnic diversity, for instance, enhance [33] or diminish [34] social cohesion and cooperation in public goods situations? And, more generally, what historical, economic, and political circumstances lead people to make greater contributions to public goods such as engaging in conservation projects? In order to gauge cooperative behaviour among stakeholders belonging to existing governance systems, a number of research methods can be used. For the Western Solomons, we used a simplified version of a voluntary contribution *public goods game* (PGG) from experimental economics. The game is designed, in part, to understand prosocial behaviour (or voluntary actions such as sharing that can benefit others or groups), and it examines people's behaviour when individual and group interests conflict with each other [35]. Preliminary results indicate that religious and ethnic homogeneity favoured prosocial behaviour among players in each village and that free-riding was more common in socially heterogeneous hamlets. Once more, this kind of information is essential for designating MPA and other kinds of management regimes.

2.1.4. Sea Tenure and Ecological Assessments. Current interdisciplinary studies are analyzing the relationship between changing customary (traditional) or semicustomary (hybrid or nascent) management systems and the status of artisanal fisheries [36, 37], food security and health [38], and the effects of introducing diverse fisheries management schemes [13, 39]. This interest originates from the general failure of centralized and science-driven coastal fisheries programs in the Pacific region and a need to find alternative means of managing coastal marine resources. In the Western Solomons, we investigated the relationship between changing fishing intensity and management systems and the abundance of species that play a critical role in the resilience and vulnerability of coral reef ecosystems. Using a combination of marine science methods (see [40]), we investigated the ecological impact of localized subsistence and artisanal fishing pressure on parrotfish fisheries in Gizo Town (with weak sea tenure) in the Western Solomon Islands and used this information to conduct a comparative assessment of parrotfish abundance in open-access and customary closed-access coral reefs in nearby Kinda and Nusa Hope villages (with functional sea tenure). The results suggested that the erosion of customary sea tenure is fostering the rapid decline of already vulnerable fisheries around urbanized regions of the Western Solomons and that functioning customary management systems, even with high population densities such as in the Kinda and Nusa Hope areas, can positively affect the management and conservation of parrotfish fisheries. Other studies [37, 41] have also utilized marine science to examine whether customary practices conserve resources, and this research generally suggests that they do.

2.2. Human Foraging Strategies. Researchers seldom identify human foraging strategies in a given region when designing marine conservation programs. Yet, it is indispensable to study fishing behaviour, including spatiotemporal human resource exploitation patterns (e.g., seasonal changes in fishing gear), human responses to variability in inter- and intrahabitat relative productivity (as determined by catch rates) and the influence of this variability on fishing strategies, and human threats to particular marine habitats. This information can help in the design of permanent and seasonal closures modelled in accordance with human seasonal foraging patterns. Simply stated, integrating fishing behavioural patterns into program design enhances people's compliance with conservation or any other form of fisheries management.

2.2.1. Human Behavioral Ecology and Fishing. Human behavioural ecologists have employed optimal foraging theory models to predict various aspects of human foraging behaviour. In the Western Solomons research, hypotheses drawn from the patch-choice model and the marginal value theorem (MVT) [42] were tested to study fishers' patch choices and time use across spatiotemporal variation. Predictions from these models were utilized to analyze the seasonal movements of fishers, to forecast the decisions that fishers make in the types and abundance of fish that they prey on, the use frequency of marine habitats, and the fluctuating intensification of fishing efforts. For example, when using the patch-choice model, the hypothesis that overall time allocation to a habitat type (set of patches) increases when seasonal productivity for that habitat increases and is higher than that of other habitats was tested. On the other hand, overall time allocation to a habitat type decreases when seasonal productivity for that set of patches declines and is lower than that of other habitats.

Researchers can use two related methods to test this hypothesis: focal follows and self-reporting diaries. First, focal follows involves keeping time-motion records for fishers and measuring their catches. The diary method consists of recruiting randomly selected subjects to keep diaries of their fishing activities. Through direct observations and self-reporting diaries, seasonal foraging data for a sustained period of 10 years (1994–2004), covering more than 10,000 foraging events and 15,000 hours of fishing activities, have been compiled in the Western Solomon case study. In Roviana and Vonavona, these data were used to explore the effects of village and habitat type on mean net return rates and fishing event duration. The mean net return rate measurement is equivalent to the energy gained during fishing (the kcal value of the edible catch) minus the labour input (labour costs incurred during foraging, including travel, search, and handling times) divided by the total residence time at a fishing ground.

In general, results showed that overall effort was directed to the habitats with the highest yields and that fishers moved between habitat types, fishing grounds, and species assemblages across different seasons to maximize their mean net return rate. More specifically, the results provided a better understanding of (1) the distribution of fishing methods and the geographical disparities in yield and effort, (2) different relative habitat productivities across seasonal and spatial variations, and (3) the changes in time use as a response to resource abundance or scarcity. Variance in fishing return rates and effort data for different habitats in regional villages not only showed differences in foraging strategies but also hinted at the effectiveness of each community's resource-management strategies. The research generated data on local foraging patterns that aided in the MPA designation process. More generally, this type of research can help provide understanding of the strong interdependences between human foraging and the marine ecosystem, as well as possible environmental impacts of human activities—information that is vital for designing EBM or hybrid EBM-CM plans.

2.2.2. Geographical Information Systems (GIS) and Human Foraging. Socio-spatial information, such as artisanal fishing data, along with biophysical information can be incorporated into a GIS database for designing marine conservation programs (e.g., [43, 44]). In the Western Solomons case, human foraging strategies were distinctively conceptualized spatiotemporally by querying the GIS database and then displaying the data derived from the queries. The GIS was used to link the cartographic spatial data set of indigenously defined resource patches (615 sites collected with GPS receivers) with nonspatial attribute data (foraging data set). This allowed an analysis of the spatiotemporal relationships between particular marine habitats and the patches within them, on the one hand, and changes in their relative productivity and associated temporal increases or decreases in foraging effort by fishers of various regional villages to exploit these resources, on the other. More specifically, a query was run with the GIS that extracted the fishing events associated with each of the three locally recognized tidal seasons in the region (e.g., Roviana Lagoon). The visual representation of the foraging analysis made details more apparent and consequently gave a deeper understanding of intrahabitat variability and human responses to and strategies for dealing with this variability. In short, such knowledge can assist in designing marine conservation that is less disruptive to people's fishing strategies and, therefore, their livelihoods (see [45]).

2.3. Indigenous Ecological Knowledge. Scientists and policy makers are increasingly realizing the importance of incorporating indigenous ecological knowledge into inshore fisheries management (e.g., [46, 47]). Essentially, local fishers have first-hand experience and knowledge of the environment that they exploit, including knowledge about the direct assessment of local marine stocks and how they change over time, which is an expertise marine biologists rarely have. The value of local knowledge and practices for marine resource management is not just hypothetical because research has shown that marine protected areas that integrate IEK into their design can be successful biologically and socially [13, 22]. In this sense, indigenous ecological knowledge can be very helpful for designing conservation programs.

2.3.1. GIS and Indigenous Ecological Knowledge. In the context of artisanal fisheries management, GIS coupled with ethnographic and marine science research has proven useful in delineating and cataloguing reefs belonging to the Miskito Indians in coastal Nicaragua [48], for mapping fishing spots in southeastern Brazil and helping local fishers use this knowledge to defend their territories from industrial trawlers [49], and for systematizing indigenous ecological knowledge into geospatial data to guide fishery management in Bang Saphan Bay, Thailand [50]. Socio-ecological and spatial analyses can be particularly useful for delimiting the fragmentation and distribution of locally identified habitats across a particular region. Habitat mapping is important for cataloguing habitat diversity and extent and for identifying sites that incorporate the ecological processes that support biodiversity, including the presence of exploitable species, vulnerable life stages, and interconnectivity among habitats for designing marine protected areas [51].

In the Western Solomons, we developed a reliable and participatory way to produce maps of the benthos and associated biological communities. First, we developed a qualitative definition of benthic communities, which incorporated both physical and biological characteristics [52], using an indigenous classification of benthic habitats commonly found in some of the areas targeted for conservation. Next, we employed a large format plotter to print a two-foot by four-foot hard-copy map of the planned MPA (with a scale of approximately 1 : 3,500). Five men and five women were selected to be the photo interpreters based on their knowledge of the marine environment and their fishing experience. The participants identified the main reefs and principal benthic characteristics and jointly drew the boundaries of abiotic and biotic substrates using a felt-tip marker directly on the photograph. The resulting paper map with the respective benthic types was scanned, and the image files were loaded into the GIS for georectification. After georeferencing, each of the boundaries was traced using on-screen digitizing techniques that created polygons (shape files) of each of the benthic substrates (Figure 1). This local information was ground-truthed through an actual underwater visual census conducted by local field assistants. Once the marine science data was logged into the GIS, we ran a spatial query that selected all of the points from the marine science survey layer found within each polygon of the indigenously defined, dominant benthic attributes, and we ran a point-to-point comparison for an accuracy assessment of indigenous ecological knowledge.

Thereafter, fishers were interviewed to map resident taxa and associated biological events of significance at each habitat type and to identify fishing areas within the boundaries of the proposed MPA sites. These interviews allowed for a better understanding of local conceptualization of the marine environment (Figure 2). Fishers guided us in a small boat around the perimeter of each named area and named and ranked (according to abundance) the presence and distribution of common fish species and the locations of spawning, nursery, burrowing, and aggregating sites for particular species within each recognized ground and associated benthic habitat. The spatial extent of the area (represented as polygons) and the location of particular biological characteristics (represented usually as points) were collected with Global Positioning System (GPS) receivers and imported into our GIS database as a layer. To ground-truth this information, we conducted visual counts through a static seven-minute fish survey from the surface at each site, during which the selected fish species were observed within a radius of five metres. Relative abundance measures were calculated for all species in each general habitat type to compare their distributions across the MPA regardless of habitat size (rough cover percentage). Finally, to determine whether the Baraulu participants were significantly better than chance-guessing at which fish species were present in which areas, fish observations were matched to local assessments through various methods detailed by Aswani and Lauer [53].

The analysis of both data sets showed that equivalence between indigenous aerial photo interpretations of dominant benthic substrates and *in situ* field dive surveys ranged between 75% and 85% for a moderately detailed classification scheme of the benthos, which included nine locally defined abiotic and biotic benthic classes for the MPA seabed. For the second analysis, the visual fish census showed a strong correspondence between the qualitative deductions of the local informants and the quantitative analysis of noncryptic species' general habitat distribution and relative abundance. In sum, this research showed the accuracy of local indigenous knowledge of dominant benthic substrates and specific resident taxa, and it also revealed that participatory engagements with local peoples can aid in successful implementation of MPAs, and, by extension, in the design of contextualized EBM plans.

2.3.2. Indigenous Ecological Knowledge and Marine Science. Indigenous ecological knowledge tied with current marine science knowledge can facilitate the identification of species and associated habitats that most urgently need protection. In Aswani and Hamilton [54], we wanted to assess the commensurability of indigenous ecological knowledge with marine science for identifying ecological processes that support biodiversity, including the presence of species with significant ecological functions, vulnerable life stages, and interconnectivity among populations of certain species. Three main aspects of Roviana indigenous ecological knowledge about bumphead parrotfish (*Bolbometopon muricatum*) were identified as being most relevant for management and conservation through a blend of marine science and

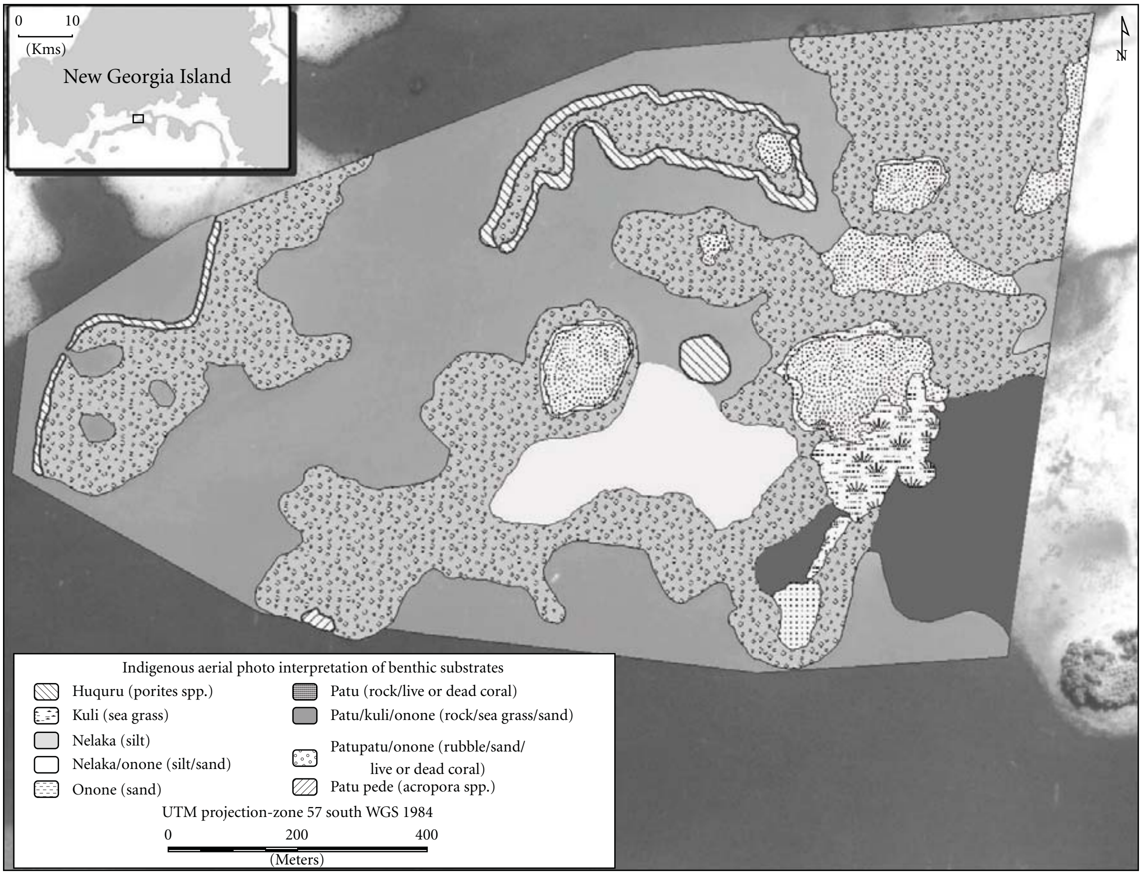

Figure 1: Informants' demarcation of predominant abiotic and biotic substrates on the aerial photographs of the Baraulu MPA, Roviana Lagoon [45].

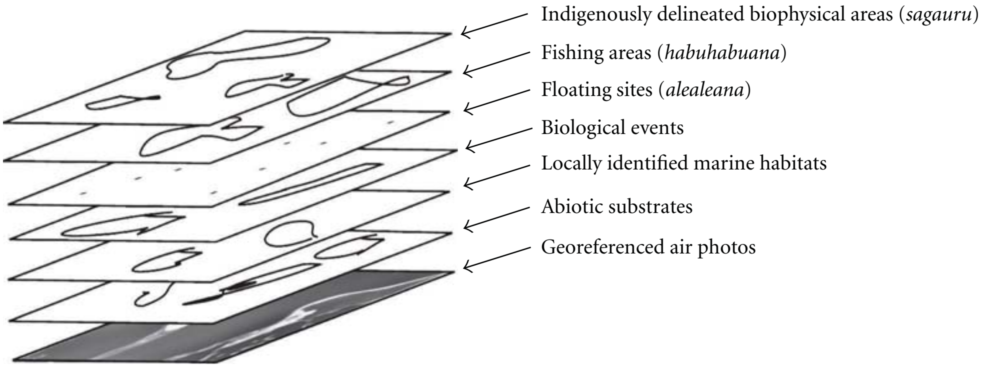

Figure 2: Indigenous hierarchical cognition of the seascape as represented by layers (or themes) in the GIS [45].

anthropological methods (e.g., interviews, creel surveys, and UVCs). We studied (1) local claims that fishing pressure has had a significant impact on bumphead parrotfish populations in the Roviana Lagoon, (2) the claim that only small bumphead parrotfish are ever seen or captured in the inner lagoon and that very small ones are restricted to specific, shallow, inner-lagoon nursery regions, and (3) the assertions made by local divers that bumphead parrotfish predominantly aggregate at night around the new moon period and that catches are highest at that time. Research results supported claims one and two, but did not support proposition number three.

Nevertheless, the results showed that in Roviana Lagoon, where many ecological and social changes have transpired within the lifespan of fishers, knowledge regarding ecological transformation can be detailed and useful. This research allowed for (1) verifying that the bumphead parrotfish is a species in urgent need of protection, (2) aiding in understanding how different habitats structure the size distribution of bumphead parrotfish, (3) helping in identifying sensitive locations and habitats that need protection, including shallow inner-lagoon sites that serve as nursery areas, and (4) becoming informed about how lunar periodicity affects bumphead parrotfish behaviour and catch rates. This information, in turn, allowed for the design of MPAs that integrated local knowledge with marine science—an approach that is of fundamental significance for designing hybrid CM and EBM plans.

2.4. Large-Scale Environmental Disruption and Socioecological Research. The long-term well-being of coastal populations is dependent upon coastal ecosystems and the critical economic and ecological services that they provide, including storm buffering and fisheries production. Yet the services provided by interface habitats are being degraded worldwide at an alarming rate [7]. This ecological degradation makes coastal populations increasingly vulnerable to massive environmental disruptions such as earthquakes and ensuing tsunamis. Researchers have suggested that rural populations with functioning customary/local management systems possess enough adaptive management qualities to make them more resilient (i.e., the capacity to absorb shock and transformation) to rapid environmental change (e.g., [55, 56]). Large-scale disturbances like hurricanes and tsunamis have provided researchers with an opportunity to evaluate, after the fact, if or how resilient those systems were to these disturbances.

On April 2, 2007, an earthquake measuring 8.1 struck the Western Solomons, which generated a tsunami that caused significant damage affecting both human and ecological communities. The scale of impact from the earthquake and tsunami varied greatly across different sites. In many villages this has caused a loss of the associated habitat biodiversity that previously supported a productive fishery—the basic source of household protein and income for communities of the region. For all the tragedy, this event offered our research team a unique opportunity to assess across this impact gradient the factors that may lead to the social, economic, health, and ecological resilience of coastal communities when they are faced with large-scale environmental disturbances. We asked the following. What are the socioeconomic, health, nutritional, and ecological consequences of catastrophic environmental events on coupled human and ecological systems? What are the human ecological responses (e.g., provisioning strategies) of coastal populations to environmental catastrophe? What social factors, such as cultural norms, property regimes, economic welfare, and regulatory enforcement, may lead to some communities being more socially resilient than others when faced with environmental disruption? And finally, do customary management systems increase the ecological and social resilience of coastal communities in the face of rapid change?

To answer these questions we are currently using a combination of interdisciplinary qualitative and quantitative research methods (many of which have been detailed in this paper) to (1) measure the socioeconomic effects of rapid and large-scale environmental disruption, (2) assess the concomitant responses of coupled human and ecological systems, and (3) evaluate potential drivers of system resilience across an impact gradient stretching from east to west in the Western Solomon Islands. In sum, resilience has long been recognized as an important component of effective resource management, but it has become increasingly important with the new emphasis on ecosystem-based management of marine systems. Our Western Solomons research program presents a good "before-and-after" experimental situation in which to measure the social and ecological vulnerability and resilience of coastal communities when faced by large environmental disturbances (as we have pre-earthquake social and ecological data for some affected communities). Grasping the human and natural responses to rapid ecological change is crucial to designing EBM plans and conserving marine ecosystems and associated services, particularly in the context of a changing climate and increasing human population [57].

2.5. Climate Change and Socioecological Research. Pacific Island communities are already experiencing the impacts of global and local climate change. They are especially susceptible to specific changes brought about by climate vulnerability (e.g., temperature variations, modifications of water flows and weather patterns, soil and water salinity or acidity, rain cycles, erosion, and coral bleaching). These changes have dramatically increased the levels of climatic unpredictability [58] and, consequently, the risks associated to the primary productivity and survival for coastal communities. Coastal communities are often also experiencing disproportionate levels of poverty, exposure to pollutants, or abusive external appropriation of the resources of their area. Climate change exacerbates the negative impacts of these marginalizing characteristics [59]. The possible socio-ecological adaptations associated to climate change may present multiple forms including environmentally driven migration, changes on the economic practices such as fishing and agriculture, forestry (e.g., intensification), institutional transformations, or new trading strategies [60, 61]—processes that can be measured using a wide range of social and natural science methods, some of which have been detailed in this paper.

Research on climate change is mostly done by physical or natural scientists. Socioecological research on climate change, however, affords research that measures the perceptions of local populations to the effects of climate change [62]. Social research on climate change combines scientific with the local perspectives on the issue. The advantage is that the local perspective allows researchers to gauge on the ground the social and ecological effects of an elusive macroscale phenomenon such as climate change. A local analysis is fundamental because climate change research requires the combination of diverse geographical scales (local, regional, international) and different levels of analysis.

Because social research in climate change lies at the intersection between scientific knowledge and local definitions of reality, an investigation requires the conceptual definitions of "change." Different social groups with different definitions of what is change or climate, for instance, are interacting in a dialogue that may result on important misunderstandings if there is no previous agreement on the meaning of the key concepts discussed. Currently, we are implementing a project in the Western Solomons designed to identify and analyze the local perception of “change” as well as measuring different local adaptations to such transformations. While we seek to identity transformations associated to climate change, our survey instruments are not designed around the concept of “climate change” but rather around any perceived changes around multiple dimensions of social and ecological reality. This is done to avoid *a priori* informant response bias and contamination (e.g., by information heard on the radio) [63].

Western Solomon communities are good candidates for climate change and adaptation research because (1) they are directly dependent on the environment and they still have a dominant subsistence economy (fishing and horticulture), (2) the environment they rely upon is fragile and fragmented and the different ecological patches of its landscape react differently to climate change, and (3) we have two decades of retrospective marine ecology and socioeconomic data. Local perceptions regarding climate change are being recorded through the use of various methods detailed in this paper (see, e.g., Section 2.1.3). Once compiled and analyzed, results of local perceptions will be matched against scientific studies (e.g., agricultural pests, lagoon hydrology) currently being conducted by our scientific team at the University of Queensland, Australia, to bring together the twin elements of traditional and scientific understandings for assessing the vulnerability of remote coastal communities living in the New Georgia Group, Western Solomon Islands. This will facilitate to fine-tune our resource management strategies (e.g., the current MPA network) to help local communities’ better cope with environmental unpredictability associate to climate change.

3. Discussion

Environmental research and resource management plans that divide biophysical aspects of a system from social ones are inadequate [55, 56]. Social and ecological systems are strongly coupled and highly complex, and they are changing rapidly, which places the social-ecological system at the centre of research that addresses the impacts of ecological change on human societies [64]. Today, methods for studying coupled human and natural systems are still being developed, and improving our conceptual framework and research methods for studying socio-ecological systems is fundamental to designing EBM. In addition, current studies ignore the role of individual actors in shaping the outcomes of coupled social–ecological systems—thus replicating the shortcomings of the ecosystems approach of the 1960s and 1970s—and this needs to be corrected through the use of actor-based models if we are to understand socio-ecological systems and the actors within them [57].

In the case of the Pacific Islands, existing forms of customary management offer a significant socio-ecological context for hybridization with EBM. It is important to remember that customary management is not designed to conserve biodiversity but rather to allow participants to manipulate the environment for human benefit and well-being through various socially embedded management techniques (which may or may not be successful in resource management). In Oceania, there are a number of challenges in harmonizing EBM with CM systems, and simultaneously being in sync with provincial and national regulations and policies [65]. The first and most important step, however, is to integrate EBM with existing localized forms of customary management at ecologically and socially relevant scales [9]. There are a number of conceptual and operational principles that make these two systems of management actually amenable to hybridization.

First, indigenous people in the Pacific Islands conceptualize their territorial estates holistically, whereby they do not dichotomize land and marine spheres of ownership. Sea space and land space exist continuously, and indigenous cognitive categories do not dissociate these realms as westerners do [66]. Quintessential examples include the Hawaiian *ahupua’a* [67], the Fijian *vanua* [68], and the Marovo *puava* [17]. In Roviana, Western Solomons, people do not cognitively disassociate land and sea estates. The word *pepeso* literally means ground, but it is used as an inclusive property domain that is divided into four main zones: the mainland, the lagoon, the outer barrier islands and their adjacent sea-facing habitats, and the open sea. The ocean is then divided into named sites that represent biophysical resource exploitation areas, geomorphologic features that allow or obstruct people from navigating, cultural and historical markers that define the seascapes, areas of significant biological events (e.g., spawning aggregations), and areas nesting major and minor marine habitats (see [69]). This indigenous environmental cognition corresponds with one of EBM’s core principles—the interconnectivity between and within terrestrial and marine ecosystems. The indigenous environmental conceptualization differs, however, in that it is embedded in indigenous sociocultural and religious practices in a way that EBM is not in Western society. Nevertheless, a holistic view of the environment is a first step towards reconciling these distinct world views.

Next, in many Pacific Island nations, islanders have *exclusivity/excludability* rights over their territorial states, and this allows for the implementation of many of EBM management tools, particularly limiting effort through a number of management strategies (e.g., taboo sites or de facto marine protected areas). Indigenous tenure rights identify particular users as having exclusive rights over resources and the ability to exclude nonmembers from accessing and using them. Rights of inclusiveness are distinguished via a number of sociocultural rules detailed previously. Entitlements, in any form, allow users access to a benefit stream while excluding nonmembers. The degree to which entitlement holders can exercise their territorial rights to exclude interlopers and punish inclusive members (thus managing their resources) varies from island to island and is often contingent upon the strength of traditional self-governance, population pressure, fishery commercialization, and a country’s legal recognition of customary sea tenure, among other things [31]. Key here is that exclusive rights afford stakeholders the capacity to institute spatial, temporal, gear, effort, species, and catch restrictions [10], or tools that are fundamental in fisheries management and EBM. Inclusive stakeholders, therefore, can

(1) protect vulnerable species and habitats (i.e., biodiversity and ecosystem function) and (2) protect susceptible life history stages (i.e., spawning and nursery grounds). In sum, tenure systems and associated customary management techniques, like EBM, can result in the protection of ecosystem structure and function, and they are place based, thus allowing stakeholders to restrict human activities that are detrimental to a local ecosystem.

Finally, as noted by Berkes [70, pages 17–18] customary management does not only entail ownership and use control of resources but a set of practices and perceptions that are embedded in the whole indigenous sociocultural, economic, and political systems. This socio-ecological system, therefore, nests (1) indigenous ecological knowledge of plants, animals, and the land- and seascape, (2) a resource management system in which IEK is put into practice to use and manage natural resources, (3) a set of social institutions such as customary sea tenure, which establishes the codes of social relationships between resource users and managers, and (4) a worldview that shapes environmental perceptions and gives meaning to the observed natural environment. The success of this integral system, in turn, is shaped by *adaptive management*, or the capacity of the system to change when faced with new social and environmental circumstances, and *social learning*, in which people learn about environmental uncertainty and feed this knowledge back into the management system. This is entirely in line with the core principles of EBM.

An essential objective of EBM is to integrate ecological, social, economic, and institutional perspectives, recognizing their strong interdependences [4]. Yet this aim has not been realized in actual management situations. Why, then, impose top-down, state-sponsored EBM plans in Pacific Island nations, when analogous management systems already exist in many parts of the region—especially systems that, as illustrated, share so much in common with EBM? In actuality, their similarities provide a fertile ground for the hybridization of traditional and modern environmental management systems. Note that this is relevant beyond Oceania, as localized systems of CM occur informally in many parts of the world, including the United States (e.g., [71]). In sum, if we are to cross-fertilize EBM and CM to create a holistic, hybrid management strategy, we need to identify, for both systems, the governance and management mechanisms at various spatial and temporal scales that result in positive institutional outcomes in terms of environmental sustainability, social equity, and institutional endurance.

EBM needs to resonate with local governance and ideational frameworks of references for its acceptance and integration with local systems of management. In the design of an MPA network in the Solomon Islands, my team and I selected MPA sites for their ecological and social value through a combination of local considerations and social and natural science research. Across many villages, traditional authorities and fishers in general agreed that an MPA neighbouring the village was the most feasible management strategy. Catch, size, and gear restrictions are difficult to enforce given certain cultural preferences and the extent of most sea territories, but the spotting of interlopers entering and exiting the MPA is not as difficult. Many sites were also selected through various research strategies detailed in this paper, including (1) an ethnographic study of regional customary sea tenure (CST) to assess, among other factors, the feasibility of implementing fisheries management in the area, (2) the incorporation of the visual assessments of local photo interpreters, who identified benthic habitats, resident taxa, and spatiotemporal events of biological significance, into a GIS database, (3) the coupling of indigenous ecological knowledge with marine science to study aspects of life history characteristics of vulnerable species, and (4) the incorporation of fishing time-series data (1994–2004) into the GIS to examine spatial and temporal patterns of human fishing effort and yields. The objective of the MPA network is to protect biodiversity and to sustain and improve ecological resilience in a cultural and socioeconomically viable fashion. This, in turn, will allow coastal communities to develop better responses to stochastic environmental events associated with global climate change, which invariably is what EBM fundamentally is.

4. Conclusion

This paper offers social and ecological scientists various integrated methods that transcend the false divide between the natural and social sciences, and it illustrates research approaches (among many) that integrate social and ecological analysis for studying human-environmental relations. The paper also illustrates how we can use these socio-ecological methods for conceptualizing natural resource management programs such as hybrid EBM and CM plans. From a local perspective, the systematic articulation of local ecological knowledge and cultural values through the natural (e.g., marine science) and social (e.g., anthropology) sciences can better promote local participation in the design and development of environmental management and produce a more inclusive approach to conservation. Community members in Oceania can better understand the biological value and the use restrictions of a management program when it builds upon local cultural practices with which the community members are familiar—a situation that facilitates rule enforcement and monitoring. Indeed, community-based management and CM are not a panacea for current environmental and socioeconomic problems in the region, but they offer the only viable and socially just context for meaningful resource management. More generally, coupled studies of marine and social processes can foster management regimes that are more adaptive and effective and that move toward holistic, ecosystem-based marine conservation in the region.

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Research Article

Scenarios for Knowledge Integration: Exploring Ecotourism Futures in Milne Bay, Papua New Guinea

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Scenario planning, a method for structured thinking about the future, offers an important tool for integrating scientific and stakeholder knowledge at different scales to explore alternative natural resource management and policy options. However, actual examples of such integration are rare. A scenario planning exercise was conducted in Milne Bay Province, Papua New Guinea, to integrate knowledge among scientists, ecotourism experts, and ecotourism stakeholders to explore possible futures for Milne Bay's nascent ecotourism industry. Four scenarios focused on climate change and technology, highlighting the risks and opportunities associated with rapid information exchange, and options to develop alternative ecotourism activities despite climate change impacts on natural assets. Although ecosystem-based management strategies were not investigated in detail by participants, all scenarios recognized and identified important cross-scale partnerships required to achieve sustainable management of natural resources and to promote ecotourism. An evaluation of changes in perceptions at the beginning and end of the scenario exercise suggests that participants became more aware of social and ecosystem processes occurring at broad spatial and temporal scales.

1. Introduction

Marine ecosystem management operates in a context of high uncertainty due to processes that occur at and across multiple spatial and temporal scales [1, 2]. This is particularly so in the Pacific Islands, where uncertainty in marine management stems in part from local cultural norms that can influence resource use and conservation decisions [3–5] and a general lack of data to support decision-making [6, 7].

In this context of uncertainty, planning for the future presents a challenge and is confounded by complex system dynamics such as nonlinearity and reflexivity—people's actions in response to future expectations can, in fact, lead to a different future than they expected [8]. Furthermore, beliefs about the future may be based on different epistemologies or knowledge systems [9]. Indeed, because the future is yet to happen, there is no "true" state of the future and, therefore, alternative characterizations or images of the future that illustrate a range of possible states may collectively provide the most insight into what the future might hold [10].

Scenario planning is a structured process of exploring the future in situations when uncertainty is high and controllability is low [11]. Alternative scenarios produced through such a process are in effect conceptual models or stories that describe how the future may unfold. In such uncertain, uncontrollable situations, scenarios have an advantage over more quantitative models (such as systems dynamics or agent-based models) in their flexibility, transparency, and, utilization of narrative to describe possible futures in all their complexity. Well-suited to participatory processes where there is a need to engage stakeholders without scientific or technical backgrounds, scenarios have been used in a range of resource-dependent communities in Asia and Africa for a decade or more [12–14]. To our knowledge, scenarios have not been widely applied in marine ecosystem management in the Pacific.

Though scenarios are increasingly used to explore the future, there has been little consideration of their role in integrating knowledge of different stakeholders, including scenario developers (but see [15]), and of their potential

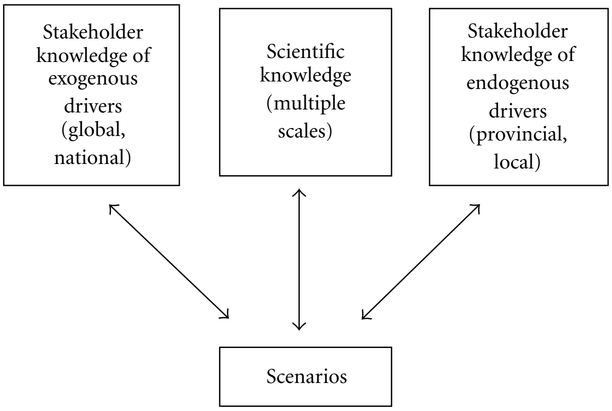

Figure 1: Process of knowledge integration through scenarios. The arrows extend in both directions to indicate an iterative process of information flows between the scenarios and the different knowledge sets.

as boundary objects; that is, they link individuals with different training, interests, and backgrounds [16]. Scenarios have at least two potential integrative abilities: first, they can integrate knowledge and underlying epistemologies of different actors, such as scientists, resource users, and decision-makers. While scientific knowledge can be obtained at multiple scales, from local to global, it often lacks detail and cultural context. Thus, even if future events can be predicted with reasonable confidence by scientific methods, it is difficult to predict how people will respond or indeed pre-empt these events. Scenarios, by bringing together participants' knowledge and scientific information in various forms, can produce a future understanding greater and better informed than any one information source alone. Second, it is difficult to predict how different events and human responses will interact across global, national, and local scales. Comprising information at multiple scales, scenarios help to identify drivers of change that are both exogenous and endogenous to the system of interest, as well as cross-scale drivers, that are not possible to evaluate by looking at information from one scale alone. The effectiveness of scenarios for multiscale analysis of ecosystems and human well-being was demonstrated in several Millennium Ecosystem Assessment projects, for example, in Southern Africa, the Mediterranean, Caribbean, and Northern Highland Lake District in Wisconsin [15, 17, 18].

The relationship between scenarios and knowledge is bidirectional; just as knowledge contributes to the building of scenarios, scenarios contribute to the expansion of knowledge (Figure 1). Scenarios can also be used to evaluate knowledge in several ways, by (1) indicating where knowledge needs to be updated as new information is available or perceptions of the future change, (2) assessing the relevance and credibility of scientific knowledge used to build scenarios, and (3) revisiting assumptions that underpin scenarios [18].

In this paper we view knowledge as comprising multiple realms of information, in line with Berkes' [19] description of a knowledge-belief-practice complex that includes not only traditional ecological knowledge but also environmental practices, social institutions, and world views. Knowledge also encompasses knowledge holders' perceptions of key drivers of future change and response options [20]. Much of the knowledge discussed in this paper relates to perceptions of the future which, despite the impossibility of "knowing" the future, are deeply rooted in individually and socially held knowledge [21, 22]. Knowledge systems are not always explicitly identified as such, and the integration process is often a subtle, tacit one.

Table 1: Drivers of change for Milne Bay's ecotourism industry, from most to least frequently mentioned by participants as a negative or positive driver.

Driver	Positive	Negative
Education	12	—
Technology	10	1
Climate change	—	9
Overharvesting and exploitation	—	9
Population growth	—	8
Industrialisation	2	6
Information and media	6	1
Government system and structures	—	5
Infrastructure	5	—
Growth in demand for ecotourism	5	—
Accessibility/transport	—	4
Corruption	—	4
Legal framework	3	1
(Rising) costs of fuel	—	3
Disease introduction and spread	—	3
Multiculturalism	1	2
Values	2	—
Urbanisation	1	1
Agricultural practices	1	—
Migration to Milne Bay	—	1
Crime/law and order	—	1
Resource demand	—	1

This paper discusses the use of a scenario process to integrate knowledge to explore possible futures for the ecotourism industry in Milne Bay, Papua New Guinea. Milne Bay's high biophysical and cultural diversity—the essence of its ecotourism appeal—imply that ecotourism will achieve the most success if it is planned and undertaken in the vein of ecosystem-based management [23, 24]; that is, it is managed at the provincial (i.e., landscape) scale and acknowledges social-ecological system complexity. An important imperative for knowledge integration exists in ecosystem-based management, which is inherently focused on management at multiple levels [25] and thus requires knowledge about the ecosystem to be drawn from different scales and, consequently, different knowledge sources. Scenarios provide a mechanism for integrating knowledge temporally (into the future) as well as spatially.

The scientific objective of the scenario process was to trial a method for better understanding of how the future is perceived by a particular stakeholder group, and the objective of the ecotourism industry was to better understand risks, opportunities, and strategies for future development. We explored knowledge integration through scenarios in two ways: (1) by bringing together scientific knowledge and provincial-scale stakeholder knowledge in a workshop and (2) by evaluating changes in perceptions before and after the scenario workshop. We highlight divergence in views that may need resolution and gaps where more information is needed, noting other scenario processes that have explored similar issues. Lastly, we discuss the utility of scenario planning for developing decision-making processes for marine ecotourism and multiscale ecosystem management strategies.

2. Methods

2.1. Study Area. Milne Bay Province, which includes the eastern end of mainland of Papua New Guinea (PNG) and some 435 islands (Figure 2), is an area of high national and global conservation significance due to its ecological diversity [26]. Though PNG's marine ecosystems are considered to be in excellent condition [27], degradation due to overharvesting is an acknowledged threat to marine resources in Milne Bay [28]. The past decade has seen community-based coastal and marine resource management and conservation advocated in the province [28, 29]. Ecotourism is being promoted by nongovernment and PNG government organizations as a preferred form of economic development because it potentially provides sustainable livelihoods for communities based on nonconsumptive utilization of natural assets, while also generating an incentive for local communities to conserve these assets. Thus ecotourism is a means of ecosystem-based management that delivers ecological as well as livelihood and well-being benefits [24].

In this light, members of Milne Bay's nascent ecotourism industry have begun expressing an interest in learning how to establish sustainable ecotourism. There is also a desire in the province to place control of tourism in local hands. In the past, tourism in PNG has, in large part, been conducted by multinationals who often take the funds out of the country. In Milne Bay Province there is a push toward ecotourism, following local and international recognition that the province in particular offers unique natural features, wildlife, and culture that tourists demand. Compared to other provinces that have allowed international firms to deplete their resources without sharing profits, a more conservation-oriented ethic exists in Milne Bay. However, a lack of infrastructure and institutional capacity are noted as major challenges [29], compounded by factors that are largely beyond the province's control that can impact tourism such as recent global economic shocks and climate change.

2.2. Workshop with Ecotourism Stakeholders. In June 2008, an ecotourism workshop in Alotau, the provincial capital, brought together industry stakeholders, including ecotourism operators, representatives of the Milne Bay Tourism Bureau, and representatives of nongovernmental organizations with an interest in ecotourism to discuss "big-picture" issues for the industry. Invitations to the workshop were sent to all known ecotourism stakeholders in the province, and twenty-one responded positively and attended. The workshop was facilitated by a locally based nongovernment organisation, with sessions run by two international scientists and two ecotourism experts. The workshop entailed a series of discussions over three days to discuss types of ecotourism, challenges faced, and approaches for understanding and overcoming these challenges. One of these sessions was devoted to a rapid (one-day) scenario-planning exercise to identify key drivers and uncertainties affecting the ecotourism industry, to consider alternative scenario storylines for its future, and implications for management of the natural assets underpinning the industry.

Following an introduction to the overall workshop goals, presentations were given by scientists and tourism experts on biodiversity conservation in Milne Bay, definitions and examples of ecotourism, the theory of scenario planning, and methods and examples of scenarios developed elsewhere. The scenario planning exercise built on previous experiences used to examine ecosystem services in a Southern African river basin and to explore alternative development trajectories for the Great Barrier Reef region [17, 30, 31]. The exercise involved a series of steps: (1) identifying a guiding question and timeline, (2) identifying drivers of change, (3) ranking drivers of change for importance and uncertainty, (4) identifying two axes of uncertainty and four scenario quadrants, (5) forming breakout groups to develop storylines for each of the four scenarios, and (6) presentation and discussion of the scenarios, including implications for managing ecotourism and ecosystems that support it.

The identification of a guiding question first required agreement on a definition of ecotourism. Ecotourism was defined as "responsible travel to natural areas that conserves the environment and improves the wellbeing of local people, and an enriching experience in which local communities' cultural relationship with their environment, developed over many generations, is shared by the guide with the traveller." In small groups, participants identified natural and cultural assets (marine and terrestrial) that they considered important for ecotourism on a map of Milne Bay Province (Figure 3). The group identified its guiding question as "Will it still be possible to have sustainable ecotourism in 2040?" The year 2040 was selected by asking participants to recall key events and trends in the past as well as considering scientific data and projections for population growth, climate change, and other variables that were highlighted in the presentations. Participants identified major changes such as collapse of the bêche-de-mer fishery, doubling of human population, changes in agricultural production, and PNG's independence, all having occurred within the past 30 years, serving as a frame of reference for envisioning the future. Thirty years also corresponds roughly to one generation, allowing participants to envision life when their children reach their age.

The group then identified drivers that might influence the outcome of the guiding question. Each participant was

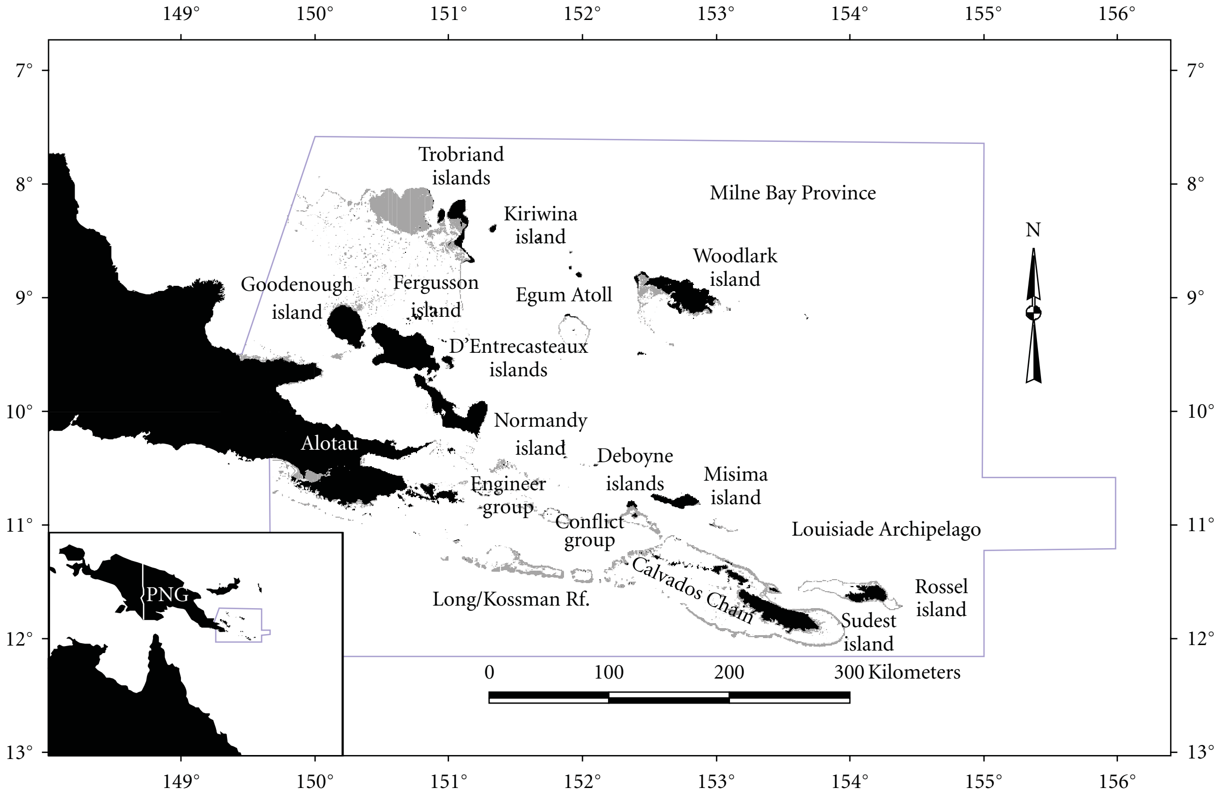

Figure 2: Map showing Milne Bay Province. Black areas represent dry land, and grey areas coral reefs and coastal habitats.

Figure 3: Composite map of important natural and cultural assets supporting ecotourism identified by participants.

Table 2: Perceptions of biggest threat to Milne Bay ecotourism, biggest opportunity for Milne Bay ecotourism and time required to establish a successful ecotourism industry in Milne Bay, pre- and post-scenario exercise.

Biggest threat	Number (%) of participants responding, pre-exercise	Number (%) of participants responding, post-exercise
Poor management of (eco)tourism industry	5 (27)	1 (5)
Poor governance	4 (21)	4 (20)
Extractive industry/overharvesting/exploitation	3 (17)	3 (15)
Economy	2 (11)	3 (15)
Geography	1 (6)	0 (0)
Change in biophysical environment/climate	1 (6)	8 (40)
Understanding and awareness	1 (6)	0 (0)
Media	1 (6)	0 (0)
Political will	0 (0)	1 (5)
Biggest opportunity		
Cultural link to environment	5 (28)	3 (16)
Income for local communities	3 (17)	2 (11)
Infrastructure (e.g., international flights, transportation)	3 (17)	3 (16)
Marketing and promotion of Milne Bay	3 (17)	1 (5)
Funding and support	2 (11)	0 (0)
Biodiversity, endemism, uniqueness, and beauty of natural environment	1 (6)	0 (0)
Training of tour guides	1 (6)	3 (16)
Climate change	0 (0)	1 (5)
Technology	0 (0)	2 (11)
Marine activities (e.g., diving)	0 (0)	2 (11)
Partnerships	0 (0)	1 (5)
Friendly people of Milne Bay	0 (0)	1 (5)
Time required to establish successful ecotourism industry		
At least 1 year but less than 5 years	2 (12)	1 (6)
At least 5 years but less than 10 years	7 (41)	6 (35)
At least 10 years but less than 20 years	7 (41)	6 (35)
At least 20 years	1 (6)	4 (24)

asked to write down the three drivers that they believed would be most influential for achieving sustainable ecotourism to 2040. Participants felt that it was necessary to distinguish positive and negative drivers, and it was agreed that each person would write down three of each type. These were displayed for the group and tabulated (Table 1). From these, participants selected climate change and technology as the two drivers that they felt would have the highest impact and were most uncertain. Education was more frequently mentioned than either of these as a positive driver, but there was thought to be less uncertainty associated with the future direction of education. In addition, overharvesting, while mentioned as frequently as climate change, was thought to have less uncertainty associated with its impacts.

Climate change and technology became the focal axes of the scenarios. The group identified unpredictable elements of climate change as changes in sea level rise, carbon credits, changes in temperature and extreme events, and their impacts on natural assets. Uncertain elements of technology were identified as the commitment of government to improve rural communications, impact on lifestyles, speed of adoption, market opportunities, cost, better sources of energy, micro-hydropower, the spread of environmental information, and government policies. To stimulate the development of the scenarios, the scenario facilitators suggested four possible ways that these two key uncertainties, climate change and technology, could combine.

(1) A climate change crisis happens in the near future and low-cost technology is available in Milne Bay Province.

(2) Climate change brings about gradual changes and low-cost technology is available.

(3) A climate change crisis happens in the near future and low-cost technology remains unavailable.

(4) Climate change brings about gradual changes and low-cost technology remains unavailable.

Four groups were formed, and each group was assigned to one of these combinations, with the task of sketching a brief, logical storyline, focusing on two questions: (1) under this scenario, how would you achieve sustainable ecotourism by 2040? and (2) what do you think are the most important collaborations or partnerships to achieve successful ecotourism in Milne Bay Province? The groups were also asked to name their scenario.

2.3. Evaluation of Participants' Perceptions before and after Scenarios. Little evaluation has been done of the impact of scenario processes in the stakeholder communities in which they are used [16] and in influencing participants' perceptions of the future and their ability to envision the future. We were interested in gauging the effect of the scenario process on participants' responses to questions about future ecotourism; therefore, one day before and one day after the exercise, participants were asked to individually answer the following open-ended questions.

(1) What do you think is the biggest threat to ecotourism in Milne Bay Province?

(2) What do you think is the biggest opportunity for ecotourism in Milne Bay Province?

(3) How long will it take to establish a successful ecotourism industry in Milne Bay Province?

Responses were analyzed for thematic content, and in the case of question (3), quantitative content (i.e., the number of years). Themes were identified and responses were categorized according to the most appropriate theme or themes. Responses with similar themes were grouped into a smaller number of categories (i.e., "Increase in extractive industry" and "Oil palm, mining, and logging" were both categorized as "Extractive industry/overharvesting/exploitation"). Responses in each category were then tallied.

3. Results

The working groups developed four scenarios based on interactions of the most uncertain drivers, the speed and nature of climate change, and the availability of low-cost, readily adoptable technology. Summaries of the four scenario narratives are presented below. As these were written for the purpose of presentation and discussion amongst the four groups, narratives were written in an informal style, with references to locally familiar place-names, for example. Below the participants' original text was preserved as much as possible, except for where clarification was needed.

3.1. Four Futures for Milne Bay

3.1.1. Down but Not Out, In Fact, Better Than Ever: New Life (Climate Crisis, Technology Available). High-level seas surge, flooding local roads. Coastal zones and small islets disappear under water. High rainfall events cause rivers to flood and there is severe erosion. Coastal homes are lost. The central business district of Alotau is flooded. The road to East Cape is cut, and the North Coast fringe is lost to sea level rise. Thanks to low-cost technology, everybody has access to mobile phones, even on the islands, and some have internet. Thus they are aware of the risks of climate change and are ready to respond.

The effect of the climate change "crisis" is to stimulate action, to start a new life. Looking to 2040, there will be a need for proper planning to relocate infrastructure, roads, health centers, schools, villages, and guesthouses. There will be mangrove replanting, Coast Care, conservation, education, awareness, and a focus on practical on-ground actions. An emphasis will be placed on environment and community life. Business activities will be green-certified and eco-friendly, links will be made into carbon markets, with support from overseas funds. Energy will be provided by a mix of hydropower, wind generation, solar, and biodiesel. Internet advertizing and promotion of the region as an ecotourism destination will be standard practice—Milne Bay's green culture becomes its selling point.

Because of the need to relocate villages and services and build new infrastructure, the climate change crisis presents an opportunity to incorporate technology appropriately into villages. This requires partnerships with organizations specializing in appropriate technology, the environmental, forestry, sustainable agriculture, planning, civil engineering, electrical and communication sectors, and with donor agencies (such as AusAid, the European Union, Japan International Cooperation Agency and the United Nations), carbon traders, and the Government of PNG.

3.1.2. Kula Connections: Sailing to the Future (Gradual Climate Change, Technology Available). Climate change is a risk, but in the absence of an immediate crisis, there is time to prepare for it. The Kula Ring, a traditional system of trade between the islands, is reborn in the Information Age. Technology allows better information exchange, networking between tourism businesses and partners (e.g., NGOs), and education, energy, and transport improvements. With this information exchange comes a coordinated approach to diversifying ecotourism products.

There is a risk of increased information exchange that leads to the loss of cultural uniqueness, authenticity, and the ownership of ecotourism opportunities to foreign investors, but this can be addressed through legislation and increased awareness, again using networks and partnerships to assist. Technology can also support use of alternative energy, fuel-efficient transport, better communication between operators and with partners, tourist markets, and global connections. This is complemented by better education at the village level, including about ecotourism.

3.1.3. Escape to East Cape: Island Hoppers (Climate Crisis, Technology Unavailable). Sea levels continue to rise at the current rate. Low atolls disappear, including Survivor Island at Haloweya and small islands in the Conflict and Engineer groups. Sea currents become stronger, jeopardizing travel by traditional sailing canoes, and making diving and snorkelling unsafe. There is migration from the affected islands to the mainland, creating tension between those displaced and

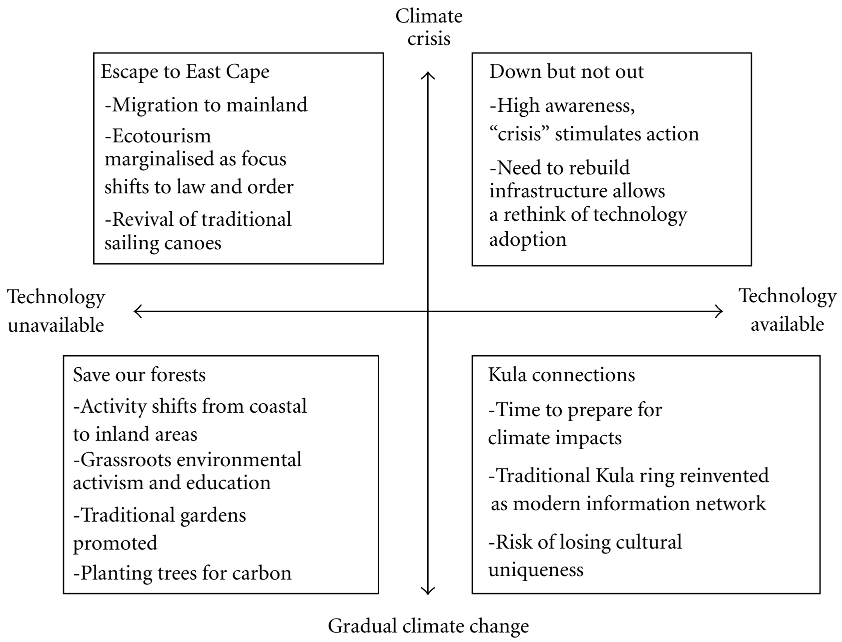

Figure 4: Four scenarios based on interactions of the most uncertain drivers identified by the stakeholder group: the speed and nature of climate change and the availability of low-cost, readily adoptable technology.

residents. Some tourism attractions, such as white sandy beaches and critical wildlife habitat, are lost.

Ecotourism becomes a marginal industry. There is a lack of effective communication, information, and transportation for tourists and locals alike. However, around Milne Bay the use of traditional canoes increases, and interest is revived in promoting cultural tourism, but the canoes need to be better built so that they are more reliable—especially without a mobile phone network for emergency calls. Tourism persists, but in a cautious "island-hopping" style; visitors consist only of the few most adventurous explorers.

Priorities are law and order to maintain security and conflict reduction. However, education and awareness are high on the agenda, and Alotau becomes a hub of research activity on climate change impacts in the Pacific. Actions include (1) forging relationships between groups at multiple scales to share information, much of it through word-of-mouth, (2) proactive lobbying of government and NGOs for funding to improve communications, (3) improving government action to resettle migrants, and (4) introducing food crops tolerant of salinity rise for local food supplies and tourists.

3.1.4. Save Our Forests (Gradual Climate Change, Technology Unavailable). Milne Bay reverts to low-technology, grassroots approaches to environmental awareness and conservation. Anticipating rising sea levels, people shift their activities from coastal to inland areas. Wise use of traditional farming—whereby gardens are passed down to children—is promoted, rather than clearing virgin forest and causing hillside soil erosion. People plant more mangroves and traditional trees and quickly engage in the carbon trade and lobby for government policies to help protect forests before more severe climate changes occur. Strategies also include teaching environmental issues in schools, including global climate change and carbon trading, using media to raise awareness, preserving cultural values of skull caves, awareness of sacred sites and protocols, preserving wildlife, teaching young ones to respect the environment, and training resource owners, NGOs, churches, and Local Level Government.

3.2. Comparison of Pre- and Post-Scenario Workshop Responses. The pre- and post-scenario perceptions regarding biggest threats and opportunities to ecotourism in Milne Bay Province and the time required to establish a successful ecotourism industry in Milne Bay Province are shown in Table 2.

Climate change and related environmental change was the most frequently mentioned threat at the conclusion of the scenario exercise (40% of participants), compared to only one participant (6%) mentioning it at the start. Poor management of the ecotourism industry was much less frequently mentioned (from 27% before to 5% after) while economy was slightly more frequently mentioned (from 11% to 15%) and extractive industry and poor governance remained similar. Understanding and awareness, media, and geography, collectively mentioned by 18% of the participants at the start of the exercise, were not mentioned at the conclusion, while political will was mentioned by 5%.

Among the biggest opportunities identified before the exercise were the cultural link to the environment (28%), income for local communities (17%), infrastructure (17%), and marketing and promotion of Milne Bay (17%). After the exercise, an equal number of participants (16%) mentioned the cultural link to the environment, infrastructure, and training of tour guides. Post-exercise responses were more

Table 3: Action items identified during the workshop to support goals identified in scenario process. Each item was assigned to an individual or group to lead.

(1) Create a list of web-links and other contact details and circulate to workshop participants.
(2) Create a list of inbound tour operators from the Port Moresby airport with contact details for Milne Bay Tourism Bureau (MBTB) use.
(3) Provide examples of Tourism Profile Surveys for operators to consider (via MBTB).
(4) Create a list of free web tools operators can use (always advising MBTB so they are aware).
(5) Distribute photo of map created on Day 1 of workshop.
(6) Circulate presentations to all participants.
(7) Circulate report from this workshop.
(8) Provide copy of the image of the decimated landscape of Madagascar shown in the workshop as an example of poorly-managed tourism, to raise awareness.
(9) Develop a Code of Practice that differentiates ecotourism businesses from mainstream tourism.
(10) Establish system of Dive Fees, following aspects of Raja Ampat (Indonesia) model, through the following steps:
    (a) Build awareness with the Minister
    (b) Develop 5-year strategy
    (c) Work with policymakers to write legislation
(11) Begin data collection to undertake Value Chain Analysis of ecotourism industry (analysis of long-term changes that might affect individual operators and their connections to others in the market).
(12) Meeting of participants with MBTB to discuss collaboration in the future and any role they might play to assist, identify further actions and draft visitors' survey.

diverse, with climate change, technology, marine activities (e.g., diving), partnerships, and friendly people of Milne Bay all noted as "opportunities", although not identified before.

More participants (30%) stated that it would take longer (>10 years) to establish a successful ecotourism industry in Milne Bay after the exercise than before, when only 12% stated that it would take this long. After the exercise, four participants said that it would take at least 20 years.

4. Discussion

4.1. Interpretation of Scenarios. The scenario workshop revealed four conceptual models of Milne Bay Province: one a crisis-inspired, technology-embracing paradigm shift (Down but Not Out), one a high-technology, information-propelled future, in which people are proactive but cautious (Kula Connections), one championing a back-to-basics, grassroots activism (Save our Forests), and one of struggling through, with increasing tensions accompanying rising seas (Escape to East Cape). The four scenarios revealed both risks and opportunities associated with the two key drivers, climate change and technology. For example, while climate change impacts were initially viewed as threatening, participants noted opportunities associated with climate change such as the development of alternative ecotourism activities, and for the region to become a center for climate change research. Conversely, while low-cost technology was initially viewed as beneficial, participants recognized threats to ecotourism posed by rapid information exchanges over high-speed communication networks. Interestingly, the two scenarios that dealt with a climate change crisis explored solutions to possible problems in the most detail.

It appeared that the terms "climate change" and "technology" were overwhelmingly interpreted by the scenario groups as, respectively, "sea level rise" and "information." The narrow focus is not unexpected given the short time that groups were given to work on their scenarios but may also reflect an understanding of these issues that is limited to actual experiences, such as the loss of coastline and infrastructure, and the importance of radios, mobile phones, and internet. In particular, slower or more subtle impacts of climate change on ecotourism, such as coral bleaching, were not explicitly identified by participants. As a possible consequence of this narrow focus, management strategies for vulnerable natural assets underpinning ecotourism were not explored in any detail. Only two scenarios, "Down but Not Out" and "Save Our Forests" discussed ecosystem management, and actions were largely limited to community scale intervention such as mangrove planting to protect coastlines from sea level rise. In an extended exercise, scientific information could provide more detailed dynamics of the driving forces and projected impacts of climate change and technology while provincial stakeholders could provide locally meaningful contextual details such as place-names, language, history, cultural norms, as well as detailed observations over a long time period [21]. By integrating both forms of knowledge, a wider range of implications of these drivers can be addressed [15].

Scenarios have been used in other studies to explore tourism and its vulnerability to climate change. For example, the Caribbean Sea Ecosystem Assessment evaluated changes in Caribbean ecosystems and ecosystem services and options for responding to these changes [15]. Reliance on tourism was identified as a major uncertainty around which scenario storylines were developed. New marine diseases and sea level rise were discussed as particular threats to the tourism industry as consequences of a changing climate. Scenarios have also been used to explore the future role of tourism and ecotourism in a developed country context and, specifically, how ecosystem degradation impacts on tourism appeal and, in turn, regional economies and property values [11, 31].

The role of technology in supporting tourism development does not seem to be well-explored in scenario exercises, although technology has frequently been identified as a key driver in many scenario processes [31], likely due to the magnitude of technological impacts and their uncertainty in influencing the future. Probing a wide array of direct and indirect technological developments and their potential consequences for ecotourism in Milne Bay would be a significant, but necessary, undertaking in follow-up scenario work.

Discussion of the scenarios suggested that building social networks and partnerships between members of the ecotourism industry and affiliated organizations, such as international tourism bodies and nongovernmental organizations, is particularly important. Participants also discussed the need to adopt long-term plans and visions for the ecotourism sector, to avoid progressing down an undesirable pathway from which there is no easy return, and to reach consensus on aspects of tourism regulations, marketing, and promotion so that standards can be developed. Action items were identified at the close of the workshop to support these goals (Table 3).

4.2. Insights and Future Directions. The use of scenarios, like other participatory modelling processes, to integrate knowledge about the future stipulates careful consideration of objectives and outcomes [32]: is it to support local people to understand scientific information, to persuade local people to adopt scientists' views, to elicit local perspectives for the value they add to scientific understanding, to learn from each other, or to test methodologies? Scenarios can effectively do all of the above. In our case, the scenario process and evaluation indicate that scenarios helped participants to think about the future in new and different ways, to reveal where views about the future diverge, and where understanding is lacking.

Our evaluation of changes in perceptions at the beginning and end of the scenario development process suggests that among participants, changes in perceptions occurred regarding major drivers of change and effective responses: awareness increased of processes occurring at broad spatial and temporal scales and the need for longer-term planning. In interpreting these results, it should be noted that (1) no standard definitions were given for the terms "collaboration," "partnership," and "successful;" (2) participants' interpretations of the question about length of time required to establish a successful ecotourism industry appeared to vary, with some responding about individual tourism operations and some about the industry as a whole; and (3) scenarios were not the only activity undertaken during the workshop. Despite these possible shortcomings, the evaluation does provide at least a general picture of how beliefs about the drivers of tourism may have evolved over the course of the workshop.

We offer a few insights on the role of scenarios in integrating knowledge. First, we acknowledge that scenarios rarely integrate information explicitly, but they do so implicitly by building stories based on different information sources. Scenarios risk being a "knowledge dump": a process of "free-floating" [33] exploration whereby issues of accuracy and precision, weighting, standardization, and resolution of discrepancies do not often receive attention. That said, there is a trade-off between quantification and transparency and flexibility. It may be useful to develop both quantitative and qualitative scenarios to suit a range of purposes [15].

Second, the sequence of information insertion is important. There is a need to gauge perspectives on perceptions of future change before and after information is presented, and we have included such an evaluative component in our ongoing research. However, there is another trade-off between giving too little information to enable participants to address a full range of drivers that impact them, risking biased or unfounded conclusions, and giving too much information, risking confusion or disinterest. Finding the right balance is key. A related challenge emerges in evaluating perspectives and how they change without actually influencing them before the evaluation takes place.

While scenarios can help to build consensus [34], a diversity of knowledge and perspectives on the future can be of great value for learning [15]. Future uncertainty means that surprise is likely, and the most robust strategy is often to invest in a range of options. For this reason, ample space and time is necessary to accommodate differences in opinion.

The experience above lays the groundwork to further develop and refine the scenarios for application to ecotourism and broader ecosystem management in Milne Bay, where the scenarios approach as a future exploration and knowledge integration tool remains novel. In follow-up scenario work, the future visions described in the workshop could be developed in parallel with future visions at the scale of the ecotourism operators and their communities or villages. The village-scale perspective could provide a local reality check for the scientific aspects of the scenarios, while also offering a level of detail beyond that afforded at the provincial scale. A next step for using these visions might entail presenting the four regional scenarios to local stakeholders, eliciting their views and responses and feeding these back to the regional scenarios. Alternatively, scenario development could begin at the village scale and be presented to provincial stakeholders. Such cross-scale scenario development is useful for effectively dealing with the complex problems presented in futures analysis and tends to increase the relevance of scenarios at all scales of interest [18].

4.3. Development of Ecosystem-Based Management to Support Ecotourism. Ecotourism is widely promoted in Milne Bay as a potential panacea for reconciling the need to improve livelihoods with the conservation of globally recognized marine and terrestrial biodiversity values [29]. In spite of the benefits of ecotourism being implicitly understood by the stakeholders at the workshop, there was little discussion of the need for ecosystem-based management *per se* to conserve the natural assets underpinning the industry. Specific management actions were only mentioned in two scenarios, and these largely related to community scale planting of mangroves to protect coastline from sea level rise. However, elements of ecosystem-based management were present in the scenarios and deliberations that followed, such as the need to plan ecotourism at a large landscape scale that incorporates a range of terrestrial and marine ecosystems, and for ecotourism operators to involve and ensure benefits to local villages to discourage activities that are ecologically detrimental.

The scenarios workshop may have had a subtle influence on progressing ecosystem-based management of marine and terrestrial assets by raising awareness of broader temporal and spatial scales. The importance of cross-scale partnerships was recognized, and specific stakeholders identified, in all four scenarios. These were mentioned in terms of promoting ecotourism and sustainable natural resource management, and specific post-workshop actions were identified to develop them. Such partnerships are known to be crucial for the successful development of ecotourism in developing countries, since they provide multiple sources of knowledge, financial, human, and social capital [35], and are a prerequisite for establishing adaptive co-management of complex social-ecological systems [36, 37]. Consequently our scenario planning approach may have accelerated the process of establishing ecosystem-based management in Milne Bay by increasing awareness and social networks amongst the ecotourism stakeholders at the workshop and identifying further partnerships necessary for consolidating the sustainable development of the industry.

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Review Article

Creating Effective Partnerships in Ecosystem-Based Management: A Culture of Science and Management

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An ecosystem-based management research partnership between the Hawaiʻi Institute of Marine Biology and Office of National Marine Sanctuaries, specifically with the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve and, later, the Papahānaumokuākea Marine National Monument, provides a case study to analyze integration of scientific research into management plans through collaborative communications. Ecosystem-based management seeks input from disparate stakeholders and requires effective communication systems for the public, science, and management partners that bypass differences in organizational culture and communication styles. Here, we examine a successful partnership within the framework of ecosystem-based management to survey and evaluate cultural differences, understand what facilitates collaborative communication, highlight factors that impede a successful partnership, and identify areas for improvement. Effective communication has been achieved through an analysis of the organizations cultures and structures to better define communication links. Although specific differences were noted in organization and style, successful integration was accomplished through techniques such as the development of symposia and semiannual reports. This paper will explore the organizational culture analysis and structure evaluation, which are components of a larger study. This science management integration project is an example of how organizational analysis can lead to recommendations for improved communication and integration of science and management.

1. Introduction

Single-species management has often failed to deal with the multitude of issues associated with complex, isolated, and large ecosystems. To address this, ecosystem-based management (EBM) has emerged, which uses a holistic perspective to focus protection on a large area as opposed to specific species. Marine EBM has now been broadly accepted in policy, science, and management as crucial for effective marine conservation and resource preservation [1–5]. A key component to successful EBM programs is the integration of science into the management process. Since EBM has grown at such a rapid pace, it is necessary to ensure that the practices of science and management work together. This is often a challenge because each operates by and responds to different mandates, time scales, and authorities. The science-policy continuum can be improved through practical management strategies that are capable of incorporating policy-relevant research [6]. EBM relies heavily on scientific inquiry for an understanding of the status and changes related to the managed environment. As science management integration becomes more commonplace, issues associated with the respective cultures of each field arise. Even though managers and scientists agree on the necessity of incorporating science into management, very little research has been conducted to examine how this can be accomplished in practice. The recent increase in large-scale marine protected areas throughout the Pacific and use of EBM has demonstrated the need for showcasing successful examples of science management integration. This paper will examine how organization structure, communication styles, and cultural differences can impact integration of science and management. It also examines how analysis of these differences has been applied to the Northwestern Hawaiian Islands Research Partnership (NWHI-RP) and the analysis recommendations. The NWHI-RP will be used as a case study applying businesses management models to better understand the differences within science and management.

2. Review of Science Management Integration

The current literature on the relationship between science and management has repeatedly called for more communication between scientists and managers [7, 8]. This consensus solution is in principal a practical and appropriate one. However, it lacks a true analysis of the underlying issues and fails to develop detailed recommendations relating to the integration of science and management relationships or communication methods. The ability for scientists to communicate with managers has been referenced as a common struggle, particularly within EBM [9–13]. For example, in 1999, the UNESCO World Conference on Science adopted a declaration on the use of scientific data, which included recommendations of frequent science communications training. This was echoed in 2005, when the George Wright Society, a nonprofit association devoted to scientific and cultural values of protected areas, made additional requests including improved communication, incorporation of management needs into ecological monitoring, and inclusion of scientific results into management and planning. Recently, the Marine Conservation Biology Institute (MCBI) also expressed similar concerns in their report *Recommendations for the Management of the New Pacific Remote Monuments* [14]. While there have been many calls to action, the NWHI-RP has been implementing collaborative communication mechanisms to integrate science and management since the partnership was initiated five years ago. The partnership provides an excellent model of how to accomplish these ill-defined goals and will be further explored in this paper.

How scientists convey their research to managers, policy makers, and the public plays an important role in decision making within EBM [15]. In the last two years, the US federal government has released two planning documents that outline the need for both science in management and the further development of EBM. The *White House Council on Environmental Quality Final Recommendations of the Interagency Ocean Policy Task Force* [5] and the NOAA *Coral Reef Conservation Program Roadmap for the Future* [16] both present EBM as a critical technique for handling future ocean conservation. With plans to increase EBM, greater reliance on scientific research will be needed as a source for planning information. Therefore, a better understanding of the science-management connection is required to enhance accountability and relevance in EBM partnerships [15]. Over the last ten years, as scientists have been encouraged to participate in meetings, where policy and management issues are discussed, increasing demands have been placed on scientists to translate their research to management [6]. Unfortunately, there has been limited exploration or testing of this in case studies. A detailed literature search was completed in 2009 exploring the concepts of communications and integration in EBM. While a considerable amount of work has been published on the subject, few studies have developed pragmatic and practical applications or examples. As collaborative, ecosystem-based approaches to management increase in frequency, partnership evaluations are needed to better understand the institutional challenges surrounding EBM [17]. Looking at organizational design and culture is central to improving understanding of the relationship between science and values in management decision making [17].

2.1. Review of Barriers to Effective Communication. The published literature calls for two-way communications between scientists and managers [6, 13, 18]. Standard, one-way communication from scientists to managers has lost popularity due to the ineffective relationships that have developed and the general disfavor of linear information [6]. Collaboration through science management communications has become more common, but there continues to be transmission issues that require examination [12]. Science can play a large role in the management and policy process, particularly with more science-driven management techniques such as EBM. While joint communication allows for a better exchange of information between management and science parties, there are still challenges due to the nature of these disciplines. One of the common challenges has been identified as the language in use, which can impede comprehension of the information presented. Both science and management communications need to be liberated from technical language and abbreviations in writing, while maintaining the integrity and purpose of the source information [13, 18].

The management and policy literature has suggested that scientists should report in a more general and practical format for those that lack training in the scientific field and to facilitate a comprehensible platform for nonscience team members to better understand the materials [9]. Scientific data are now being used in the design of management tools and in identifying knowledge gaps and contentious issues [13, 19]. On the other end of the spectrum, many scientists feel that managers should have some technical understanding of the scientific process and the ecosystems in which they are working [20]. Intellectual autonomy from management also needs to be present when carrying out scientific endeavors to ensure scrutiny, peer review, and dissent [19]. Concerns over academic integrity have often been at the forefront of the communications debate. Thus, while both the scientific and management communities have explicitly stated the need to have reciprocal communication, this has been challenging due to cultural and institutional divides. As a result, many agencies have begun to employ specific science communication experts whose sole role is to facilitate dialogue between managers and scientists.

2.2. Review of Science Management Cultural Differences. The cultural differences present in the science and management fields influence communications in many ways, often inhibiting comprehension of content and placing emphasis on the differing attitudes and perceptions in each area [12]. Scientists and managers who are ingrained within these cultures inherently have different concepts and understandings of natural systems and work practices [19]. Adding to these complexities are numerous differences amongst managers and scientists in the distinctive international, federal and regional agencies [12]. Conflicts between science and management have occurred because of different time and work mandates. The time limitations and restrictions placed on decision makers and the longer terms associated with scientific research create a major area of disconnect between the fields in terms of expectations, deadline creation, and outcome implementation [7, 13]. For example, scientists rely heavily on journal publications targeted to others in their field to communicate their research. Not only do they convey their work through these publications, but their research is often communicated on the basis of long-term time frames, which often operate in years rather than months or weeks [21]. Management, on the other hand, operates in a field that is time sensitive and based in accordance with politics, leading to shorter deadlines [7]. The time scale differences are particularly challenging within EBM, where scientific assessment of entire ecosystems can take many years. Expectations have been placed on both scientists and managers to improve coordination and communication of their information when working with each other. Scientists must first write research grants and obtain funding and then present research that is publicly distributed and application oriented, while managers gain a greater understanding of the research presented to them.

2.3. Review of Measuring Science Management Cultural Differences. Communication is the basic social process in which cultural senses are cultivated [22]. Within organizational studies, culture has been represented as a social factor that keeps an organization together and expresses the values and beliefs of its members [23]. These values or patterns of belief are manifested by symbolic devices that can be identified through an organizational cultural audit [24]. Science management integration within EBM can be challenging because the cultural differences of participating agencies are often not assessed. Alignment of organizational culture within both science and management is possible by reviewing work structure and systems to ensure strategic integration and communication [25]. Cultural compatibility does not necessarily mean that two organizations need to be alike but more that there is a general understanding of how the other works [24]. Considerations that should be taken into account when evaluating the cultural compatibility of science and management include the job satisfaction of individual employees, differing decision making and management methods, language, work practices, and organizational structure. The surrounding environment is also a powerful element that shapes work relationships and processes. Desk objects, bulletin board content, and employee interaction can directly reveal an organization's culture.

3. Analysis of Science and Management Integration in the NWHI-RP

3.1. Background of the NWHI-RP. The NWHI-RP is a collaboration between the Hawaiʻi Institute of Marine Biology and Office of National Marine Sanctuaries, specifically with the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve and, later, the Papahānaumokuākea Marine National Monument. The Hawaiʻi Institute of Marine Biology (HIMB) is a research facility that focuses on marine ecosystem science and an institute in the School of Earth Science and Technology at the University of Hawaiʻi at Mānoa. The Northwestern Hawaiian Islands (NWHI) is a biologically diverse ecosystem, relatively free of anthropogenic impacts, making it an ideal site to study ecosystem function. In 2006, the highest level of protection possible under the United States law was afforded to the area creating the Papahānaumokuākea Marine National Monument (PMNM). Three jurisdictional agencies act as cotrustees and are responsible for the conservation of the Papahānaumokuākea Marine National Monument; they include two federal agencies, Department of Commerce (National Oceanic and Atmospheric Administration (NOAA)) and Department of the Interior (US Fish and Wildlife), and the State of Hawaiʻi [26]. Research has been carried out in the NWHI for many years, but the formalized partnership between HIMB and the NOAA Office of National Marine Sanctuaries was not finalized until 2005 (one year prior to the Monument designation). The Office of National Marine Sanctuaries is the trustee for the United States system of marine protected areas. The research partnership with HIMB was designed to generate data to assist decision makers using EBM. Research emphasis has included understanding connectivity through movement patterns and genetic population structures, characterizing and determining levels of coral health, mapping and monitoring ecosystem threats such as climate change, and providing education and outreach on the related science activities [27]. Prior to the partnership, existing management and science agencies did not frequently share their work in a formalized setting. The NWHI-RP has worked hard to overcome communication challenges and is a successful example of science management integration and collaborative communications. The NWHI-RP will be used as a case study applying business management models to better understand the differences within science and management. The NWHI-RP offers a unique opportunity to examine the processes that currently combine the knowledge of scientists, managers, and other support staff and make recommendations that will facilitate a more open dialogue.

3.2. Science Management Integration Project. In June 2009, the NWHI-RP began the Science Management Integration Project to identify contemporary needs and challenges including communication mechanisms for the public and science management partners within. The Science and Management Integration Team (SMIT) was a small group of eight participants comprised of managers, educators, and

Table 1: Science management organizational culture analysis.

	HIMB (science)	Commonalities	PMNM (management)
Office space allocation	Offices are spread out across many labs and buildings. Very few common areas.	Space allocation based on seniority. Common areas used for breaks, group meetings, and so on.	Offices more centrally located next to each other. Common areas are regulated by importance of the event.
Objects and signage display	Animal field guides, scientific posters, and lab publications.	Workplace safety posters, job announcements, nature pictures, and maps.	Pictures of staff, outreach material.
Communications	Frequent verbal communication, mass communication through email list serve. Little written communication. Two-way communication. Semiformal to informal.	Written and verbal. Frequent use of email.	Less verbal communication except for offices in close proximity. One-way communication. Formal.
Social interaction	Frequent and casual interactions. Flexible work environment with nonfinancial rewards (e.g., travel and work in remote ecosystems like the Northwestern Hawaiian Islands). Lower turnover in staff.		Infrequent and formal interactions. Unpredictable schedule, crisis management. Formal government environment. Higher staff turnover.

scientists spanning a variety of seniority levels. The team was responsible for participation in focus groups pertaining to the organizational structure, partnership culture, and recommendations to better integrate science and management within the partnership. The overarching goal of the project was to develop a resource that would improve communications between the science and management institutions of the NWHI-RP. Several methods of evaluation were used in this project to develop a full analysis and case study. The science management evaluation was a year-long study conducted within three phases to collect information, analyze, and produce recommendations. Several types of analyses were completed including a literature review, attitudes and perceptions survey, focus groups, and organizational analyses (including a Strengths Weaknesses Opportunities Threats (SWOT) analysis, organizational culture analysis, and organizational structure evaluation). This paper will explore the organizational culture analysis and structure evaluation, which are two components of a larger study evaluating the NWHI-RP.

3.3. Partnership Culture. The differences in science and management culture often inhibit understanding and challenge integration of the two areas. The idea of assessing organizational culture focuses attention on the qualitative influences or shared frames of reference among entities [23]. Differences between science and management can inhibit comprehension of content and place undue emphasis on differing attitudes, perceptions, and prejudices [12]. Organizational culture can be assessed in a variety of ways using observations, interviews, or questionnaires [24]. It is important to examine where cultural similarities exist between HIMB and PMNM in order to understand where integration can be implemented.

The SMIT was tasked with assessing the organizational culture of the NWHI-RP by observing four different elements of each agency. The similarities and differences were compared against several attributes including interoffice communications, social relations, office space allocation, signage display, and any other related observations (see Table 1). Commonalities were shown between HIMB and PMNM related to shared area use and workplace displays. Both agencies differed in their space allocation, which influenced how partners interacted with each other. PMNM resides in two office buildings, while HIMB has wide-spread offices and labs across an island approximately 29 acres in size. Other differences in organizational culture were apparent in the methods of social interaction and message styles employed by the members of each community. An informal and verbal communication approach was common at HIMB, while a more formalized and written process was emphasized by PMNM.

The results shown in Table 1 are consistent with the current literature, reflecting differences in science and management communication styles. All of the attributes discussed above contribute to the makeup of each agency and the dynamics within the NWHI-RP. These attributes are significant but are not the sole factors in measuring the effectiveness of a partnership. Cultural audits are rarely conducted in EBM but are important so that partnerships have an understanding of the similarities and differences within each agency involved. Once cultural differences are identified, attempts to decrease gaps between science and management can be made. Much of this is echoed in the analysis of the organizations structures as well.

3.4. Partnership Structure. The structure of an organization will dictate how people communicate and accomplish tasks

[28]. Drawing from business models, there are three basic types of structures that commonly occur in organizations and include hierarchical, flat, or matrix [29]. A hierarchical organization is a traditional structure with authority heavily weighted at the top and layers of workers and support staff below with each subsequent layer having less autonomy than the preceding one [29]. A flat or horizontal organization has authority spread evenly throughout the entire structure, with little or no management between workers fully involved in decision-making processes [29]. Lastly, a matrix organization pools employees and assigns duties based on particular projects [29].

As part of the science management integration assessment, the structures of both NWHI-RP entities were analyzed in order to understand how communications lines were influenced by organizational structure. Development of partnership structure was based on the SMIT analysis and employee staff listings provided. Differences in structure occurred depending on individual perceptions. HIMB, the science entity of the partnership, was identified as having a horizontal organization because of the autonomy given to scientists to pursue work in their specific research area. PMNM, the management side, was characterized as a hierarchical organization, common to government agencies. Since both partnership organizations were shown to have different structures, it is necessary to look at the communication processes between the two.

The horizontal structure of HIMB is influential on how scientists participate in the organization and the opportunities that are afforded to staff to provide input on partnership choices and research. Lead administration at HIMB seeks input from principal investigators in order to make science decisions. However, HIMB has little lateral exchange on specific projects despite the efforts to maintain a flat structure. Some of this is influenced by the differences in research areas from the participating scientists. Organizational differences between the two agencies are mostly found between the support positions and job duties. Differences in organizational expectations contribute directly to job types and job satisfaction. Single versus multiple task positions can influence the work scope and scale. Within HIMB, there is more project-oriented work, which leads to specific knowledge development and focus. In the PMNM offices, multitask work scales are more common, leading to varied work plans and numerous projects.

Both HIMB and PMNM are in a continuous state of evolution, and their organizational structure is a main source of change and restructuring. Partnership communication between the management and science agencies is most frequently done at the administration level between the HIMB director, the lead partnership coordinator, and the PMNM superintendents. Several communication gaps were demonstrated by this analysis, particularly between staff within each agency and across the partnership. For example, during the field season, scientists must coordinate with each other and with management staff on topics relating to permit applications, research, and field logistics. Individuals who hold responsibility for numerous projects are often difficult to reach. This problem represents one of the biggest communication obstacles that the partnership is faced with. Over the past few years, expansion in staff positions has aided with the work load allowing for better communication.

4. Partnership Communications

To compensate for the changing dynamics and differing organizational structures, planned mechanisms for partnership interaction and communication have been instituted to ensure integration of science into management. Communication of partnership activities occurs regularly as a result of symposia and informal meetings, semiannual reports, and outreach.

4.1. Symposia and Meetings. Presentations regarding the scientific research in the Northwestern Hawaiian Islands are delivered to managers and other partners semiannually through two-day symposia. This opportunity allows scientists and managers to come together to review the science, ask questions, and elaborate on any related issue or management concern. Within the NWHI-RP, scientists have learned to develop their presentation skills for management audiences, breaking down research to apply to management needs. Infrastructure has been set up through the partnership to assist with this using media training and “brown-bag” lunch presentations to facilitate communication between the management and science agencies. Managers have adapted to this as well, communicating on a more frequent basis their expectations and information needs. As the partnership science continues to develop, more participants and spectators are attending these meetings, widening the collaboration and discussion of science and management. In-between symposia, smaller semiannual meetings are held to provide updates to a more direct group. Quarterly lectures are another technique used for bringing together science and management partners. One-hour presentations during lunch are given from both managers and scientists to update the group on relevant issues related to the partnership. A variety of subject matters have been covered from research cruise planning, student presentations, to science-policy roundtable discussions. These meetings allow partnership participants to interact with each other and communicate in an informal setting.

4.2. Semiannual Reports. From the NWHI-RP symposia and meetings, the research is then translated into a semiannual report that is distributed to managers, related federal agencies and other partners. As more information is generated, the demand for the report has grown. Scientific findings are reiterated in a condensed and digestible format removing technical language and including illustrations and project summaries for easier reading. The report originally was produced quarterly and now alternates between a more thorough annual edition and a brief newsletter. The decrease in coverage frequency has allowed for more detailed reporting and better accommodates the timeframe associated with

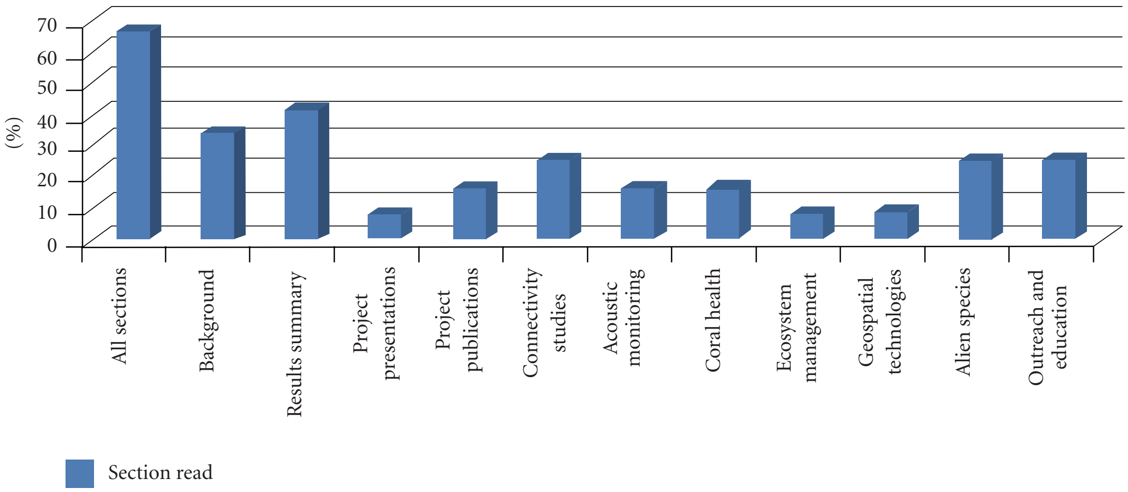

Figure 1: HIMB NWHI research partnership semiannual report sections read. (Survey participants had the option of selecting more than one section with the exception of those who selected all sections.)

Table 2: The NWHI-RP communications methods since 2007 for management, public, and elementary school audiences.

Management		Public		Elementary school	
Method	Numbers	Method	Numbers	Method	Numbers
Semiannual meetings and symposiums	6 events 477 people	Continuing education	6 courses 104 people	Elementary school (i) teacher workshops (ii) career days (iii) marine curriculum	27 events 9,242 people
Brown bag lectures and round table discussions	19 events 736 people	Family education	27 events 6774 people	Ecosystem Penpals Student Exchange Project	4 teachers 70 students
Semiannual research reports	6 reports 984 people	General public (i) science tables at community events (ii) evening lectures	25 events 8,831 people	Future Marine Scientist Mural Painting Project	3 teachers 152 students
No. of people	2,197	No. of people	15,709	No. of people	9,471
Total no. of people reached (since 2007) 27,377					

scientific studies. In December 2008, an anonymous evaluation was conducted to determine if readers were finding the report information clear and transferable to management. According to the survey, 67% of respondents read all the sections within the report. The activity summaries and partnership background were ranked as the easiest sections to comprehend and were the most frequently read (see Figure 1). All survey respondents agreed that the report was useful and informative, with 75% stating that they were dependent on the report for research updates. Respondents also stated that the report language "appropriately reflected their level of scientific understanding." Evaluations were positive, but criticisms concerning the "lack of focus on future direction" and "management implications" were also cited. This echoes the continued need for inclusion of management applications to the science presented.

4.3. Outreach. Within the partnership, scientists have been able to present their research to both managers and the public, while simultaneously producing peer-reviewed publications. Since 2007, studies from the partnership have been shared with over 27,000 people through public events, class presentations, and community involvement (see Table 2). (The outreach information presented here reflects the education efforts related to the NWHI-RP only from the HIMB and does not include the multitude of outreach and education related to the PMNM.) Over 50 undergraduate and graduate students at HIMB have also been supported through the NWHI-RP. Many of these students have been involved in outreach through the partnership gaining experience in sharing their research with the public and speaking to general audiences. The NWHI-RP has implemented several communication plans to ensure that the marine science being conducted in the PMNM is applicable to both management and the public. Science concepts are included with interdisciplinary outreach programs to build public involvement. Encouraging community to cultivate a sense of place in the partnership, and this unique ecosystem, requires the development of programs that bridge relationships with local schools and neighborhoods. The outreach effort implemented by the NWHI-RP has successfully accomplished this.

5. Recommendations for Improved Communication

Following the literature review, organizational analysis and cultural evaluation of the NWHI-RP, a few recommendations have been made from the SMIT to improve communication between managers and scientists. While these recommendations are targeted at the NWHI-RP, they can easily be applied to other EBM partnerships or science agencies. Few recommendations for science management integration within EBM have been made in the literature aside from better communications training for scientists and incorporating management needs into science results. These are important aspects of science management integration but fail to provide any practical examples or recommendations to accomplish this. Using the existing outreach efforts, the NWHI-RP has been able to improve its overall communications. Further development of programs and analysis through the science management integration project will allow for continued improvement in communication.

Existing collaboration and communication efforts within the NWHI-RP has improved productivity by fostering employee relations and awareness of each other's work. While the partnership has been successful at implementing several communication methods, further collaboration should be encouraged. Two-way communications has been cited as one of the greatest challenges in EBM [6, 13, 18], but regular interactions in the partnership have already shown to create a positive mechanism for partnership communications. It is recommended that the semiannual meetings and symposia incorporate more group discussion and creative brainstorming sessions on key management issues. In order to facilitate more efficient communication in the partnership, one meeting per year should be dedicated to presenting science and management results and another one for group discussion. There should also be greater emphasis on balancing the presentations to include more management-orientated concepts and concerns. Another way to encourage further discussion through informal communication is by organizing gatherings outside of work to discuss specific science topics.

The NWHI-RP semiannual reports have already undergone revision based on the evaluation that was completed in February 2009. Science reporting is an important component of the research occurring through the partnership and EBM in general. Science writing needs to be readable by both managers and nonscience audiences. Critical to understanding research, a science glossary with key terms and a species index were added to the semiannual reports. This allowed for general understanding of the terminology without losing the important components of the research. Inclusion of a section on management activities and describing management implications of the research is still needed to better integrate the partnership literature. The recognition and promotion of the NWHI-RP amongst the public is also essential to the support and understanding of research and both the HIMB and PMNM agencies. As research projects are completed, publications and media releases targeted at the general population should be encouraged. Continued participation at public events both related and unrelated to marine science and conservation will also help to increase partnership recognition. Community fairs, concerts, and fishing tournaments are all excellent places to share information about science and management initiatives.

6. Conclusion

The science management integration analysis conducted on the NWHI-RP is an effective way of evaluating EBM partnership communications and science management integration. Using techniques such as organizational analysis and surveys, evaluation of how science, and management interact can be vital to the success of science management partnerships. The NWHI-RP is a pragmatic example of an evolving EBM partnership that continues to improve its communication and ability to integrate science and management. For over five years, HIMB and PMNM have been working together to use ecosystem-based science to inform management and develop integrative research. The lessons learned provide a starting point for other management and science groups looking to support EBM. To further improve on this successful model, the NWHI-RP has implemented the Science Management Integration Project to identify contemporary needs and challenges including communication mechanisms for the public and science management partners within. As outlined here, the partners use several different modes of inquiry and presentation in its science communications plans with both management and the public to meet the multidisciplinary needs of EBM. Challenges in science communications with the partnership and EBM in general continue to exist, but by improving our understanding of both the science and management disciplines, the deficiencies in these fields are eroded, and this paper highlights a successful model for collaborative communication and the integration of science and management.

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Research Article

Reimaanlok: A National Framework for Conservation Area Planning in the Marshall Islands

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The development of *Reimaanlok*, a national framework for the planning and establishment of community-based conservation areas in the Marshall Islands, is outlined. A team composed of international experts and local resource management professionals selected and modified an ecoregional planning approach, defined key concepts, selected conservation features and targets, compiled biogeographical information from scientific and local knowledge and carried out a national-level ecological gap assessment. Past development of community-based fisheries and conservation plans was reviewed and the lessons learned informed the development of a robust community-based planning process for the design and establishment of conservation areas on individual atolls, integrating ecosystem based management (EBM) theory, traditional knowledge and management, and the particular socio-economic needs of island communities. While specific geographic, historical, cultural and economic characteristics of the Marshall Islands have created a framework that is unique, several aspects of this process offer ideas for national strategic conservation planning in other Small Island Developing States where there is a paucity of scientific data, significant and increasing threats, and where decision-making about the use of natural resources occurs primarily at the local level.

1. Introduction and Background

Coral reefs are degrading globally at an increasing rate [1, 2]; this is expected to worsen, as localized impacts including overfishing and land-based pollution are compounded by the array of impacts from climate change and ocean acidification [3, 4]. Few pristine reefs exist even now [5, 6], underpinning the conservation priority of such refuge reefs to enhance reef persistence in the future. Global efforts to mitigate the drivers of global climate change are crucial [7], but limiting localized impacts on reef ecosystems through improved resource management and conservation is essential for long-term adaptation [8–10]. Systematic conservation planning using spatial prioritization is becoming a widely used approach [11, 12] to identify representative networks of protected areas that will be resilient in the face of these increasing threats [13]. At the same time, in the Pacific Islands, centuries-old customary marine management was in decline but is now experiencing a "renaissance" in the form of community-based management [14].

In the face of global losses of biodiversity, the Marshall Islands retain some of the healthiest and most pristine coral reef systems anywhere in the world [15, 16]. In recent years, however, biodiversity in the Marshall Islands has become threatened by increased pressures on fisheries, climate change, and sea-level rise, increased urbanization and pollution, and a loss of the traditional subsistence lifestyle central to the identity and well-being of the Marshallese people [17, 18]. These trends have strengthened commitment within the Marshall Islands to establish and manage community-based conservation areas in addition to other resource conservation strategies. In 2006, the President of the Marshall Islands signed the Micronesia Challenge, a commitment by Micronesian countries and territories to "Effectively Conserve 30% of Nearshore Marine and 20% of Terrestrial Resources by 2020" [19].

To this end, in the Marshall Islands the development of a national framework for the planning and establishment of community-based conservation areas sought to reconcile international imperatives for conservation with the need for a locally-driven approach underpinned by a sense of ownership and the intimate environmental knowledge of local people [20]. This project and the resulting document were called "*Reimaanlok*"—Marshallese for "looking to the future, together." *Reimaanlok* incorporated a national-scale ecological gap assessment along with the development of a locally appropriate process for the empowerment of Marshall Island communities to establish and manage conservation areas. Here, we discuss the process of integrating traditional knowledge, local needs, modern conservation planning methods, and learning about these components in a locally led project.

2. The People, Biodiversity, and Management Needs of the Marshall Islands

Twenty-nine low-lying coral atolls and five low coral islands rise over 6,000 meters from the seabed to the surface of the equatorial Pacific and comprise the islands known to the Marshallese as *Aelōn̄ Kein* (Sea Sky Land) (Figure 1). The Exclusive Economic Zone (EEZ) of the Marshall Islands is over 2 million km^2, and less than 0.01% (183 km^2) is land. A total of 1,225 individual islands and islets make up the *Ratak* (Sunrise) chain in the east and the *Ralik* (Sunset) chain in the west. The atolls consist of biotic limestone on a deep basalt core, built over millions of years by coral reefs that grew as the basalt core slowly subsided [21, 22], creating a coral reef system extremely rich in productivity, diversity, and complexity. The modern islands only formed between 2,000 and 4,000 years ago, amid a slight lowering of sea level [21]. The region was settled by the direct ancestors of today's Marshallese around 500 BC [23]. Today, around 60,000 people live in the Marshall Islands, with two-thirds of these in the urban centers of Majuro and Ebeye, and the remaining living in low population density on twenty atolls and four islands [24].

Marshallese are excellent seafarers, canoe builders, and fishermen whose life has always been closely related to the ocean and its many creatures [25]. In the past, traditional fishing methods ranged from the simple line and hook to nets, traps, spears, clubs, rope, and coconut fronds and were accompanied by complex taboos, social hierarchies, procedures, and magic chants that integrated the spiritual, social, and economic lives. Methods were specialized for specific fisheries, fishing grounds, and seasons [25]. While some traditional fishing methods remain in use today, many are being lost along with the social and cultural complexities that essentially led to sustainable use of marine resources. Rising population levels, capital investment in the fishery sector, and increased international trade in fishery products have resulted in an erosion of the prevalence of traditional methods and associated sociocultural organization and are resulting in unprecedented levels of fishing pressure on both the nearshore and pelagic fisheries [17, 18]. However, fish and other marine resources remain important subsistence and commercial foods, the catching and sharing of which revive culture and community [25, 26].

Though scientific study of the islands has been limited due to their remoteness, those studies that have been carried out reveal a rich catalogue of biodiversity, including over 1000 species of fishes [27], over 362 species of corals [16, 28], 40 sponges, 1655 molluscs, 728 crustaceans, 128 echinoderms, 27 marine mammals, and 5 turtle species [29].

From 1946 to 1958, the US military carried out 67 tests of nuclear weapons on Bikini and Enewetak [30, 31]. While the atolls of Bikini, Enewetak, Rongelap, Ailinginae, and Utrik received the bulk of radioactive fallout from these tests, most atolls in the Marshall Islands received some radiation [32]. Impacts on biodiversity have been significant; while hard coral communities in Bikini Atoll have largely recovered after five decades, local extinctions of lagoonal specialist species [16], high concentrations of cesium-137 in terrestrial biota [33], and massive craters more than a mile across provide a lasting legacy of this history. Conversely, the nuclear legacy has yielded a *de facto* form of biodiversity protection as previously highly habitable islands are now unpopulated and access has been severely restricted or prohibited.

While the Marshall Islands Government has the authority at a national level to manage, sustainably develop, and conserve its natural resources, decision making about the use of the resources occurs almost entirely within local communities. Local governments have jurisdiction over the resources within five nautical miles of its shores, but decisions are often made under the guidance of traditional leaders. Traditional conservation practices, governed by *iroij* (chiefs), were designed to protect and manage natural resources in order to secure reliable food supplies. One of the methods remaining in use in limited areas is "*mo*"—the traditional system to designate parts of land, a whole island, or a reef area, as a restricted site. Special permission from the *iroij* was required to visit a *mo,* and harvesting would be done only for special occasions or in times of critical need, such as a drought. The rules and regulations for *mo* varied across the archipelago and would often involve rituals and chants, and violations were believed to result in consequences mystical in nature [25]. Other measures were in place to manage the sustainable harvest of populations including seasonal harvesting restrictions, size limits, and prohibition of extraction of gravid females [29]. While some evidence of these traditional management measures remain, even stronger is the evidence of their erosion and the lack of modern management measures effectively taking their place [17].

To fill this gap, various efforts have been made to establish community-based conservation areas throughout the Marshall Islands. Some have been led by the Marshall Islands Marine Resources Authority (MIMRA) with the support of regional fisheries agencies as part of the development of sustainable local fisheries (for example, Arno and Likiep);

Table 1: Definitions of *Reimaanlok* concepts and terms as developed in workshops.

Term	Definition
Nearshore Marine Resources (NMR)	Resources below the high water mark oceanward to a depth of approximately 100 m, and including the entire lagoon. Given this definition, there are 14,067 km^2 of NMR in the RMI.
Effective Conservation	Management that (a) maintains or improves atoll ecosystems, their biodiversity, health, productivity, and integrity, (b) sustains artisanal subsistence use of resources, and (c) protects and preserves areas of significant natural and cultural heritage. Areas under Effective Conservation have (a) publicly developed, legitimately recognized, and actionable management plans with clear objectives, (b) long-term biological and socio-economic monitoring and evaluation against management objectives, and (c) some form of recognized customary or legal rules and compliance system. Areas under Effective Conservation are part of a national system of conservation areas that includes representation of all habitat types and special conservation targets.
Types of Conservation Areas in the Marshall Islands-Type I-Subsistence Only	This area is managed for subsistence noncommercial use. In international standards, this relates to IUCN Category VI-Managed Resource Protected Area. The management area may include some Type II-Special Reserve no-take or highly restricted areas as part of the management regime.
Types of Conservation Areas in the Marshall Islands-Type II-Special Reserve	This area is subject to a high level of protection, and occasionally a very low level of subsistence or special occasion activities. In international standards, this relates to IUCN Category Ib-Wilderness Area. Examples of this are the atolls of Ailinginae and Bikini that have high levels of protection and restrictions on human activities

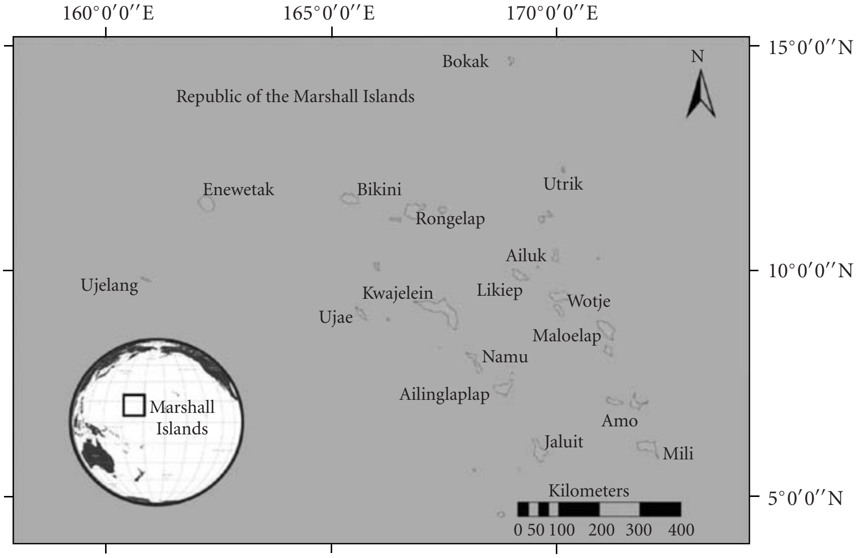

Figure 1: Map of the Marshalls Islands.

some have been led by the national Environment Protection Authority (RMIEPA) with a focus on balancing biodiversity conservation with sustainable livelihoods (for example, Jaluit Atoll Conservation Area). In addition, some communities and leaders have pursued the establishment of conservation areas independently, through issuing local government ordinances and working with international researchers (for example, Ailinginae, Ailuk, and Bikini).

As this range of conservation initiatives developed, with varying degrees of success, the need for an overarching framework for conservation area planning became apparent in order to provide clear direction for national agencies on how they could best assist local communities and to provide a focus for funding and assistance from international donors. The development of the *Reimaanlok* framework and of accompanying processes and guidelines was driven by this need.

3. Towards a National Framework for Conservation and Sustainable Resource Management

The development of an overarching national framework of conservation planning and resource management was led by a core team of international specialists and local resource

Table 2: Conservation features and targets in the Marshall Islands.

(a) Coarse-scale conservation features and targets: Broad categorization of habitats and ecosystems that encompass all the biota of the Marshall Islands.

Feature	Type I target subsistence only	Type II target special reserve
Terrestrial		
Agroforests	50%	
Indigenous broadleaf forests	20%	10%
Wetlands	80%	
Marine		
Deep lagoon	30%	0–5%
Lagoon pinnacles	30–40%	0–15%
Lagoon slope	50%	0–15%
Ocean leeward reef *liklal*	30–50%	0–10%
Ocean Reef	100%	
Ocean windward reef	30–50%	0–10%
Reef flat	30–50%	0–10%
Reef pass and channel	80–100%	0–30%

(b) Fine-scale conservation features/special features. Important areas for species, rare or imperiled communities, places of cultural significance. These are features considered worthy of conservation consideration that are not adequately dealt with under the coarse-scale features above.

Feature	Type I target subsistence only	Type II target special reserve
Terrestrial		
Bird Island	100%	50%
Breadfruit forest *mā*	100%	0%
Climax forest communities: *Pisonia grandis kan̄al* and *Neisosperma oppositifolium kōjbar* forests	20%	10%
Mangrove area *jon̄, bulabol* and *kimeme*	90%	?
Pemphis acidula forest *kōn̄e*	100%	50%
Pond *pat*	60–80%	?
Shrubland and grassland	100%	50%
Turtle nesting beach	100%	100%
Windward forest *jān̄ar*	100%	
Marine		
Clam site	50%	30%
Fish spawning aggregation area (SPAG)	100%	NA
Point with extended ocean reef *bōke*	?	
Reef hole *nam*	30%	
Seagrass meadow	100%	

? indicates that these targets remained undetermined.

(c) Species conservation features.

Terrestrial
Aquatic shrimp
Arno skink
Horticultural species *bōb* (*Pandanus tectorius* clones), *iaraj* (taro)
Land crabs *atun̄, baru wan, barulep*

(c) Continued.

Avifauna
Bristle-thighed curlew *kuk-kuk/kewak*
Great Frigatebird *toulōn̄* (f), *ak* (m)
Micronesian pigeon (including the Ratak subspecies) *mule*
Short-eared owl
Short-tailed albatross
Marine
Bigeye tuna *bwebwe*
Black-lipped pearl oyster *di*
Bumphead parrotfish *mem*
Cetaceans
Cowries and other shells *libuke*
Fisheries target species
Game fishes
Giant clams
Giant grouper *kidriej*
Green sea turtle *wōn/jebake* (brown color)
Hawksbill turtle *jebake*
Lobster *wōr*
Manta ray *boran̄*
Napoleon wrasse *lappo*
Other turtles *wōn*
Rare coral species
Sea cucumber *jibenben*
Sharks *bako*
Spotted eagle ray *imel*
Three-banded anenome fish *banij*
Whale shark

Notes on Tables 2(a), 2(b), and 2(c). The values in Table 2(a) for coarse-scale conservation features are area based; thus, the % refers to a portion of the total area of that habitat type. The values in Table 2(b) for fine-scale conservation features are based on occurrences. That is the % refers to a portion of the total number of occurrences of the target. For example, if 200 climax forest communities in the Marshalls are identified, then 20 (10%) should be protected and another 20 managed for subsistence use only. A total of 40 areas (20%) should be under effective conservation. Often the fine-scale features are too small to easily map (consider a turtle nesting beach), and so the targets are set by occurrences rather than by area. Conservation targets are location and area based; therefore, there are no targets set for species conservation features (Table 2(c)). Some conservation features do not have targets associated with them due to uncertainty within the planning team about appropriate targets. It is expected that the importance of these conservation features and appropriate goals will be determined during atoll-level conservation planning processes.

management professionals, including all the authors of this paper. A far larger group of people from all government and nongovernment resource management agencies operating at a national level was involved in the development of the framework through workshops, interviews, and reviewing documents. This planning process was used as an opportunity for local institutions to create and manage a program through a process of group learning and consensus building [34]. The intent of this was to build "locally adaptive institutions" [35] for effective conservation in the Marshall Islands.

3.1. Conceiving of a "Hybrid" Approach to Conservation Management. For conservation efforts to be successful and sustainable, conservation programs should be carried out within the constraints set by the local culture [36]. Some features of community-based management are universal and fundamental to its success: ownership of the resources and the intimate knowledge of the environment held within a community [37, 38]. Meanwhile, conservation planners have developed spatially explicit, systematic approaches to design an ecologically representative and functional network of conserved areas (usually referred to as ecoregional planning or systematic conservation planning) [11–13].

Often, in ecoregional planning processes, the approach taken is to identify a portfolio of sites to be considered and, from these, to select actual sites as priorities for conservation [11, 13, 39, 40] based on a systematic evaluation of the locations of conservation targets, the gap assessment and other factors (see, e.g., Green et al. [41] and The Nature Conservancy [42]). The challenge for the *Reimaanlok* team was to combine the modern western concepts of systematic conservation planning with indigenous knowledge and

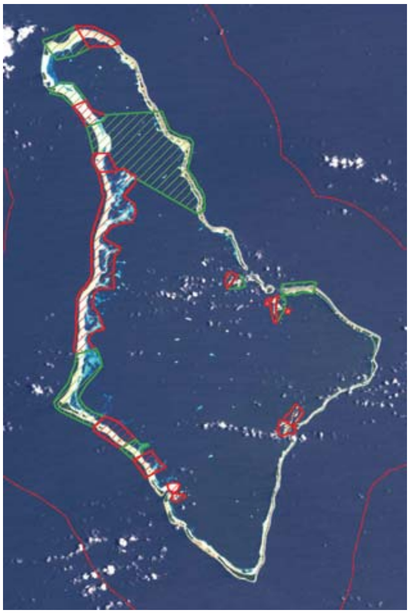

Figure 2: Example of mapping of existing conservation areas on Jaluit Atoll. Type I areas (managed subsistence use only) are mapped in green and Type II areas (high level of protection) are mapped in red.

management actions to form “hybrid” [20] or “multicultural plans” [36].

The team spent much time debating an approach that would work for the Marshall Islands and developing the process and the conceptual framework for building the plan. This resulted in a commitment to carry out several steps in the ecoregional planning process including identifying conservation features, setting conservation targets, collating biogeographic information, and carrying out a gap assessment. Importantly, in this national-level planning process, it was decided to stop short of identifying a portfolio of possible sites and prioritizing these sites for conservation action because “the biodiversity of each atoll is important to those people who live on it, all atolls have areas worth conserving, and only the community and landowners of that atoll have the right to determine which sites they will conserve” [43]. Instead, a detailed process for conservation planning at the level of each atoll was developed to ensure that the process would be led by local stakeholders and resource owners. This approach still enables the objective of a representative network of conservation areas to be met, because each of the Marshallese atolls have a similar array of habitats and geomorphology, in contrast to other countries, where heterogeneous terrain and habitat means establishment of a representative network often involves selecting very specific sites.

3.2. Selecting an Ecoregional Planning Framework and Defining Concepts. Initially, the core team considered various models for an ecoregional planning framework (see Redford et al. [11] for a review of various approaches) before settling on The Nature Conservancy’s “Designing a Geography of Hope” [39]. Primarily, this was chosen to ensure that the terminology and concepts aligned with those used in other Micronesian countries (especially Palau and the Federated States of Micronesia), where TNC has been active in conservation planning [42]. To ensure stakeholder input and participation, a series of workshops was held to discuss and develop (a) objectives for conservation in the Marshall Islands; (b) conservation features: those elements of biodiversity to be conserved; (c) conservation targets: how much of each conservation feature is to be conserved; and (d) definitions for key concepts including “Effective Conservation” and “Nearshore Marine Resources” from the Micronesia Challenge commitment (Table 1).

From the start, Marshallese staff worked closely with international conservation planners to determine the process and define these underpinning concepts in what became an ongoing dialogue of two distinct forms of cultural knowledge about how to do conservation [20, 36]. This meant grappling with such fundamental concepts as “protected areas,” a favored term in the global conservation vernacular but an unfamiliar concept in the Pacific islands, where traditional management schemes are more sophisticated than a simple “keep out” [14, 20]. As a result, this discourse has empowered the Marshallese team members to engage in the debate about conservation methods on an equal level with international “experts.”

3.3. Selecting Conservation Features. Conservation features were defined as the elements of biodiversity and related cultural features that will be the focus of conservation and management planning efforts. Very simply, they are the things that are to be conserved or managed. A “coarse-filter/fine-filter” approach to consider conservation features at different spatial scales was adopted for this [40]. Conservation features were grouped into three types:

(a) *coarse-scale conservation features/environmental units* broad categorization of habitats and ecosystems that encompass all the biota of the Marshall Islands;

(b) *fine-scale conservation features/special features* Important areas for species targets, rare or imperiled communities, and places of cultural significance;

(c) *species conservation features* threatened species, endemic/restricted range, flagship species, species of cultural significance, and species of economic importance.

Conservation features for the Marshall Islands were identified in three workshops of the national planning team, a literature review and extensive consultation with national and international experts familiar with the biodiversity, and ecosystems of the Marshall Islands. The list was subsequently refined over a period of six months in discussions (Table 2).

3.4. Collating Scientific and Local Knowledge about People and Biodiversity. A spatial database of conservation features, patterns and intensity of use, cultural aspects, and existing management areas is a prerequisite for systematic conservation planning. Information about biodiversity in the Marshall Islands was compiled into a Geographic Information System (GIS). The spatial elements of the GIS were digitized from multiple data sources, including high resolution satellite imagery (including ASTER, Landsat, and QuickBird), nautical charts, and coral reef habitat maps developed by the Institute for Marine and Remote Sensing (IMARS) [44]. These maps provided a vector-based delineation of coarse-scale marine conservation features on a national scale.

Information about special biodiversity and cultural features was collated from review of literature and from interviews with local knowledge experts and scientists. Local and traditional knowledge on occurrences of conservation features was gathered by interview with more than 15 people knowledgeable about resources and special features in different atolls. Simple maps and data recording sheets were used to collect the information, which was then entered into the GIS. This process yielded the recording of over 500 special biodiversity or traditional management locations across the entire Marshall Islands.

While there is, in general, a paucity of scientific data on biodiversity in the Marshall Islands, the project was successful in creating processes to collect, document, and use local and traditional environmental knowledge. At the national level, this data augments the scarce scientific data to better inform the systematic planning process. The real value, however, is that the process of collecting and discussing, and thereby valuing and validating, local and traditional environmental knowledge is crucial to reducing inequities in knowledge and power between scientists and local people [34, 36] and is a prerequisite for ensuring participation and ownership [34, 37] and, therefore, success of conservation efforts. This cultural empowerment creates opportunity for long-term collaboration and dynamic development of information [36] between outsiders and locals, brings creativity to the challenge of conservation [34], and contributes to building adaptive institutions.

3.5. Setting Conservation Targets. Once occurrences of conservation features had been mapped, a consensus-based process was used to establish long-term national conservation targets for these features (Tables 2(a) and 2(b)), intended to meet or exceed the Marshall Islands' commitment to the Micronesia Challenge. The Micronesia Challenge targets are inline with internationally accepted good practice: for example, 30% protection of marine resources was achieved in the Great Barrier Reef Marine Park [45] and the Channel Islands [46] and has been highlighted as the minimum amount necessary to allow reefs to persist in the long term [47]. Guided by these commitments, and to improve resolution of the national conservation targets, a further guideline was explicitly stated to aim for 30% of Nearshore Marine and 20% of terrestrial areas under effective conservation on *each* individual atoll. It was recognized, however, that, while for some unpopulated atolls the achievement of this goal may be easy, for others, such as the heavily developed atoll of Majuro, it will be much more difficult. The setting of targets and their division into levels of protection as Type I areas (subsistence use only) and Type II (special reserve) reflects the thoughts of the planning participants on the degree of protection required by different features, taking into account the rarity and condition of occurrences of features, and their vulnerability to harvesting pressures.

This process was subject to all the uncertainties that often hamper conservation planning including a limited understanding of the area that needs to be protected to maintain habitats and species and to ensure the persistence of ecological processes [12, 40, 48]. While it was an important process to determine conservation targets, the discussions in the workshops highlighted the need to keep in mind the objective of maintaining the community support for resource management as more important to long-term effectiveness than achieving the exact targets [49].

3.6. Ecological Gap Assessment. Existing and planned conservation areas were mapped (see Figure 2 for the example of Jaluit Atoll) and categorised as Type I (managed subsistence use only) or Type II (high level of protection). A gap assessment was carried out using GIS analysis to determine how successful these existing conservation areas are in meeting the conservation targets. This gap assessment showed that existing or proposed conservation areas covered 18% of total Nearshore Marine Resources in the Marshall Islands (Table 3). Coverage was varied as many atolls have no conservation areas, while others, such as Bikini or Ailinginae, are 100% protected. Importantly, this assessment did not cover the effectiveness of the current management or degree of implementation, as monitoring and evaluation systems are not properly in place.

3.7. Key Principles for Establishing Community-Based Conservation and Management. The national framework recommends replicating community-based management in several atolls, moving away from identifying priority areas nationally to use existing administrative arrangements that support community-based management. Local buy-in and efficiency of resource management is best where the communities' needs drive the process [14, 20, 38], yet many Marshallese atoll communities lack the resources and capacity to establish management plans without assistance from national agencies. Previous experiences of developing community-based fisheries management plans and other conservation plans were discussed within a group of local resource management professionals. The challenges of these projects were discussed, and translated into several key principles for establishing community-based conservation and management in the Marshall Islands.

(1) *Focus on Community Leadership and Social Sanctions.* In the past, the focus has been on western-style mechanisms for compliance, such as local or national government regulations, legal enforcement, and the use of the judicial system for sanctions. Discussion revealed that local regulations had often not been officially signed off by the local governments and, even where they had, there was substantial noncompliance. It was determined that the most effective

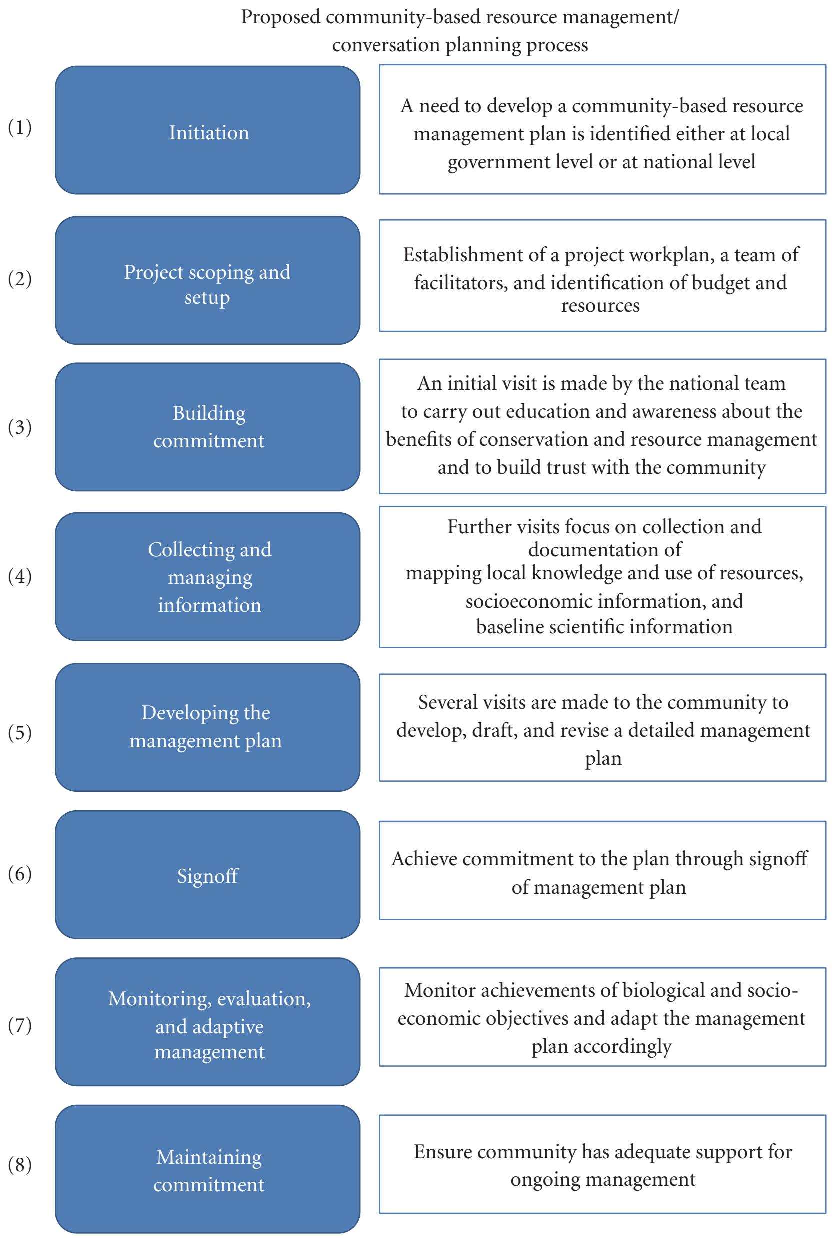

Figure 3: Summary diagram of the process for community-based conservation and resource management planning.

compliance could be achieved within a community through direction from traditional leaders and other respected leaders, accompanied by associated social sanctions. Regulations and legal authority were considered a secondary priority.

(2) *Projects Are Initiated by the Community.* Often, in the past, the projects had been initiated by people outside the community and when discussed in light of the perceived successes and failures, this was thought to be an inefficient use of valuable institutional resources as it had a low chance of being fully successful. It was decided that support would be prioritized for those atolls and communities that actively request assistance for the development of conservation plans.

(3) *Ensure Adequate Time and Commitment of Resources by Marshallese Agencies.* Review of past success and failure revealed that insufficient time and resources had been committed to individual communities to ensure consensus and buy in to the management planning process. Previously, plans had often been written by international "experts" with only one or two visits to an atoll community by national staff. It was decided that the development of each plan should involve considerable long-term community engagement with numerous consultations, facilitated by Marshallese staff from national agencies

Table 3: Gap assessment: current area under conservation against the goals for coarse-scale conservation features.

Feature	Total area (km^2)	Area under conservation (km^2)	Percentage under conservation	Target
Ocean reef	627.33	108.35	17%	50%
Lagoon slope	1120.48	258.82	23%	50%
Reef pass and channel	646.70	133.89	21%	80%
Lagoon pinnacles	77.82	9.64	12%	40%
Reef flat	1354.58	316.88	23%	50%
Total nearshore marine	3826.91	827.58	22%	30%*
Deep lagoon	10239.65	1727.16	17%	30%
Total marine	14066.56	2554.74	18%	—
Land	184.65	28.94	16%	20%*
Total	14251.21	2583.68	18%	

Area under conservation refers to an estimate of the amount currently described in management plans or local government ordinances as being under Types I or II of management and also those areas proposed in the near future to be under management.

*Micronesia Challenge Commitment

(Figure 3). This extended time commitment would allow for the development of trust between national staff and communities, time for *bwebwenato* (talking stories), sharing knowledge, discussion of a variety of resource management options, and, most critically, time to reach genuine consensus on the processes for managing the resources by the community. It was further determined that there was need for greater commitment to ongoing support for atoll communities in monitoring and evaluation and in enabling adaptive management far beyond the initial multiyear management planning exercise.

(4) *Use Appropriate Tools for Community-Based Planning.* It was discussed that one of the limitations of past work had been a lack of adequate tools available to support problem analysis and decision making within the community. The tool most often used in the past was the “problem-solution tree” (see, for example, King and Faasili [50]) which had been useful for its simplicity but was no longer sufficient to frame the discussion of conservation and resource management within the communities. The team decided that a wider range of tools was required and that these tools should be customized to the particular cultural context of the Marshall Islands. The Locally Managed Marine Areas Guide for Practitioners [51] was adopted as the basic toolkit, having been developed for this purpose for Pacific Islands. The team developed other tools specifically for the Marshall Islands context including atoll-level conservation area design principles that incorporate ecological and socio-economic considerations and a culturally specific process for the collection and documentation of local and traditional knowledge using community-based mapping [43].

(5) *Integrate Multiple Realms and Objectives: Marine, Terrestrial, Human.* To improve upon approaches building on only a single conservation objective, it was decided that resource management and conservation plans should be holistic and consider coastal management issues along with terrestrial and marine biodiversity conservation, in the context of local food security and economic needs. Apart from the obvious utility of integrated conservation planning, this approach also reduces consultation fatigue in communities and duplication of efforts by national and international agencies. This latter issue is particularly important in a relatively small country like the Marshall Islands with a limited pool of human resources.

Based on these principles a working group developed the 8-step *Process for Community-Based Fisheries and Resource Management Planning*, as a set of guidelines for facilitators to assist communities in the development of community-based resource management and conservation plans (Figure 3).

4. Conclusions

The development of *Reimaanlok* responded to international imperatives for the establishment of a national protected area network (in particular the Convention on Biological Diversity Program of Work on Protected Areas and the Micronesia Challenge) while ensuring that the detail of the conservation objectives and targets, the policy settings, and the program design were applied to the context of the Marshall Islands, with its particular mix of western style government and traditional governance and cultural structures. As a result, *Reimaanlok* did not attempt to identify specific sites for conservation areas but rather carried out a national-scale ecological gap assessment and developed the principles, process, and guidelines for the design, establishment, and management of conservation areas that are fully owned, led, and endorsed by local communities based on their needs, values, and cultural heritage. In informing the development of the plan, a combination of scientific rationalist knowledge, provided largely by visiting international scientists, and local and traditional knowledge of ecosystems, biodiversity, and sociocultural information was used. All this information is equally valid and was treated as such. The intention of the *Reimaanlok* process was to serve as a framework-building process to allow for implementation of on-ground conservation outcomes.

While there are geographic, historical, cultural, and economic characteristics of the Marshall Islands that require this framework to be specific to these particular circumstances, several aspects of this process offer ideas for national strategic conservation planning of Small Island Developing States more generally. In particular, it is important to engage with global agendas for biodiversity, but equally important to find the most appropriate way within each country's own system to achieve those objectives, while making use of international assistance, where it is useful.

A Note about Terminology

In *Reimaanlok: National Conservation Area Plan* for the Marshall Islands, we adopted the terminology from The Nature Conservancy's model for ecoregional planning. To minimise confusion, we have adopted terminology in this paper that is considered to be more widely used in the conservation literature. If the reader goes on to examine *Reimaanlok* directly, "conservation features" are referred to there as "Conservation Targets" and "conservation targets" as "Conservation Goals."

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Review Article

Comparative Phylogeography of the Coral Triangle and Implications for Marine Management

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Extreme concentration of marine biodiversity and exploitation of marine resources in the Coral Triangle pose challenges to biogeographers and resource managers. Comparative phylogeography provides a powerful tool to test biogeographic hypotheses evoked to explain species richness in the Coral Triangle. It can also be used to delineate management units for marine resources. After about a decade of phylogeographical studies, patterns for the Coral Triangle are emerging. Broad connectivity in some species support the notion that larvae have maintained gene flow among distant populations for long periods. Other phylogeographic patterns suggest vicariant events resulting from Pleistocene sea level fluctuations, which have, at least occasionally, resulted in speciation. Divergence dates ranging back to the Miocene suggest that changing land configurations may have precipitated an explosion of species diversification. A synthesis of the marine phylogeographic studies reveals repeated patterns that corroborate hypothesized biogeographic processes and suggest improved management schemes for marine resources.

1. Introduction

The Coral Triangle is well recognized as the global apogee of marine biodiversity, with species richness incrementally decreasing from this region eastward across the Pacific Ocean and westward across the Indian Ocean [1, 2]. This center encompasses much of Indonesia, Malaysia, the Philippines, Brunei, Timor L'Este, Papua New Guinea, and the Solomon Islands and is also variously referred to as the East Indies Triangle (e.g., [3–5]), the Indonesian and Philippine Region [6], the Indo-Malay-Philippine Archipelago [7, 8], and a variety of other names [2]. It has also been referred to as the Indo-Australian Archipelago (e.g., [9, 10]) although this is a misnomer for the Coral Triangle biodiversity hotspot, since it does not include Australia [1] and has geological origins transcending Eurasian and Indian−Australian tectonic elements [11]. In addition to its biodiversity reputation, the Coral Triangle is also unfortunately well known for peaks in threats to marine biodiversity, particularly for reef-building corals and coral reef fishes [12–14] and the need for improved marine resource management [1].

From a geological perspective, the Coral Triangle hotspot is relatively young [15]. Throughout the Paleogene (∼65–23 mya), tropical ocean formed an essentially continuous belt around the globe, with the Atlantic and Pacific basins connected by the Tethys Sea. During much of this time, the global center of marine biodiversity was found in the western Tethys Sea, as indicated by fossil beds in what is now the Mediterranean Sea [15–17]. In the late Eocene, this center shifted east to what is now the Arabian Peninsula, with the initial collision of Africa and Eurasia and the rifting of the Arabian plate [17, 18]. Continued west−to−east collision of Africa and Eurasia then constrained both of these hotspots, and finally closed off the Tethys Sea about 19 mya, and the center of biodiversity moved to its current position in the middle of the Indo-Pacific. A large component of biodiversity in the Coral Triangle must then consist of taxa that shifted their ranges from earlier centers of diversity [19–21] (see Harzhauser et al. [22] for a detailed example from the Tridacnidae).

Around the time that taxa from the diminishing Tethyan hotspots began to invade the Indo-Pacific, tectonic processes were producing more diversification *in situ*. Until the beginning of the Miocene about 23 mya, diversity within the Coral Triangle was surprisingly low across many taxa, ranging from zooxanthellate corals to mangroves (“The Paleogene Gap”) [16, 17]. At about this time, roughly coincident with the closure of the Tethys Sea, the Australian plate began to collide with island arcs in the Pacific, and the southeast margin of the Eurasian plate, dramatically altering surface circulation and effectively defining the modern basins of the Indian and Pacific Oceans [23]. Numerous phylogenetic studies of Indo-Pacific fish and gastropod taxa have found that most diversification occurred following this collision, during the Miocene [21, 24–27], and some have even found a distinct pulse of lineage diversification associated with the timing of the collision around 20 to 25 million years ago [20, 28]. Thus, the initial formation of the complex Coral Triangle seascape in the middle of the Indo-Pacific appears connected to its high levels of biodiversity.

While the timing of the appearance of the much of the biodiversity of the Coral Triangle is apparent, the mechanisms that promoted the concentration of biodiversity remain unclear. Published conjectures on the evolutionary processes behind this biogeographic phenomenon are probably more numerous than any other single topic in marine biogeography (recently reviewed in Hoeksema [2]). The many hypotheses that attempt to explain the diversification and persistence of species can be generalized as accumulation, origin, overlap, and refuge hypotheses. The center of accumulation hypothesis suggests peripatric speciation on islands peripheral to the Coral Triangle [40, 41], followed by subsequent biogeographic dispersal and accumulation in the biodiversity hotspot. Alternatively, within the Coral Triangle, complicated marine currents and a history of sea level changes have variously connected and isolated marine populations. This complex interaction of geological and oceanographic processes could have promoted vicariance, and therefore the Coral Triangle has been proposed as a center of concentrated speciation that played a major role in the origin of the Indo-Pacific fauna [6, 42, 43]. The Coral Triangle is also an obvious area of potential admixture, or overlap, of diverse Indian and Pacific Ocean biotas such as geminate pairs of fishes [3, 44] and spiny lobsters [45, 46]. This separation of Pacific and Indian Ocean biotas coincides with a major marine biogeographic break referred to as the Sunda Shelf Barrier [47, 48]. Perhaps most consequentially, the marine habitats of the Coral Triangle are highly diverse and extensive. The Sunda and Arafura shelves represent the largest tropical continental shelf area on earth [49]. This abundant and varied habitat has led many to hypothesize that the Coral Triangle is an area of relative refuge from extinction [9, 16, 50].

Although hypotheses to explain the biodiversity of the Coral Triangle abound, the empirical work is limited and has not yet provided much clarity [51]. Traditional area cladogram tests have been attempted [4] but these are inconclusive: “It is possible that, with the addition of more taxa, additional patterns would emerge. Much more systematic work within the East Indies is required to resolve this problem” [52]. However, phylogenetic and phylogeographic tests of the above hypotheses also vary in their conclusions, seemingly dependent on the taxon, methodology and sampling strategy. Some taxa appear to show an abundance of peripatric speciation (e.g., [53, 54]) while others seem to be diverging within the Coral Triangle (e.g.,[29, 34, 55]). Many taxa show evidence that the extensive and varied habitats of the Coral Triangle help to lower their risk of extinction [25, 26] while there is molecular and paleontological evidence of frequent local extinctions on peripheral islands [56–60].

It has repeatedly been noted that the above hypotheses are not mutually exclusive—that all of the above processes are potentially building biodiversity in the Coral Triangle [7, 8, 51]. A similar conclusion has been reached for the diversity center in the Caribbean [61]. This nonexclusivity, together with broadly similar predictions from each hypothesis and a flock of inconsistently applied definitions has often shed more heat than light on the Coral Triangle hotspot [10, 62]. For example, the distinction between vicariant and peripatric speciation can be blurred, especially for marine species, because evolutionarily significant levels of gene flow among disjunct populations can be maintained by infrequent pulses of long-distance larval dispersal [63, 64]. Perhaps what is needed is a new hypothetical framework that focuses on process rather than pattern (e.g.,[65]).

At present, the most urgent question about Coral Triangle biodiversity is how it can be protected in the face of assorted anthropogenic alterations of the marine environment [12, 14]. To do this, we will need to be able to precisely identify the evolutionary processes by which marine species in this region (1) diversify and (2) persist. Comparative phylogeography provides a means to test specific hypotheses regarding these processes [66, 67]. Diversification and persistence are also the two main processes that underpin all hypotheses that attempt to explain the biodiversity of the Coral Triangle. In terms of diversification, what now seems clear is that many taxa that are recognized at the species level and above largely precede the sea−level fluctuations of the Pleistocene [16, 17, 20, 26, 28]; for possible exceptions see [3, 45]. However, phylogeographic surveys of the Coral Triangle have uncovered numerous cryptic lineages that may represent newly formed (or forming) species [29, 33, 34, 53]. Perhaps by studying these recent speciation events in detail, we can better understand the tempo and mode of speciation in and around the Coral Triangle. In addition, the population boundaries delineated by concordant patterns in phylogeographic studies can serve as management units for fisheries management and marine protected area planning [40, 68–71]. With regard to the persistence of marine species, the major evolutionary process to consider is gene flow. Marine habitats are generally patchy at many spatial scales, and this is particularly so for the reef fauna of the Coral Triangle. Most reef species ranges in this region span broad stretches (∼1–500 km) of pelagic ocean that can only be crossed by a pelagic larval stage. While genetic methodologies tend to be swamped by ecologically relevant levels of gene flow, they can be useful in detecting areas across which gene flow is low or nonexistent, or mediated by intermediate “stepping-stone” populations [34, 71]. Furthermore, coupling genetic connectivity studies with oceanographic models can help reveal barriers to larval dispersal and source (upstream) versus sink (downstream) population dynamics that will be helpful in establishing networks of marine protected areas [72]. Phylogeographic pattern relates primarily to genetic connectivity at evolutionary time scales and not necessarily to demographic connectivity at more ecological time scales [73–75]. However, the presence of shared phylogeographic breaks is evidence of demographic independence of phylogeographic regions. Phylogeography in the Coral Triangle is still very much in its nascent phase. Our purpose is to review phylogeographic patterns that have thus far been uncovered in the Coral Triangle and to determine if these patterns can be used to improve marine management schemes.

2. Invertebrate Phylogeographic Pattern

Early phylogeographic studies spanning the Coral Triangle region showed evidence of pronounced divergence among Pacific and Indian populations. Lavery et al. [76] first reported this pattern of Pacific−Indian Ocean divergence in the coconut crab, *Birgus latro*. Similar patterns were subsequently reported in the blue sea star, *Linckia laevigata* [77, 78], the tiger prawn, *Penaeus monodon* [79], and the crown of thorns sea star *Acanthaster plancii* [80], which has arguably fragmented into four distinct species [32]. Explanations for this pattern uniformly invoke vicariance among Pacific and Indian Ocean basins during Pleistocene low sea level stands. While these early studies provided the first glimpses of lineage diversification within and around the Coral Triangle, they often included only a few, if any, populations from within the Coral Triangle, limiting the inferences that could be drawn regarding evolutionary processes within the Coral Triangle.

Extending phylogeographic studies into the Coral Triangle have revealed a more complex picture of processes acting in this region. Early studies on *Linckia laevigata* indicated Pleistocene vicariance [77], and subsequent studies with more intensive sampling within the Coral Triangle support the notion of a Sunda Shelf barrier (Figure 1) but also show that the Coral Triangle is a region of admixture of Pacific and Indian Ocean lineages [30, 88]. Further genetic structuring of *L. laevigata* within the Coral Triangle has also been demonstrated in the western Philippines using allozymes [31]. Early allozyme genetic studies on *L. laevigata* revealed genetic differences between the Indian and Pacific Ocean populations dominated by two different color morphs: royal blue morph in the Western Pacific and an orange or apricot morph in the Indian Ocean [78]. Williams [89] demonstrated that orange and blue morphs shared the same mitochondrial DNA. However, allozyme and COI nucleotide sequence analysis suggested genetic differentiation between sympatric blue and orange color morphs found in the Kalayaan Island Group in western Philippines [90]. Moreover, there was significant fine-scale genetic structure among populations of the both color morphs in the South China Sea and Sulu Sea. Crandall et al. [30] showed evidence of regional isolation of *L. laevigata* in Cenderawasih Bay, a phylogeographic break in eastern Indonesian that is seen in another sea star, *Protoreaster nodosus*.

The first phylogeographic studies to focus intensively within the Coral Triangle examined the mantis shrimp, *Haptosquilla pulchella* [91, 92]. The initial study indicated strong population genetic breaks between the Lesser and Greater Sunda Islands and populations to the north [91]. Expanding the range of the mantis shrimp study eastward [39] indicated that an additional population break for *H. pulchella* transects the Bird’s Head region of Papua New Guinea (Figure 1). This led to a hypothesis that the oceanographic feature referred to as the Halmahera Eddy may serve as a barrier to larval dispersal westward into the Celebes, Molucca, and Banda Seas [29]. This eddy is a result of the New Guinea Coastal Current (an arm of the Southern Equatorial current) interacting with the Equatorial Counter Current [39] (Figure 1). The resulting eddy limits east to west water transport across the Molucca Sea, presumably limiting larval dispersal and gene flow as well. Phylogeographic data from two additional mantis shrimp species [29], *Haptosquilla glyptocercus* and *Gonodactylinus viridis* as well as 10 additional species of stomatopod [Barber et al., *in review*] corroborate an eastern Indonesian population break east and west of Halmahera and also a break near the southern Sunda Shelf (Figure 1). While these studies as well as earlier work on *Birgus latro* and *Penaeus monodon* suggest that genetic structure in the Coral Triangle is a common feature of crustaceans, work on the symbiotic shrimp, *Periclimenes soror,* shows no evidence of structure across the Coral

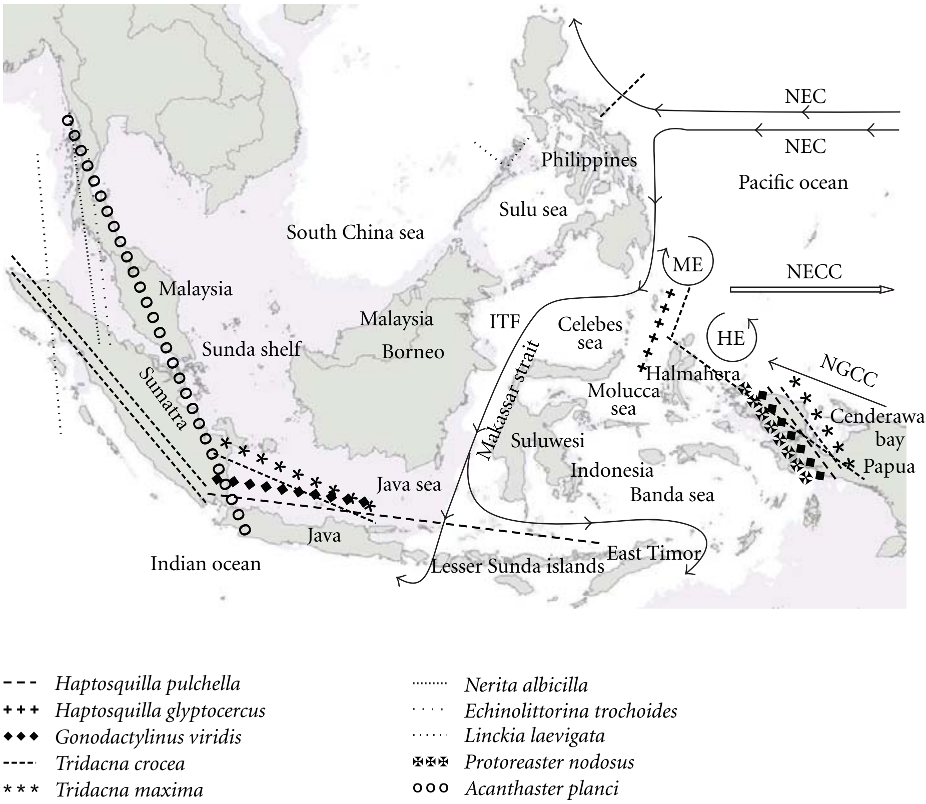

Figure 1: Major oceanographic surface currents and phylogeographic breaks in the Coral Triangle inferred from relative frequency pie chart figures of highly divergent clades, lineages, or haplotypes from published papers on invertebrates (*Haptosquilla pulchella* [29], *Haptosquilla glyptocercus* [29], *Gonodactylinus viridis* [29], *Linckia laevigata* [30, 31], *Protoreaster nodosus* [30], *Acanthaster planci* [32], *Nerita albicilla* [33], *Tridacna crocea* [34–36], *Tridacna maxima* [37], and *Echinolittorina trochoides* [38]). HE : Halmahera Eddy, ME : Mindanao Eddy, ITF : Indonesian Throughflow, NEC : Northern Equatorial Current, NECC : Northern Equatorial Counter Current, and NGCC : New Guinea Coastal Current (after Schiller [39]).

Triangle, despite strong phylogeographic structure in their host sea stars, *Linckia laevigata* and *Protoreaster nodosus* [30].

Studies of both bivalves and gastropods reveal population breaks across the Coral Triangle. Independent studies on the giant boring clam [34, 35], *Tridacna crocea* show phylogeographic breaks at the Sunda Shelf and in eastern Indonesian (Figure 1). On the eastern Philippine seaboard, north−south genetic structure broadly concordant with the bifurcation of the Northern Equatorial Current as well as significant fine-scale genetic differentiation was found for *T. crocea* populations [36]. Similarly, fine−scale genetic structuring in *T. crocea* populations in the shelf and shoal reefs of western Philippines has been demonstrated using allozymes [31]. Another giant clam, *Tridacna maxima*, shows a deep phylogenetic break in the Java Sea, between Eastern and Western Indonesia [37]. The periwinkles, *Echinolittorina trochoides, Echinolittorina vidua* [38], and *Nerita albicilla* [33], also show population breaks that correspond to the western Sunda Shelf Barrier (Figure 1). However, as with sea stars, this pattern is absent in the parasitic gastropod, *Thyca crystallina,* even though there is strong structure in its host, *Linckia laevigata* [30, 88]. Additional evidence of structure within the Coral Triangle comes from limpets of the *Patelloida profunda* group [93] and the abalone *Haliotis asinina* [94]. The former study showed clades associated with Pacific and Indian Oceans, although the age of these lineages date back to the Miocene, suggesting a much deeper history to the patterns in this group.

Studies on additional invertebrates provide further evidence of population structure across the Coral Triangle. Regional structure is seen in the barnacle *Chthamalus malayensis* [95], in the coral reef sponge *Leucetta chagosensis* [81], and the scleractinian coral *Heliofungia actiniformis* [96]. However, sampling was insufficient to show exactly where these genetic breaks occurred in the Coral Triangle. Regional phylogeographic breaks were not present in two species of reef-building corals, *Pocillopora damicornis* and *Seriatopora hystrix*, although high levels of genetic divergence among many populations were observed [97].

3. Fish Phylogeographic Pattern

Tests of phylogeographic pattern using marine fish have varied spatial coverage across the Coral Triangle. Perrin and Borsa [98] demonstrated an apparent population break between Sulawesi and Borneo with the nearshore pelagic Indian Scad, *Decapterus russelli* (Figure 2), but the only sample site in eastern Indonesia was on northwestern

Sulawesi. Ablan [99] suggested four separate management units based on population data from *Dascyllus trimaculatus* [82] and *Thalossoma hardwickii* [83] corresponding to the Sunda Shelf, the South China Sea, the Pacific Ocean, In contrast to invertebrate and the Philippines plus eastern Indonesia. Leray et al. [84] also demonstrated a broad geographic break consistent with a Sunda Shelf barrier for *D. trimaculatus*. Drew and Barber [87] demonstrated a strong genetic break consistent with the western Sunda Shelf Barrier in the Lemon Damsel *Pomacentrus moluccensis*. Lourie et al. [85] studied four species of seahorse around Southeast Asia and found population breaks within the Philippines, north−south and east−west across the Coral Triangle, and corresponding to the western Sunda Shelf Barrier (Figure 2). Timm et al. [55] tested connectivity with the False Clown Anemonefish, *Amphiprion ocellaris*, and found population breaks corresponding to the southern Sunda Shelf Barrier, easternmost Indonesia, and a broad north−south break (Figure 2). Based on allozyme analysis, Magsino et al. [86] demonstrated a phylogeographic break in *Siganus fuscescens* consistent with the Northern Equatorial Current Bifurcation in eastern Philippines (Figure 2). This population break in *S. fuscescens* was further validated by analyses of the mtDNA control region that also suggests isolation of the South China Sea basin and fine-scale structuring within the South China Sea and southern Philippine Sea [100]. Although phylogeographic pattern in fishes supports Sunda Shelf, easternmost Indonesia breaks, and the northeastern and southeastern Philippine break consistent with some invertebrates, corroboration is lacking for other phylogeographic breaks.

Phylogeographic structure has been detected in a number of fish species studied widely across the Indo−Pacific with limited samples within the Coral Triangle and therefore could not detect breaks within the Coral Triangle. These include the surgeonfish *Acanthurus triostegus* [101], the milkfish *Chanos chanos* [102], the parrotfish *Chlorurus sordidus* [103], and the snapper *Lutjanus fulvus* [104]. High levels of microspatial genetic structure have been detected in the Banggai cardinalfish, *Pterapogon kauderni*, but this is limited to a small area in eastern Indonesia [105–107]. Other studies sampled disparate sites or limited genes within the coral triangle and broadscale phylogeographic breaks cannot be inferred. These include the clownfish *Amphiprion ocellaris* [108], the wrasse *Thalossoma hardwicki* [83], the snapper *Pristipomoides multidens* [109], the scad mackerel *Decapterus russelli* [110], and the Spanish mackerel *Scomberomorus commerson* [111].

4. Species without Apparent Phylogeographic Breaks across the Coral Triangle

In addition to evident barriers to gene flow across the Coral Triangle, a number of species exhibit apparent lack of phylogeographic breaks across the region. This includes the sea urchins *Eucidaris*, *Diadema*, and *Tripneustes* [112–114], the marine snails *Echinolittorina reticulata* [38] and *Nerita plicata* [33], the nearshore pelagic scads *Decapterus macrosoma* and *Decapterus macarellus* [115], the trumpetfish *Aulostomus chinensis* [116], three species of surgeonfishes of the genus *Naso* [117, 118], and the Eastern Little Tuna *Euthynnus affinis* [119]. Although sites were not sampled within the Coral Triangle, the Bigscale Soldierfish, *Myripristis berndti*, also apparently does not show phylogeographic structure across the Indo−West Pacific [120]. The lack of phylogeographic structure across the Coral Triangle is surprising given Pleistocene fluctuations in sea level that potentially restricted gene flow. These species may have continued to successfully disperse through the Coral Triangle during periods of glacial maxima, reestablished gene flow quickly after glacial maxima, lost divergent lineages, undergone selective sweeps, or simply did not span the Coral Triangle during glacial periods [30, 121]. One other possibility is that the genetic markers or sample sizes used were not adequate to detect population structure.

5. Concordant Phylogeographic Pattern

The numerous marine phylogeographic patterns in the Coral Triangle, above, strongly support a western Sunda Shelf Barrier. The Sunda Shelf was emergent during Pleistocene low sea level stands, which would have limited larval transport and genetic exchange among Pacific and Indian Ocean populations on either side of the shelf, promoting lineage diversification. Similarly, the increasing numbers of studies focused within the Coral Triangle are beginning to corroborate an eastern Indonesia barrier in vicinity of the Mindanao and Halmahera Eddies (Figures 1 and 3) where physical oceanographic processes constrain water exchange, and thus larval transport and gene flow. However, the number of studies in this region is still limited. Furthermore, sample coverage is particularly sparse in some areas, especially in the Philippines, Malaysia, Papua New Guinea, the Solomon Islands, East Timor and the Borneo, Sumatra, and Banda Sea regions of Indonesia, making it difficult to corroborate barriers to lineage diversification elsewhere.

Phylogeographic patterns in invertebrates (Figure 1) are highly concordant in the western and southern Coral Triangle but coverage of sample sites in the northern, eastern, and southeastern Coral Triangle is sparse. Six species exhibit barriers to gene flow corresponding to western peninsular Malaysia and western Sumatra. This population level break closely follows the Sunda Shelf Barrier, a major biogeographic break between Indian and Pacific Ocean biotas [47]. The three concordant phylogeographic breaks along the southern edge of the Sunda Shelf and the Lesser Sunda Island chain also correspond to this barrier. However, the population breaks occur in the region north of Java in the Java Sea [37, 91] and between the Lesser Sunda Islands and Sulawesi [29]. Hypotheses relating to this northern orientation of phylogeographic breaks in the southern region of the Sunda Shelf Barrier still need to be formulated and tested.

Seven species of invertebrates show phylogeographic breaks in eastern Indonesia consistent with the Bird's head region of New Guinea, specifically, Cenderawasih Bay (see [29], Barber et al. *in review*). Seven species of invertebrates

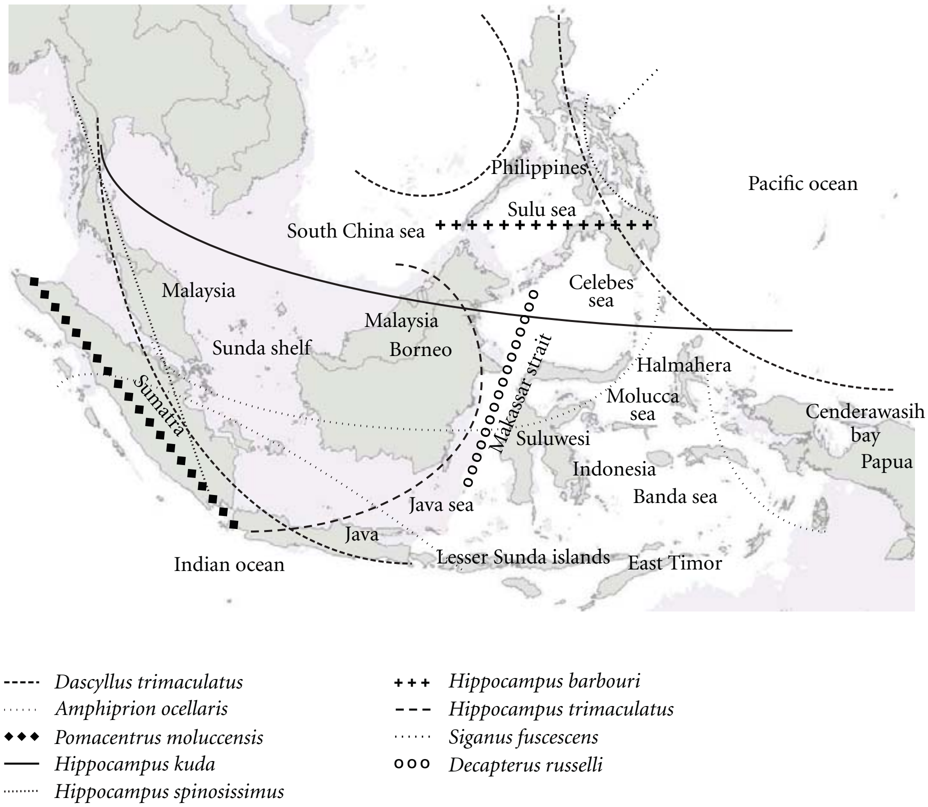

Figure 2: Phylogeographic breaks in the Coral Triangle inferred from relative frequency pie chart figures of highly divergent clades, lineages or haplotypes from published papers on fishes (*Decapterus russelli* [81], *Dascyllus trimaculatus* + *Thalossoma hardwickii* [82–84], *Hippocampus barbouri* [85], *Hippocampus kuda* [85], *Hippocampus spinosisssimus* [85], *Hippocampus trimaculatus* [85], *Amphiprion ocellaris* [55], *Siganus fuscescens* [86], and *Pomacentrus moluccensis* [87].

Figure 3: Generalized position of concordant phylogeographic breaks.

also show population structure in this region but more consistent with the area of Halmahera (see [30, 34], Barber et al. *in review*), and six species show divergence among populations among the Western Papua, Indonesia, and Papua New Guinea [Barber et al. *in review*].

In contrast to invertebrate phylogeography in the Coral Triangle, patterns from fishes are not highly concordant. Population breaks in a seahorse [85], a clownfish [55], the Lemon Damsel [87], and the Threespot Dascyllus [84] corroborate the Sunda Shelf Barrier seen in invertebrates. Similarly, data from the clownfish *Amphiprion ocellaris* corroborates an eastern Indonesian barrier (see [55], Barber et al. *unpublished data*). While phylogeographic concordance in fishes is not as strong as in invertebrates, this pattern likely has both methodological as well as biological origins.

The apparent lack of consistent concordance in fish phylogeographic patterns in comparison to invertebrates is almost certainly partially an artifact of sample coverage. Several of the recent invertebrate studies are part of coordinated efforts to intensely sample multiple codistributed taxa across Indonesia [29, 30, 33–35], while others focus sampling more widely across the Pacific and Indian Oceans [32, 34, 38]. In contrast, fish sampling in the Coral Triangle has largely been restricted to a specific region in the Philippines or in Indonesia [86, 98] has been widespread across Southeast Asia but with uneven sample coverage either within Indonesia or within the Philippines [55, 85, 99], or corresponds to a wide Indo−Pacific coverage [84, 87]. The varied levels of concordance between different sampling programs highlights the importance of systematic sampling of multiple species across broad spatial scales in order to accurately identify phylogeographic boundaries in this region. It is likely that as more coordinated sampling efforts are conducted on fish in this region that more examples of concordance will emerge, improving our understanding of the evolution of biodiversity in the Coral Triangle.

While there will certainly be more examples of concordance in fish taxa, the intrinsic differences in life histories in invertebrate and fish will likely result in more examples of phylogeographic discordance in fish than invertebrates. The characteristics and interplay of mobility of larvae and adults are typically different in invertebrates versus fishes. With the exception primarily of crustaceans, invertebrate larvae are poor horizontal swimmers [122] although they can influence their dispersal through active vertical swimming. Consequently, dispersal and recruitment in invertebrates may generally be more passive and more predictable from ocean circulation patterns than for fishes although the similarities in phylogeographic structure in the giant clam (*Tridacna crocea*) and clownfish (*Amphiprion ocellaris)* suggest that this may not be the case. Fish larvae, on the other hand, are generally more active and have been shown to return to their natal population and restrict genetic mixing between populations [123, 124]. This reduces effective population size and allows faster, stochastic sorting and can result in an unpredictable mosaic of population structure. This is exemplified in *Amphiprion* [55] and *Hippocampus* [85] that have relatively short larval dispersal durations for fish (e.g., 10–14 days in *Amphiprion*). All the invertebrates and nearly all the fishes reviewed in this study show limited mobility and/or site specificity as adults and, therefore, differences in genetic structure are expected from differences in larval mobility and biogeographic history. Exceptions to this are pelagic and wide−ranging demersal fishes and cephalopods. Dispersal and hence phylogeographic pattern in these forms can be heavily influenced by adult mobility except when localized spawning aggregations may influence genetic patterns. In this paper, only the nearshore pelagic scad, *Decapterus russelli*, is highly mobile as an adult and this species showed a unique phylogeographic break (Figure 2). Two other nearshore scad species showed no genetic structure in this area [115], which is consistent with low levels of molecular divergence found in other species of pelagic fishes [121].

6. Management Implications

6.1. Concordant Phylogeographic Breaks Suggest Broad Management Units. Phylogeographic studies in the Coral Triangle are still at an early stage but existing concordant phylogeographic breaks suggest broad management units across the western and southern Coral Triangle (Figures 3 and 4). These units appear robust because they are corroborated across multiple taxa and multiple loci [47, 69–72]. The Sunda Shelf biogeographic barrier [47], resoundingly corroborated by phylogeographic studies (Figure 3), suggests natural management divisions between east and west Sumatra and between the Andaman Sea and the Gulf of Thailand (Figure 4). A concordant phylogeographic break to the north of Java and the Lesser Sunda Islands suggest that these constitute a natural management unit. A large portion of eastern Indonesia that includes most of the seas east of Borneo appears to be a natural management unit. Halmahera to the westernmost Bird's Head region of Papua also appears to be a management unit that may either be discrete or a subunit of an eastern Indonesia management unit. Further phylogeographic studies are needed to corroborate this. This division supports ecosystem-based fisheries management efforts in the Bird's Head Seascape around Raja Ampat [125]. Populations around Cenderawasih Bay are typically divergent from those to the west, and therefore the northern Papua region could be managed separately. In eastern Philippines, two species corroborate a phylogeographic break that corresponds with the Northern Equatorial Current Bifurcation [36, 86], and this suggests that northeastern and southeastern Philippines should be treated as separate management units.

6.2. Concordance of Phylogeographic Pattern with Currents and Ecoregions. Marine management schemes that utilize population genetic data are considered stronger if combined with supporting evidence from oceanographic data and other supporting approaches [72]. The dominant surface ocean circulation features in Indonesia in terms of volume of transport [39] are the Indonesian Throughflow from the Pacific, and the Halmahera and Mindanao eddies that feed the Northern Equatorial Counter−Current (Figure 1). The Halmahera Eddy was postulated as the main reason for phylogeographic breaks in eastern Indonesia [29]. However,

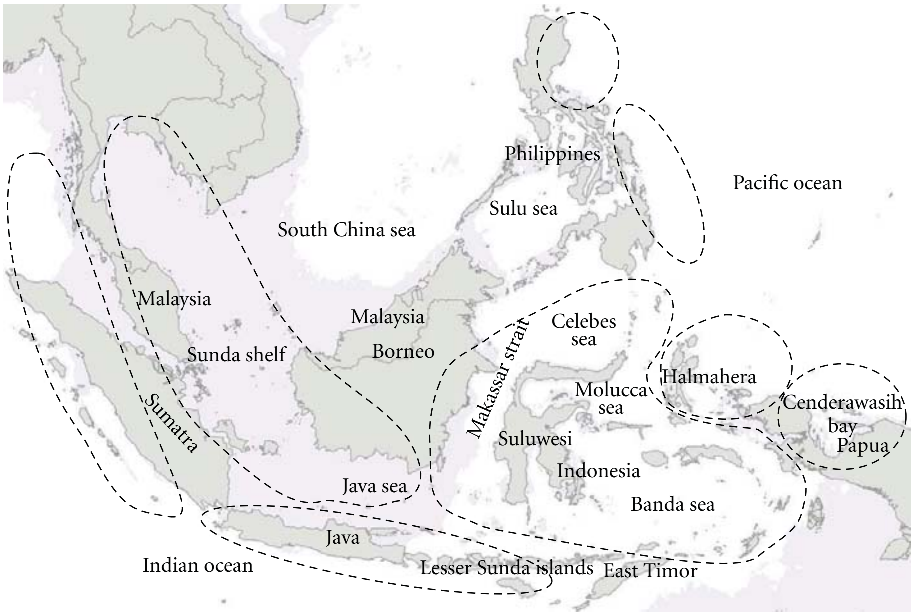

Figure 4: Approximate minimum management units inferred from concordant phylogeographic breaks. Although no phylogeographic break was evident east to west across the Java Sea, we assume that the Sunda Shelf biota is distinct from eastern Indonesia and these warrant their own management strategy.

with recent ocean circulation reanalyses it is likely that the Mindanao Eddy also plays a significant role in eastern Indonesia depending on the monsoon season [39]. Both these eddies, together with the concordant phylogeographic breaks, support the idea of delineating separate management units in eastern Indonesia. The predominantly separate ocean circulation between the Sunda Shelf and the Indian Ocean also supports the use of the Sunda Shelf phylogeographic breaks as demarcating management units. The southern Sunda Shelf break north of Java and the Lesser Sunda Islands is not strongly supported by ocean circulation. The Indonesian Throughflow suggests a strong north to south surface flow from the Makassar Straits across the Java Sea during the Southeast Monsoon [39]. However, during the Northwest Monsoon this flow is weak and the predominant current is east to west in the Java Sea that could restrict gene flow with populations to the north. While the phylogeographic patterns in this region may have historical origins, their persistence through contemporary oceanographic conditions strongly suggests that gene flow must be severely limited among these regions [29] arguing for the ecological independence of these regions.

Concordant phylogeographic pattern in the Philippines corresponds with the bifurcation of the Northern Equatorial Current. However, these are corroborated by only two published studies in the eastern Philippines [36, 86]. The mean latitude of the transition of the Northern Equatorial Current into separate northern and southern directed boundary currents has been reported as high as 15.5°N [126], but more recently it has been reported at 13.3°N, although this fluctuates to 14.0°N in January and to 12.5°N in July [127].

Additional phylogeographic and oceanographic studies are needed to refine management units across the Coral Triangle. Particularly useful will be studies that integrate estimates of genetic connectivity with predictions from computer models of connectivity based on physical oceanography so that the impact of physical oceanography on realized dispersal and connectivity can be rigorously examined in a quantitative, rather than qualitative, fashion.

Marine ecoregions based on floral and faunal composition, major physical and biological oceanographic features and expert opinion have also been proposed as a means of delineating units of marine management [1, 128]. Coupling these approaches with phylogeographic breaks may strengthen management. However, on the surface there appears to be limited agreement between units suggested by phylogeographic breaks and ecoregions proposed from metadata analysis and expert opinion [128] or patterns of coral biodiversity [1]. Proposed ecoregions do separate the Sunda Shelf from the Indian Ocean and both north and south Lesser Sunda Islands are independent units. In addition, ecoregions corroborate phylogeographic breaks separating Eastern Indonesia. Aliño and Gomez [129] also recognize northeastern and southeastern biogeographic regions corresponding to the Northern Equatorial Current Bifurcation. Coral biodiversity also suggests Cenderawasih Bay as a separate unit.

The correspondence between some of the marine ecoregions and published phylogeographic breaks suggests that some ecoregions are indeed functioning as ecologically independent units. However, there are far fewer recognized phylogeographic breaks than ecoregions. This result could be interpreted that the marine ecoregion approach is flawed. Instead, this result most likely reflects the fundamental difference in the methods used to determine ecoregions and the genetic connectivity and the limits of genetic methods to recover ecological independence among regions. Genetic patterns evolve over periods of hundreds and thousands of years. However, small levels of gene flow that can have a profound impact on genetic patterns may be inconsequential demographically [73–75]. Thus, while the presence of strong phylogeographic breaks confirms the demographic independence of two spatially distinct populations, the absence of phylogeographic structure does not necessarily indicate that two populations are connected by ecologically relevant levels of larval dispersal. It remains to be seen whether more rapidly evolving genetic markers can provide additional support to the proposed marine ecoregions in the Coral Triangle. However, the recovery of multiple phylogeographic breaks in the region of Cenderawasih Bay does indicate the demographic independence of some species in this region, suggesting that the boundaries of these ecoregions may need to be modified.

6.3. Future Directions for Management Strategy. While concordant phylogeographic patterns exist for Indonesia and eastern Philippines, data are insufficient to draw any broad−scale patterns elsewhere in the Coral Triangle, particularly for most of the Philippines and Malaysia. Corroborated phylogeographic breaks are also largely incomplete at finer scales within the Coral Triangle, although some fine−scale population structure, such as around Palawan [31], has been reported. Most fine-scale studies to date have largely focused on individual countries, rather than the entire Coral Triangle. As additional studies are conducted, more unique phylogeographic regions and management areas may be identified. Similarly, more connections among nations may also be identified. For example data for giant clams (DeBoer et al. *in review*) and stomatopods (Barber et al. *in review*) both indicate high genetic similarity between Philippine and Central Indonesian populations, indicating that management planning will likely need to span international borders.

The recovery of concordant phylogeographic breaks indicates the evolutionary, and thus demographic, independence among regions of the Coral Triangle. These results suggest management units although it should be recognized that these are general guidelines as many species do not follow the general pattern. The spatial scales of genetic structuring depend on the life history of species and local factors that affect larval transport and recruitment success. Genetic patterns are also a result of many stochastic processes and changing physical processes may result in different phylogeographic pattern. As such, it is unclear whether lack of corresponding phylogeographic breaks in some taxa are the result of unique biological factors that should be incorporated into management plans or are the result of stochastic genetic processes, despite the physical environment having the same impact on codistributed species. Given this uncertainty and the range of responses across multiple taxa in the Coral Triangle, species−specific management interventions within large−scale management units should be complemented by networks of marine protected areas that take into consideration representative habitat types to enhance protection of species and genetic diversity of highly exploited species. These nested scales of management units reflect the large-scale (evolutionary time scales or vicariance) versus small-scale (ecological and isolation by distance) factors influencing phylogeographic pattern.

7. Conclusions

Phylogeography in the Coral Triangle is young, even in comparison to the rest of this burgeoning field. Most of the studies reviewed here were published in the last ten years, and most are limited to inference from mitochondrial genes. However, the abundance of cryptic mitochondrial lineages identified thus far strongly suggests not only that biodiversity in this global marine hotspot is even higher than expected, but also that new species are forming as we write. Broadly speaking, the Coral Triangle may represent the world's largest suture zone [130, 131], in which divergent genomes from Pacific and Indian Oceans are periodically brought back into contact by rising sea levels [33, 132, 133]. Confirmation awaits results from nuclear loci, but we can readily see evidence of a suture zone in high numbers of hybrid reef fish observed at Christmas and Cocos Islands off the coast of Sumatra [133, 134], and the broad and parallel (but not identical) clines in color morphs, allozymes and mtDNA clade frequencies in *Linckia laevigata* [30, 78, 135]. The location of mitochondrial breaks reviewed here may not then represent the precise location of an allopatric barrier, but the boundary at which divergent mitochondrial genomes were reunited as they reexpanded with rising sea-levels [136, 137]. Whether the observed phylogenetic breaks have actually resulted from allopatric speciation will depend on the effective population size and ecological characteristics of each lineage (see Crandall et al. [33] for two contrasting examples).

Where did coral reef taxa find refugia during periods of lowered sea levels and glacial climactic regimes [138]? How did rising sea levels and expanding populations affect genetic diversity and local adaptation [137]? Were the resoundingly corroborated phylogeographic breaks present today, also present during previous glacial minima? Will additional studies corroborate these breaks and potentially reveal additional phylogeographic breaks? Did these phylogeographic breaks lead to lineage diversification and contribute to the extreme diversity found in the Coral Triangle? These questions and others can only be addressed with data from multiple unlinked genetic markers. Next generation sequencing technologies will soon provide relatively inexpensive access to genetic information from across the genome of many codistributed species [139]. This influx of data, in combination with information from ecological niche models [140] and biophysical models of larval dispersal [141], will allow us to address these questions with increasing accuracy.

Future studies of population genetics in the Coral Triangle will also further address management questions in this oceanographic, geologic, and biogeographic complex archipelago. Further delineation of population structure will allow management decisions to be made within a biological framework rather than in an administrative framework of convenience that may not be as effective. Assignment tests and parentage analysis are already helping to provide empirical estimates of larval dispersal within networks of marine−protected areas [142, 143]. The application of a nested small-scale management area within large scale management area approach to applied phylogeography can help preserve the rich resources and biodiversity of the Coral Triangle for future generations.

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Research Article

Not All Larvae Stay Close to Home: Insights into Marine Population Connectivity with a Focus on the Brown Surgeonfish (*Acanthurus nigrofuscus*)

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Recent reports of localized larval recruitment in predominately small-range fishes are countered by studies that show high genetic connectivity across large oceanic distances. This discrepancy may result from the different timescales over which genetic and demographic processes operate or rather may indicate regular long-distance dispersal in some species. Here, we contribute an analysis of mtDNA cytochrome *b* diversity in the widely distributed Brown Surgeonfish (*Acanthurus nigrofuscus*; $N = 560$), which revealed significant genetic structure only at the extremes of the range ($\Phi_{CT} = 0.452$; $P < .001$). Collections from Hawaii to the Eastern Indian Ocean comprise one large, undifferentiated population. This pattern of limited genetic subdivision across reefs of the central Indo-Pacific has been observed in a number of large-range reef fishes. Conversely, small-range fishes are often deeply structured over the same area. These findings demonstrate population connectivity differences among species at biogeographic and evolutionary timescales, which likely translates into differences in dispersal ability at ecological and demographic timescales. While interspecific differences in population connectivity complicate the design of management strategies, the integration of multiscale connectivity patterns into marine resource planning will help ensure long-term ecosystem stability by preserving functionally diverse communities.

1. Introduction

The recent dramatic decline of marine ecosystems [1–3] has led to an increased interest in the use of spatially explicit management strategies, such as no-take marine reserves, to promote ecosystem stability [4–9]. Yet designing marine reserves that can support a community's ability to absorb and recover from recurrent ecosystem disturbances requires an understanding of the scale and magnitude of population connectivity for a wide range of species and environments [9–13]. While there have been a number of recent, remarkable insights into larval dispersal distances for some taxonomic groups (e.g., Damselfishes [13, 14]), the lack of data for the majority of species continues to limit the integration of dispersal dynamics into reserve planning and design.

Most near-shore marine species exhibit an early pelagic larval phase (reviewed in [15, 16]) and larval duration has been repeatedly explored as a surrogate for species dispersal ability [17–20]. However, a comprehensive review found average pelagic larval duration (PLD) to be a poor predictor of genetic structure, and by extension dispersal ability, with previously reported correlations driven by species lacking a pelagic larval phase [21]. While a correlation between dispersal ability and general reproductive strategy may hold (i.e., brooders versus nonbrooders; reviewed in [22, 23]), there appears to be little evidence of a consistent relationship between species PLD and patterns of population connectivity [21, 24].

Recent reports emphasizing the influence of species ecology on dispersal and connectivity [25–30] may offer some insight into the discrepancy between PLD and other

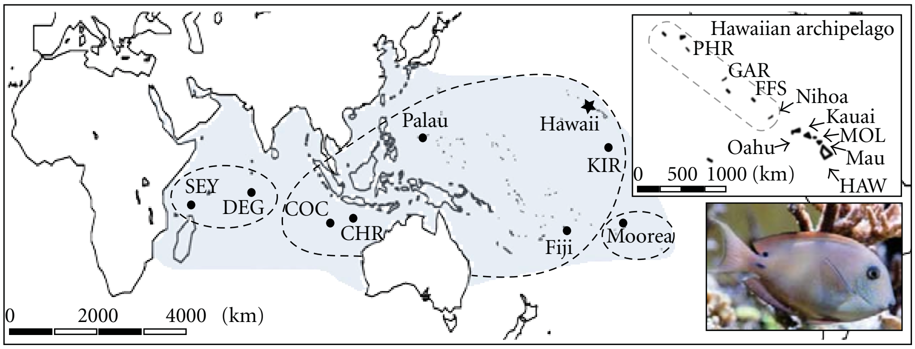

Figure 1: Location of Brown Surgeonfish (*Acanthurus nigrofuscus*) collection sites. Collections in Hawaii were made in June/July 2005-06, and elsewhere from September 2006 to June 2009. Inset details collections within the Hawaiian Archipelago, with the boundary of the Papahānaumokuākea Marine National Monument indicated by the dashed circle. Site abbreviations are as follows: SEY, Seychelles; DEG, Diego Garcia; COC, Cocos Islands; CHR, Christmas Island; KIR, Kiritimati; PHR, Pearl and Hermes Reef; GAR, Gardner Pinnacles; FFS, French Frigate Shoals; MOL, Molokai; HAW, Hawaii Island. Dashed borders on the main map indicate site groupings as determined in Samova. Photo credit: http://www.aquaportail.com/.

estimates of dispersal. For example, ecological specialists appear to be less dispersive and less successful colonizers than generalists [31]. With respect to direct larval exchange, pronounced interspecific differences in larval swimming ability and larval response to environmental signals have been identified [22, 32, 33], and inclusion of larval behavior in dispersal models can dramatically change predicted levels of local retention and larval dispersal distances [34]. The difficulty in tracking minute larvae has, however, restricted direct evaluation of dispersal distances to a small number of studies.

Whether employing induced otolith tags or multi locus parentage assignment, direct larval tracking has consistently revealed unexpectedly high levels of local larval retention [13, 14, 35–38]. In turn, this has led to the proposal that larval retention near natal sources may be a common phenomenon of reef fishes [14, 39] and of marine species in general [35]. The long-held perception that marine populations are broadly open [40–43] has now shifted towards an emphasis on the retention of larvae near source populations (reviewed in [44]), with a resulting change in recommendations for resource management [23, 37]. Yet with the exception of the Vagabond Butterflyfish (*Chaetodon vagabundus*), direct tests of larval dispersal have only been applied to fishes with small geographic ranges (<6,000 km median longitudinal range) that are restricted to either the tropical West Pacific [13, 14, 36, 37], Caribbean [35], or Mediterranean [39]. Conversely, the majority of Indo-Pacific reef fishes have longitudinal ranges exceeding 10,000 km [20], indicating that the conclusion of high larval retention may not apply to all reef species.

Dispersal ability is thought to play an important role in establishing and maintaining large geographic ranges (see [20, 45–48], but see [49, 50]). There is conflicting evidence, however, whether species' current distributions can be used to inform spatially explicit resource planning. A comparison of dispersal distances calculated from genetic isolation-by-distance (IBD) slopes for a taxonomically diverse group of reef species [51] found no relationship between dispersal ability and species geographic range size [50]. Though, because IBD analyses assume equilibrium between migration and genetic drift (i.e., equilibrium between forces adding and culling genetic diversity), IBD-based estimates of dispersal distances have been shown to differ from known values by more than 300% [52]. Biogeographic support for a positive relationship between range size and dispersal ability can be found in the least dispersive reef species; those lacking a pelagic larval phase often have smaller geographic ranges than similar species with pelagic larval dispersal [53, 54]. Likewise, genetic assessments of Hawaiian reef fishes have consistently found endemic fishes to be genetically subdivided across the 2,600 km archipelago, while more broadly distributed species reveal a lack of barriers to gene flow over the same region (see [55–58], but see [59]).

To further investigate the relationship between species range size and patterns of population connectivity, we assessed mitochondrial DNA (mtDNA) diversity in the Brown Surgeonfish (*Acanthurus nigrofuscus*) across a range that stretches from the east coast of Africa to Hawaii and Pitcairn Island in the Central Pacific [60, Figure 1]. The Brown Surgeonfish is a "generalist" herbivore that occurs in a variety of habitats from lagoons to forereefs, with feeding behavior that varies between seasons and locations [60–62]. The geographic distribution of the Brown Surgeonfish is similar to many Indo-Pacific species, covering a longitudinal distance of more than 21,000 km and straddling the well described biogeographic barrier centered on the Indo-Malay Archipelago, the Indo-Pacific Barrier (IPB [63]). A previous assessment of Brown Surgeonfish population genetic structure within Hawaii indicated extensive gene flow throughout the 2,600 km archipelago ($\Phi_{ST} = -0.006$, $P = .752$ [64]), a pattern consistent with expectations of large-scale population connectivity in widely distributed species. In addition, we contrast phylogeographic patterns (i.e., geographic distribution of genetic diversity) from the Brown Surgeonfish and other broadly distributed fishes to those from co-occurring small range species to offer some insight into how recent findings of high larval retention can be applied to marine communities and to the development of ecosystem-based management strategies.

Similar phylogeographic comparisons have provided valuable insights into species' life history [65, 66], ecology [67–69], and population history (see [24, 59, 65], reviewed in [70]). However, reliance on mtDNA markers presents some challenges. Of particular concern are the strikingly different temporal and spatial scales that genetic and demographic processes operate [71, 72]. Because most population genetic approaches integrate historical and contemporary processes, strong historical signals (e.g., colonization events) can obscure more recent patterns of gene flow [73, 74]. Additionally, demographic independence of populations can occur even when migration is high enough to inhibit genetic differentiation—meaning that a lack of genetic differentiation can not be taken as proof of frequent larval exchange [74, 75]. Therefore, rather than directly assessing ongoing larval exchange, we use findings from the Brown Surgeonfish to set up a qualitative assessment of the relationship between reef fish biogeography (range size) and population connectivity. While the increasing use of genomic molecular analyses continues to improve the resolution of fine-scale connectivity patterns (reviewed in [76]), we confine our comparison to mtDNA markers because their relative abundance offers opportunities for comparisons not yet possible with other markers.

2. Materials and Methods

Tissue collections from Hawaii ($N = 281$ [64]) were supplemented with range-wide sampling ($N = 279$; Figure 1). The combined 560 Brown Surgeonfish were collected from 17 Indo-Pacific locations with polespears while snorkeling or with SCUBA. DNA was extracted using a standard salting out protocol [77], and a 694 bp section of mtDNA cytochrome *b* was amplified using the heavy strand primer (5′-GTGACTTGAAAAACCACCGTTG-3′) from [78] and light strand primer (5′-ACAGTGCTAATGAGGCTAGTGC-3′) modified from [79]. PCR and sequencing protocols are described in [58]. In brief, polymerase chain reaction (PCR) amplification mixes consisted of 3.0 mM $MgCl_2$, 0.26 μM of each primer, 50 nM dNTPs, 1.0 units *Taq* DNA polymerase and 2.0 μL of 10x PCR buffer (Bioline USA Inc., Taunton, Mass) in 20 μL total volume. PCR thermal cycling consisted of an initial denaturing step at 94°C for 1 min, followed by 35 cycles of 94, 55, and 72°C for 30 s each, with a final extension of 72°C for 10 min. Sequencing reactions with fluorescently labeled dideoxy terminators were analyzed on an ABI 3100 automated sequencer (Applied Biosystems, Foster City, Calif) in the EPSCoR genetic analysis facility at the Hawaii Institute of Marine Biology. Only rare and questionable haplotypes were sequenced in both directions. Newly derived unique haplotypes have been deposited in Gen Bank (accession numbers HQ157717–157797). Resulting sequences were aligned in Mafft 6.62 [80].

Haplotype (h) and nucleotide (π) diversities for each collection site were calculated in Arlequin 3.11 [81] which implements diversity index algorithms described in [82]. Differences in diversity values were assessed with a one-sided T-test. A statistical parsimony network of haplotypes was constructed using TCS 1.2.1 [83].

Population structure was assessed with a spatial analysis of molecular variance (Samova 1.0 see [84]). Samova removes bias in population designation by implementing a simulated annealing procedure within the analysis of molecular variance (AMOVA) framework (Arlequin 3.11) to identify maximally differentiated groupings without *a priori* assumptions of group identity. To ensure validity of the maximally differentiated groupings, the simulated annealing process was repeated 100 times from a different initial partition of samples into K groups. The configuration with the largest, statistically significant estimate of among group differentiations (Φ_{CT}) is retained as the best sample grouping. Samova was run with values of $K = 2$ to 10 to identify the most likely number of populations. Because Samova cannot be run for $K = 1$, a separate AMOVA analysis was conducted with all collections combined into a single group. Deviations from random expectations were tested with 20,000 permutations. Patterns of pairwise genetic differentiation among individual sampling sites (Φ_{ST}) were estimated in Arlequin with the mutational model of Tamura and Nei [85], which was identified as the best fit to the data by the Akaike information criterion (AIC) as employed in Modeltest [86, 87]. We also calculated standardized estimates of allele frequency differences, D_{est} (equation 13 see [88]).

A Mantel test with 10,000 simulations was used to test for an isolation-by-distance (IBD) signature (a positive correlation between geographic and genetic distance measures [89, 90]). To provide insight into how the spatial scale of gene flow may differ across potentially interconnected islands and across large stretches of open ocean, IBD tests were conducted separately on the full data set and within Samova-defined populations.

We tested for a signature of population expansion with Fu's F_s [91] and by comparing observed and expected pairwise mismatch distributions [92] in Arlequin with 90,000 simulated samples. Fu [91] noted that F_s is particularly sensitive to deviations from a constant population size, with population expansion resulting in a significant, negative F_s. If there was evidence of population expansion, we estimated ancestral and contemporary female effective population sizes (N_{ef}) from the equation: $\theta = N_{\mathrm{ef}} 2\mu t$, with μ being the estimated annual fragment mutation rate and t is the estimated generation time. Estimates of pre- and post expansion θ were derived from the sudden expansion model of the mismatch distributions. Population ages in years were estimated from the population age parameter (τ), with $\tau = 2\mu T$, where T is the time since the most recent bottleneck. We provisionally applied a generation time of 5 years for the Brown Surgeonfish [92] and a within lineage, annual-per-site mutation rate of 1.55×10^{-8} per year [93].

3. Results

Cytochrome *b* sequencing revealed 110 closely related haplotypes ($h = 0.65$–0.91; $\pi = 0.0017$–0.0045 Table 1). Haplotype diversity in Hawaii ($h = 0.65$–0.87) is similar

Table 1: Brown Surgeonfish collection sites with sample size, haplotype diversity (h), and nucleotide diversity (π) per sample and for the overall data set (Total), with standard deviations in parentheses.

Location	N	h	π
Pearl and Hermes Reef	20	0.87 (0.06)	0.0045 (0.0027)
Gardner Pinnacles	25	0.72 (0.08)	0.0021 (0.0014)
French Frigate Shoals	33	0.72 (0.08)	0.0021 (0.0013)
Nihoa	40	0.73 (0.06)	0.0026 (0.0016)
Kauai	26	0.81 (0.06)	0.0023 (0.0015)
Oahu	39	0.70 (0.07)	0.0019 (0.0013)
Molokai	29	0.71 (0.08)	0.0024 (0.0016)
Maui	36	0.77 (0.06)	0.0030 (0.0018)
Hawaii Island	33	0.65 (0.09)	0.0022 (0.0015)
Kiritimati	35	0.89 (0.04)	0.0032 (0.0020)
Fiji	30	0.91 (0.03)	0.0031 (0.0020)
Palau	36	0.90 (0.03)	0.0028 (0.0018)
Moorea	31	0.78 (0.08)	0.0030 (0.0019)
Christmas Island	51	0.85 (0.03)	0.0025 (0.0016)
Cocos Islands	32	0.88 (0.04)	0.0030 (0.0019)
Diego Garcia	32	0.85 (0.05)	0.0030 (0.0017)
Seychelles	32	0.72 (0.07)	0.0017 (0.0012)
Total	560	0.85 (0.01)	0.0032 (0.0020)

to other peripheral collections (Seychelles and Moorea, $h = 0.72$–0.78) but is significantly lower than central Indo-Pacific collections (Diego Garcia to Kiritimati, $h = 0.85$–0.89; one way T-test, $P < .001$).

The statistical parsimony network demonstrates both the high diversity and low differentiation of haplotypes collected from sites distributed across two ocean basins (Figure 2). Abundant haplotypes are well dispersed through most sites with the exception of Moorea in French Polynesia, which exhibited a high number of geographically restricted haplotypes.

Samova identified three maximally differentiated groupings, with significant population differentiation occurring only at eastern and western edges of the range ($\Phi_{CT} = 0.452$, $P < .001$; Table 2). Central Indo-Pacific collections (Cocos Islands to Hawaii) form one large group, while Moorea is isolated in the South Pacific and Diego Garcia is grouped with the Seychelles in the Indian Ocean (Figure 1). Estimates among group differentiations (Φ_{CT}) dropped incrementally with the addition of $K > 3$ populations (data not shown) indicating a lack of further population subdivision. Pairwise Φ_{ST} and D_{est} highlight both the isolation of Moorea as well as a pattern of increasing divergence in the Indian Ocean with distance from the IPB (Table 3). Both the Seychelles and Diego Garcia were significantly different from all other locations, though the test for IBD within this region was nonsignificant ($R^2 = 0.46$, $P = .16$). Pairwise estimates of Φ_{ST} within the Samova-defined central Indo-Pacific population were near zero. Nonetheless, there was a clear IBD signature across this broad region ($R^2 = 0.61$, $P < .001$, slope $= 2.0 \times 10^{-5}$, y-intercept $= 0.038$) even though Christmas Island, located in the western Indian Ocean, was only marginally different from Hawaiian collections ($\Phi_{ST} = 0.007$–0.032, $P = .030$–$.246$; $D_{est} = -0.04$–0.166, $P = .016$–$.618$) and was genetically indistinguishable from Kiritibati, Fiji, and Palau.

Tests for demographic expansion were run on the three Samova populations. While a significant deviation between simulated and observed mismatch distributions was observed only in the Moorean collection (SSD $= 0.173$, $P = .01$), Fu's F_s was significantly negative in all three populations (Table 4). Simulations have shown F_s to be more sensitive to recent population expansion than other tests of demographic history [91], so we place greater emphasis on these tests as indicators of population expansion. Mismatch analyses indicate the time since last expansion to be on the order of 56,000 and 24,000 years in Moorea and the Seychelles/Diego Garcia, respectively, and 83,000 years in the central Indo-Pacific (Table 4). Estimates of post-expansion female effective population size derived from θ_1 were unresolved in both the Seychelles and Moorea, but was approximately 300,000 in the central Indo-Pacific population (Table 4).

4. Discussion

Several patterns are apparent from the phylogeographic assessment of the Brown Surgeonfish. First, populations are characterized by clusters of closely related haplotypes, high haplotype diversity and low nucleotide diversity, a common pattern in reef fishes (Figure 2, Table 1; [94]). Second, Samova and pairwise Φ_{ST} and D_{est} indicate that distances as long as 11,000 km do not appear to be much of an obstacle to gene flow in the Brown Surgeonfish (Table 3). Kiribati and Fiji are located at 11,900 and 8,800 km, respectively from Cocos Islands in the Eastern Indian Ocean, yet there were no indications of population differentiation across this

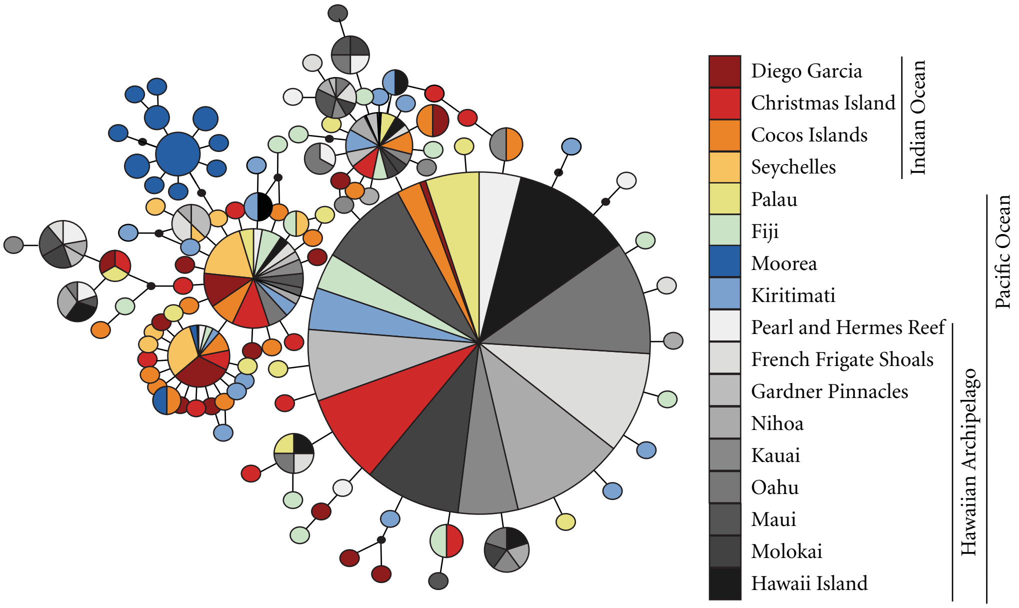

Figure 2: Statistical parsimony network for the Brown Surgeonfish. Area of circles is proportional to the frequency of the respective haplotype. Black dots represent missing haplotypes and colors represent haplotype location (see key).

Table 2: Structural analysis of molecular variance (Samova) with maximally differentiated groupings for ($K = 1$ to 3) and percent variation (%Var.) and fixation indices (Φ). Significance represented by: $^{\ddagger}P \leq .001$.

Number of groups	Groupings	Among groups		Among samples within groups		Among samples
		Φ_{CT}	%Var.	Φ_{SC}	%Var.	Φ_{ST}
1	All sites			$0.201^{\ddagger}$	20.06	
2	Moorea/All other sites	0.563	56.28	$0.082^{\ddagger}$	3.59	$0.599^{\ddagger}$
3	Moorea/Seychelles, Diego Garcia/All other sites	$0.452^{\ddagger}$	45.24	$0.053^{\ddagger}$	2.91	$0.481^{\ddagger}$

large expanse of interspersed islands and reefs. Third, Fu's F_s and coalescence estimates indicate population contractions throughout the Brown Surgeonfish's range during the most recent glacial period (~110–10 ka [95]), with subsequent population expansion, and in turn, increasing genetic diversity (Table 4).

Genetic evidence of postglacial population expansion is common in reef fishes and indicates broad ecosystem level responses to global climate change [94]. These patterns also demonstrate the temporal durability of historical genetic signals and the difficulty extrapolating demographically meaningful estimates of connectivity from genetic data. In particular, population expansion can prolong the time required for populations to reach equilibrium between the forces adding and culling genetic diversity, potentially resulting in an overestimate of population connectivity [96]. There is, however, a negative correlation between rates of gene flow and the time required for populations to attain equilibrium, meaning that well-connected populations will reach equilibrium, and therefore return accurate connectivity estimates, more rapidly than similar populations that are less well connected [90, 97]. Accordingly, while evidence of population expansion in the Brown Surgeonfish may indicate that population connectivity across the central Indo-Pacific may be overestimated, the presence of highly differentiated populations at the edge of the species range (Table 2) demonstrates ample opportunity for the establishment of genetic differentiation within the central Indo-Pacific should gene flow be truly restricted across this region. Likewise, the presence of an IBD signature within the central Indo-Pacific argues against the overestimation of gene flow, as IBD will arise only as populations approach equilibrium [98]. We therefore conclude that the lack of genetic differentiation observed across the majority of the Brown Surgeonfish's range is indicative of high population connectivity rather than a temporal artifact of nonequilibrium conditions.

The population structure of the Brown Surgeonfish is remarkably similar to the widely distributed Bluestriped Snapper (*Lutjanus kasmira*), which differs only in having an additional genetic break between Moorea and the Marquesas [68]. Notably, the Brown Surgeonfish is abundant throughout French Polynesia with the exception of the Marquesas

Table 3: Results of pairwise tests for population structure with Φ_{ST} (below diagonal) and D_{est} (above diagonal). Significance represented by: * for $P \leq .05$, † for $P \leq .01$, ‡ for $P \leq .001$, and bold for $P \leq .0004$ (Bonferroni correction for multiple comparisons). Location abbreviations as described in Figure 1.

	PHR	FFS	GAR	Nihoa	Kauai	Oahu	MOL	Maui	HAW	KIR	Fiji	Palau	Moorea	CHR	COC	DEG	SEY
PHR	~	0.031	0.059	0.032	−0.005	0.015	0.015	−0.020	0.059	0.225	0.098	0.028	**0.982**‡	0.021	0.319*	0.611‡	**0.695**‡
FFS	0.033	~	−0.031	−0.004	0.008	−0.030	−0.040	−0.036	−0.005	0.341†	0.267†	0.187*	**0.988**‡	0.134*	**0.461**‡	**0.805**‡	**0.828**‡
GAR	0.020	−0.025	~	−0.053	−0.034	−0.021	−0.044	−0.020	0.007	0.151	0.135	0.114	**0.967**‡	0.062	0.283	**0.818**‡	**0.816**‡
Nihoa	0.007	−0.001	−0.013	~	−0.022	−0.026	−0.045	−0.023	−0.023	0.200*	0.184*	0.147*	**0.971**‡	0.099	0.348†	**0.862**‡	**0.887**‡
Kauai	0.022	−0.015	−0.022	−0.017	~	−0.029	−0.027	−0.052	0.046	0.062	−0.001	0.008	**0.970**‡	−0.041	0.148	**0.674**‡	**0.675**‡
Oahu	0.027	−0.007	−0.010	−0.008	−0.024	~	−0.049	−0.034	−0.027	0.258†	0.195*	0.139*	**0.981**‡	0.079	0.362‡	**0.763**‡	**0.775**‡
MOL	0.017	−0.009	−0.013	−0.018	−0.026	−0.018	~	−0.053	−0.027	0.260*	0.218*	0.165*	**0.978**‡	0.106	0.397†	**0.837**‡	**0.868**‡
Maui	0.008	−0.007	−0.013	−0.015	−0.019	−0.008	−0.021	~	0.019	0.234*	0.168*	0.130	**0.980**‡	0.072	0.345†	**0.762**‡	**0.781**‡
HAW	0.006	0.000	−0.002	−0.015	−0.005	−0.003	−0.010	0.002	~	0.333†	0.296†	0.219†	**0.983**‡	0.165*	**0.473**‡	**0.859**‡	**0.895**‡
KIR	0.037	0.016	−0.001	0.020	0.001	0.017	0.019	0.016	0.027	~	−0.124	−0.014	**0.943**‡	0.012	−0.068	**0.623**‡	**0.628**‡
Fiji	0.016	0.004	−0.010	0.007	−0.005	0.004	0.006	0.004	0.010	−0.012	~	−0.085	**0.953**‡	−0.078	−0.097	0.477‡	**0.496**‡
Palau	0.027	0.025	0.017	0.040*	0.026	0.040*	0.041*	0.040*	0.029	0.003	−0.007	~	**0.947**‡	−0.058	0.002	0.381†	**0.486**‡
Moorea	**0.497**‡	**0.615**‡	**0.611**‡	**0.599**‡	**0.608**‡	**0.644**‡	**0.609**‡	**0.582**‡	**0.608**‡	**0.563**‡	**0.554**‡	**0.566**‡	~	**0.960**‡	**0.930**‡	**0.952**‡	**0.960**‡
CHR	0.029	0.018	0.007	0.031*	0.015	0.030*	0.033*	0.031*	0.022	−0.002	−0.010	−0.012	**0.583**‡	~	0.024	0.444‡	**0.472**‡
COC	0.051*	0.091‡	0.073*	0.100‡	0.085‡	0.117‡	0.110‡	0.092‡	0.101‡	0.023	0.022	0.006	**0.536**‡	0.012	~	0.304*	0.318†
DEG	**0.174**‡	**0.288**‡	**0.281**‡	**0.295**‡	**0.292**‡	**0.335**‡	**0.310**‡	**0.278**‡	**0.293**‡	**0.187**‡	**0.189**‡	**0.146**‡	**0.538**‡	**0.172**‡	0.065†	~	0.022
SEY	**0.240**‡	**0.355**‡	**0.357**‡	**0.359**‡	**0.369**‡	**0.407**‡	**0.385**‡	**0.339**‡	**0.366**‡	**0.236**‡	**0.244**‡	**0.196**‡	**0.583**‡	**0.218**‡	0.101†	−0.010	~

Table 4: Estimates of historical demography including pre- and post-expansion theta (θ_0 and θ_1), female effective population size (N_{ef}), mismatch analyses (sum of squared deviations; SSD), tau (τ), time since last bottleneck (age in years), and test for population expansion (F_s), with unresolved values shown as NR. Standard deviations for population parameter estimates are given in parentheses. Significance represented by: $^{*}P \leq .05$, $^{\ddagger}P \leq .001$.

	Mismatch distribution							
SAMOVA populations	θ_0	$N_{\mathrm{ef}0}$	θ_1	$N_{\mathrm{ef}1}$	SSD	t	Age	F_s
Central Indo-Pacific	0.014 (0–0.745)	130 (0–7,000)	30.57 (4.47–NR)	284,000 (42,000–NR)	0.003	1.78 (0.82–2.52)	83,000 (38,000–117,000)	$-26.73^{\ddagger}$
Moorea	0.000 (0–0.105)	0 (0–1,000)	NR (6.02–NR)	NR (56,000–NR)	0.173^{*}	1.20 (0.37–2.05)	56,000 (17,000–95,000)	$-9.38^{\ddagger}$
Seychelles/Diego Garcia	0.009 (0–0.345)	100 (0–3,000)	NR (2.60–NR)	NR (24,000–NR)	0.002	0.52 (0.02–1.12)	24,000 (1,000–52,000)	$-5.74^{\ddagger}$

(1,200 km northeast of Moorea) where it is either very rare or absent (M. Gaither pers. comm.). Gaither et al. [68] argued that population and community level differences between Moorea (Society Islands) and the Marquesas resulted from limited dispersal across the fast flowing Southern Equatorial Current (SEC), a proposal consistent with recent evidence indicating that ocean currents can have a strong influence on population connectivity [99, 100]. Considering that the Society Islands are located below the westward flowing SEC and within the southerly flowing South Pacific Current [101], oceanographic isolation may likewise explain the concordant break between Moorea and other central Pacific sampling sites observed in both the Bluestriped Snapper and Brown Surgeonfish.

The lack of pronounced mtDNA genetic structure across the central Indo-Pacific in both the Brown Surgeonfish and Bluestriped Snapper has been observed in a growing number of widely distributed reef fishes. Of the six published genetic surveys of reef fishes with geographic ranges extending from Africa to the East Pacific (27,000 km), all but the Convict Surgeonfish (*Acanthurus triostegus*) revealed little to no genetic subdivision within the Central and West Pacific [56, 68, 102–105]. Remarkably, there was no evidence of population subdivision in the Blue-spine Surgeonfish (*Naso unicornis*) from the West Indian Ocean to French Polynesia in the South Pacific [104], in the trumpetfish, (*Aulostomus chinensis*,) from West Australia to Panama [102], and in the Yellow-edged Moray (*Gymnothorax flavimarginatus*) from East Africa to the East Pacific [105].

The broad genetic connectivity consistently observed in the most widely distributed Indo-Pacific fishes highlights an emerging relationship between reef fish range size and genetic connectivity. In particular, Soldierfishes (genus *Myripristis* [24, 56]), Pygmy Angelfishes (genus *Centropyge* [106, 107]), Trumpetfishes (genus *Aulostomus* [102]), Unicornfishes (genus *Naso* [104, 108]), Moray Eels (genus *Gymnothorax* [105]), and at least some Snappers (genus *Lutjanus* [68]) and Surgeonfishes (genus *Acanthurus* [31, 109]) have demonstrated an ability to maintain genetic homogeneity across tens of thousands of kilometers.

For widely distributed species, genetic homogeneity across much of the Indo-Pacific is largely concordant with biogeographic provinces and barriers, previously defined based on species distributions. For example, the region stretching from the eastern Indian Ocean to the Central Pacific is recognized by biogeographers as the Indo-Polynesian province [110–112]. Hobbes et al. [113] observed that many Indian and Pacific reef fishes overlap at our sample location in the Eastern Indian Ocean (Christmas Island), and in some cases hybridize there. For large-range fishes, this location is commonly the western limit of a broad central Indo-Pacific population, and hence demonstrates the alignment of intraspecific phylogeographic patterns with biogeographic provinces.

This pattern of widely distributed reef fishes successfully bridging long-distances contrasts starkly with the remarkably complex patterns of population structure commonly observed in smaller range fishes. The leopard coral grouper (*Plectropomus leopardus*) is restricted to reefs from West Australia to Fiji, and a survey of mtDNA control region diversity indicated deep genetic partitions, with a minimum of six highly differentiated populations ($F_{ST} = 0.90$ to 0.94 [114]). Likewise, a comparative mtDNA survey of three restricted-range Damselfishes (*Amphiprion melanopus*, *Chrysiptera talboti* and *Pomacentrus moluccensis*) and the restricted-range Wrasse, (*Cirrhilabrus punctatus*,) revealed concordant morphological and genetic differentiation, and indicates evolutionary level partitions among the closely linked reefs of the West Pacific [115]. Small range species with planktonic larval dispersal and pronounced mtDNA population subdivision appear to be particularly common in Damselfishes (genus *Amphiprion* [115–117]; genus *Chrysiptera* [115, 118]; genus *Dascyllus* [57, 119]; genus *Pomacentrus* [119]), and Groupers (genus *Epinephelus* [55, 114]; genus *Plectropomus* [114]).

For species occurring within the central Indo-Pacific, broad genetic homogeneity should be facilitated by stepping stone gene flow across the regions relatively abundant reefs. Indeed, dispersal can be accomplished across this vast region without having to traverse more than 800 km of open ocean [120], yet even these relatively limited distances act as effective barriers to gene flow in many smaller range fishes (e.g., [114]). Conversely, the limited genetic subdivision commonly observed in widely distributed species indicate larval exchange across thousands of kilometers of open ocean, including across the world's largest marine biogeographic barrier, the Eastern Pacific Barrier (EPB [63, 121, 122]. The EPB comprises the 4,000 to 7,000 km expanse of open ocean separating the islands of the Central Pacific from the west coast of the Americas. The suite of species demonstrating recent or ongoing larval connectivity across the EPB contains members of the most common Indo-Pacific reef fish families, though notably absent are Damselfishes (Pomacentridae) and Groupers (Serranidae), identified above as taxanomic families with limited individual and geographic range.

It has been noted that mtDNA markers may not accurately reflect population histories, due to either direct selection on the marker or adjacent DNA segments [123]. However, when comparing genetic partitions among multiple species, matching patterns indicates such concerns are likely unwarranted since the biological or environmental mechanisms that drive concordance across species will likewise drive concordance across markers [70]. A notable exception to this rule is sex-biased dispersal [124, 125], though this is unlikely to be an issue in species with pelagic larval dispersal [68]. Accordingly, the broad agreement between biogeographic and phylogeographic patterns herein demonstrates that species differ in dispersal ability at biogeographic and evolutionary time-scales, which in turn would appear to indicate that species differ in the extent and magnitude of population connectivity at demographic and ecological time-scales.

How do these findings translate into policies for ecosystem-level management of reef communities? The debate continues over the extent to which genetic connectivity relates to demographic connectivity [126]. Further application of larval tracking will help identify the degree to which species and regions may differ in the scale and extent of larval exchange. However, until that time, the apparent relationship between reef fish range size and extent of genetic connectivity indicates that recent evidence of high local larval retention may only apply to species with small geographic ranges. In all likelihood, marine communities contain species with markedly different dispersal abilities [127–129], including many capable of larval exchange over thousands of kilometers.

While interspecific differences in realized dispersal would appear to complicate the development of effective marine reserves, reserve design may be simplified by focusing on the species that show the finest scale of genetic isolation [69, 130, 131]. Emphasis on short-distance dispersers requires protecting reefs on a local scale, resulting in the establishment of a network of smaller reserves [129]. While setting aside one or a few larger reserves might be politically more expedient than placing an equivalent area under protection with multiple small reserves [132], a network of smaller reserves would better accommodate differences in dispersal ability among resident species by facilitating linkages among reserves at multiple spatial scales. Under this scenario, protected populations would be sustained by either local retention within the reserve or dispersal between adjacent reserves for short to moderate dispersing species, and by larval exchange between distant reserves for widely dispersing species. Additionally, a network of smaller reserves would maximize opportunities for larval subsidy to unprotected populations by increasing the likelihood of seeding reefs outside of reserve boundaries [133], one of the primary goals of reserves designed to mitigate fisheries impacts [134]. No matter the management strategy employed, overcoming the challenges of incorporating multiscale connectivity patterns into resource management planning will ultimately help ensure long-term resource stability by preserving communities of species that differ markedly in how they respond to local and global environmental impacts.

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Research Article

Widespread Dispersal of the Crown-of-Thorns Sea Star, *Acanthaster planci*, across the Hawaiian Archipelago and Johnston Atoll

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The population structure of marine species is variable along the Hawaiian Archipelago; thus, it is important to understand dispersal and recruitment patterns for economically and ecologically important taxa to inform Ecosystem-based Management. Connectivity of the coral-eating crown-of-thorns sea star, *Acanthaster planci*, was examined from Johnston Atoll and 12 locations across the Hawaiian Archipelago. Sequences of mitochondrial DNA from 383 individuals were analyzed to infer patterns of gene flow among the Northwestern Hawaiian Islands (NWHIs), the main Hawaiian Islands, and Johnston Atoll. Population samples were genetically similar across the Hawaiian Archipelago with the exception of the west side of the Big Island of Hawaii, which was significantly differentiated from the majority of Hawaiian samples (pairwise $\Phi_{ST} = 0.0607$–0.1068, $P < .05$). Although differentiated, Hawaiʻi West shares haplotypes with every other site across the Hawaiian Archipelago. Johnston Atoll was genetically distinct from every location (pairwise $\Phi_{ST} = 0.064$–0.13, $P < .05$) except French Frigate Shoals ($\Phi_{ST} = 0.03$, $P = .10$), supporting connectivity between the central NWHIs and Johnston Atoll. Taken together with the lack of geographic population structure and haplotypes shared among all populations, these results indicate widespread larval dispersal with few restrictions to gene flow along the archipelago.

1. Introduction

The most geographically isolated island group in the world, the Hawaiian Archipelago, spans 2500 km and is composed of eighteen primary islands, reefs, and atolls separated into the remote Northwestern Hawaiian Islands (NWHIs) and the inhabited main Hawaiian Islands (MHIs). The NWHIs and MHIs are distinguishable by human habitation, geomorphology, and geological age; the MHIs are heavily populated high islands and geologically young, while the NWHIs are geologically older and predominantly uninhabitable low coral islands and atolls. The reefs of the MHIs are anthropogenically impacted from sewage outflow [1–3], alien invasive algae [4–6], overfishing [2, 7], and nutrient discharge [8], whereas the NWHIs have remained relatively pristine [7]. Fish communities and biomass in the NWHIs are unparalleled to the MHIs [7], and in terms of ranking overall “health”, the NWHIs have retained their biological richness and value compared to the MHIs [9–11].

Currently under protection as the Papahānaumokuākea Marine National Monument, the NWHIs remain shielded from most direct threats induced by human activities such as commercial fishing, military use, and tourism [11]. To inform ecosystem-based management in both the Monument and the reefs in the MHIs, it is necessary to know the direction and magnitude of connectivity across the archipelago. Ascertaining whether the NWHIs serve as a recruitment source to the MHIs or whether the MHIs serve as a recruitment source to the NWHIs should be investigated to better support implementation of ecosystem-based approaches to management.

The genetic structure and degree of differentiation among populations of surveyed marine species are highly variable along the Hawaiian Archipelago. Marine species are thought to diverge from their Pacific roots but maintain species cohesion and not diversify in the Hawaiian Archipelago [12–14]. Thus, marine species in Hawai‘i were historically expected to be generally well mixed because the spectacular species radiations seen in terrestrial species are not mirrored in the sea, and there is limited evidence to suggest divergence and diversification of marine taxa [12, 14]. Several studies supported this lack of genetic structure for the damselfish, *Stegastes fasciolatus* [15], the soldierfish, *Myripristis berndti* [16], the spiny lobster, *Panulirus marginatus* [17], and the snapper, *Pristipomoides filamentosus* [18]. In contrast to these examples, however, several marine species have also shown significant genetic differentiation within the Hawaiian Archipelago. For example, the Hawaiian grouper, *Epinephelus quernus*, exhibits genetic subdivision along the middle of the archipelago [19]. Similarly, subpopulations of the Hawaiian spinner dolphin exist between the MHIs and the NWHIs and within each region [20]. Furthermore, two genetically distinct populations of the endemic bobtail squid, *Euprymna scolopes*, have been discovered on the island of O‘ahu [21]. Finally, major restrictions to gene flow were found within the Hawaiian Archipelago for the subtidal Hawaiian limpet, *Cellana talcosa* [22], as well as for vermetid gastropods [23]. Research thus far dictates that the levels of connectivity and gene flow between the NWHIs and MHIs and among all Hawaiian islands are highly variable among species [22]. Thus, population structure must be investigated species by species to understand the dispersal and recruitment patterns for economically and ecologically important taxa until sufficient data emerge to make meaningful generalizations.

Here, we investigate the population structure of the ecologically influential, corallivorous crown-of-thorns sea star, *Acanthaster planci*. Large aggregations of the crown-of-thorns, termed outbreaks, are among the most significant biological disturbances that occur on a tropical reef [24]. Outbreaks can destroy a coral reef [24], change coral community structure [25–27], promote algal colonization [24, 28], and affect fish population dynamics [29–31]. What specifically drives outbreak formation is still unknown, and whether recent outbreaks are more of a human-induced phenomenon as a result of sedimentation and urbanization [32], run-off [32–34], or overfishing [35, 36] rather than a naturally occurring phenomenon remains under debate. Regardless of the mechanism, infestations are detrimental not only ecologically, but also economically by reducing the aesthetic value of coral reefs in locations where the economy is driven by tourism.

Coral reef tourism is a multibillion dollar industry for island nations. Net benefits from Hawaiian coral reefs alone were estimated to be USD $360 million per year [37] with 50 to 60 million a year in revenue from the dive industry [38]. Control and eradication programs have been established in several countries to manage *Acanthaster* reef impacts for ecological and economical reasons [26, 39]. Knowledge on the dispersal and connectivity patterns of this corallivore along the Hawaiian Archipelago would provide managers with information regarding potential larval pathways enabling them to monitor reef areas that may be at risk to *A. planci* aggregations and act proactively to control outbreaks and prevent spread.

This paper uses genetic markers (mtDNA) to investigate gene flow and connectivity of *A. planci* across the Hawaiian Archipelago and Johnston Atoll. Located 865 km to the south-southwest of French Frigate Shoals in the NWHIs, Johnston Atoll is the closest Indo-West Pacific source of marine species that could have potentially populated the Hawaiian Islands and has alternately been proposed as a gateway into Hawai‘i and an outpost of Hawaiian diversity. In this study, we ask the following questions. (1) Do populations of *A. planci* show evidence of genetic subdivision between and within the NWHIs and the MHIs? (2) Is there gene flow among Johnston Atoll, the NWHIs, the MHIs, or all three? (3) Do *A. planci* populations conform to a genetic isolation by geographic distance (IBD) model along the Hawaiian Archipelago?

2. Materials and Methods

2.1. Sampling. Adult *Acanthaster planci* were collected between 2005 and 2007 from Johnston Atoll and 11 sites along the 2500 km long Hawaiian Archipelago (Figure 1). Of those 11 sites, two were in the NWHIs (Pearl and Hermes Atoll and French Frigate Shoals) and nine within the MHIs (Ni‘ihau, Kaua‘i, O‘ahu, Maui, Moloka‘i, Lana‘i, Hawai‘i East, Hawai‘i West, and Hawai‘i South). Sites, Oahu and Hawai‘i East, were outbreak populations having greater than 1500 sea stars/km^2 [40]. Live stars were sampled nonlethally by snipping off an arm tip in the field by means of both free diving and SCUBA [41]. Tube feet tissue was preserved in 95% ethanol and stored at -20°C. In addition, 44 samples collected in 1982 from an unknown location of the Big Island of Hawai‘i were used in this study. For these historical samples, whole animals were collected and pyloric caeca were preserved in 95% ethanol before being stored at -20°C.

2.2. DNA Extraction and PCR. Two different procedures were used for DNA extraction and amplification based on the tissue type and age of the samples. DNA extractions mirrored the protocols described in Jessop [42] or the Hotshot boiling protocol [43].

Approximately 530 base pairs of the noncoding mitochondrial DNA control region were amplified using polymerase chain reaction (PCR) with the following primers: COTS-ctrl-fwd 5′CAAAAGCTGACGGGTAAGCAA3′ and COTS-ctrl-rvs 5′TAAGGAAGTTTGCGACCTCGAT3′ (Volger et al., unpublished). 100 μl PCR reactions were performed for tube feet samples using 30 μl of dH20, 10 μl of template, 10 μl of each primer (5 μM), and 50 μl of Promega

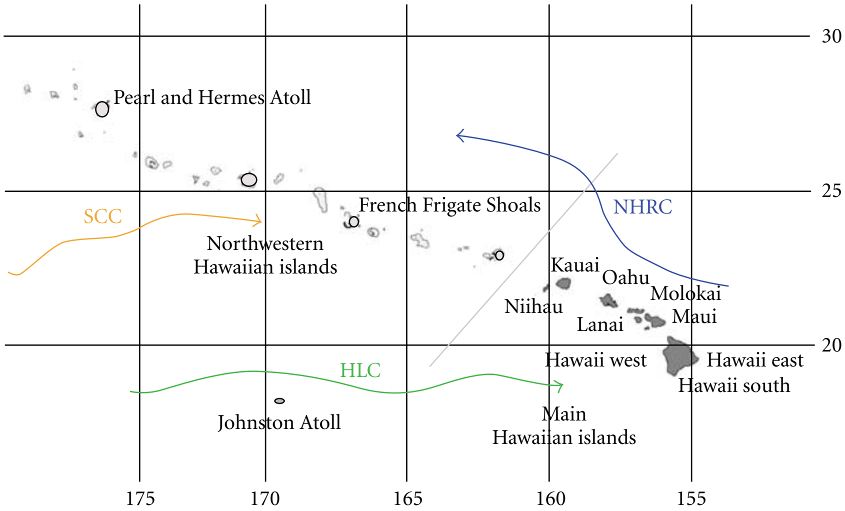

FIGURE 1: Scaled map of island and atoll collections of *Acanthaster planci* along the Hawaiian Archipelago and Johnston Atoll. High islands are represented in dark gray. Submerged reef area to a 30 meter isobath is outlined in light gray. The blue line represents the North Hawaiian Ridge Current (NHRC), the green line represents the eastward Hawaiian Lee Countercurrent (HLC), and the orange line presents the Subtropical Countercurrent (SCC).

MasterMix. The PCR for historical samples occurred in 25 μl reactions with 2.5 μl of 10X buffer, 5 μl of dNTPs (2 μM), 1 μl of $MgCl_2$ (1.5 mM), 0.5 μl of each primer (0.2 μM), 0.5 μl of template, and 1.5 U of Bioline's Immolase Taq polymerase. Thermocycling for all samples was performed with an initial denaturation at 94°C for 5 min, 34 cycles (94°C for 30 s, 55°C for 1 min, and 72°C for 1 min), and a final extension for 10 min at 72°C. PCR products from tube feet samples were cleaned using UltraClean PCR kit (MO BIO Laboratories). PCR products from 1982 samples were treated with 1.5 μl of exonuclease I and 1.5 μl of calf intestinal alkaline phosphatase (Exo-CIAP), incubated at 37°C for 60 minutes, and then deactivated at 85°C for 15 minutes.

Amplified DNA fragments were sequenced in the reverse direction, and all unique or questionable sequences were repeated using an alternate reverse primer on an ABI 3130XL automated sequencer (Applied Biosystems Incorporated).

2.3. Data Analysis. Sequences were compared, and assembled using SEQUENCHER (v4.52b; Gene Codes Corporation, Ann Arbor, MI, USA). Sequences were aligned using MANGO (multiple alignment with *N* gapped oligos) because this program uses a novel orthogonal multiple sequence alignment method that processes information of all sequences as a whole and builds the alignment vertically, avoiding the "once a gap, always a gap" alignment phenomenon [44]. Gap placement was then double checked by eye using Bioedit [45], and haplotypes were determined based on sequence identity.

A median joining haplotype network with the default weight of 10 applied to each character was created using NETWORK ver 4.5 (Fluxus Technology Ltd., Suffolk England) to illustrate haplotype variability and clustering. An analysis of molecular variance (AMOVA) was conducted using ARLEQUIN 3.1 [46]. A Kimura 2P model [47] was determined to be the most appropriate model for these data as determined by MODELTEST 3.7 [48]; therefore, all AMOVA analyses assumed this base substitution model. Haplotype diversity (h), nucleotide diversity (π), and population pairwise Φ_{ST} values were calculated in ARLEQUIN. A partial mantel test as implemented in IBDWS [49] was used to determine if genetic distance was correlated with geographic distance between islands.

3. Results

A total of 383 specimens of *A. planci* were sampled. There were 308 haplotypes, of which 125 were singletons (Table 1). Haplotype diversity was high both overall ($h = 0.98$ or 50 effective haplotypes) and within sample locations ($h = 0.968$–0.997; Table 1). The overall nucleotide diversity was $\pi = 0.027$, and within sample locations $\pi = 0.019$–0.041.

The median joining network revealed no obvious association between haplotype and geographic location (Figure 2). Haplotypes were not clustered in distinguishable groups. When haplotypes of the 1982 samples were added, there was no distinction between the older samples and the newer ones (Figure 2).

Excluding Johnston Atoll, an AMOVA to test the separation of the NWHIs and the MHIs detected no significant difference among regions ($\Phi_{CT} = 0.003$, $P = .38$), but significant differences were detected among populations within regions ($\Phi_{SC} = 0.052$, $P = .01$). Including all populations, there was an indication of population partitioning between Johnston Atoll and all sites within the Hawaiian Archipelago ($\Phi_{CT} = 0.052$, $P = .075$), with 5.24% of the genetic variation explained by these groups.

Table 1: Sample size and descriptive statistics for control region data of *Acanthaster planci* collected along the Hawaiian Archipelago and at Johnston Atoll. The "∗" indicates the Northwestern Hawaiian Islands.

Location	N	No. of haplotypes	No. of unique haplotypes	Averaged haplotype diversity (h)	Averaged nucleotide diversity (π)
Hawaiʻi 1982 Samples	44	32	11	0.978	0.023
Hawaiʻi East	29	25	6	0.991	0.023
Hawaiʻi South	34	29	12	0.989	0.029
Hawaiʻi West	42	26	8	0.969	0.024
Maui	26	20	7	0.982	0.033
Molokaʻi	25	23	11	0.993	0.034
Lanaʻi	30	25	10	0.982	0.032
Oʻahu	25	23	10	0.993	0.03
Kauaʻi	24	24	6	0.996	0.033
Niʻihau	30	21	7	0.975	0.023
∗French Frigate Shoals	13	11	5	0.974	0.019
∗Pearl and Hermes Atoll	27	26	17	0.997	0.041
Johnston Atoll	33	23	15	0.968	0.013
Total	382	308	125	0.984	0.027

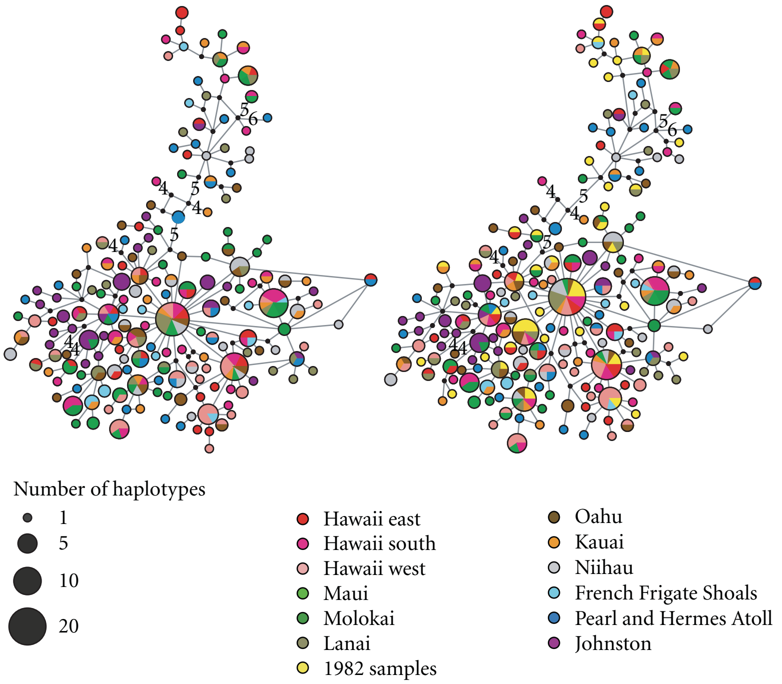

Figure 2: Median joining haplotype network of *Acanthaster planci* samples from Johnston Atoll and the Hawaiian Archipelago. The network to the right includes the samples from 1982 and the network to the left does not. Each circle represents a unique haplotype connected by a line to those that differ by one or more base pairs. Those lines that represent >4 bp differences were labeled, but lines are not to scale. Nodes on the lines indicate missing haplotypes. Each haplotype is color coded by region and size of the pie chart is proportional to frequency. The smallest colored circles represent a singleton haplotype and the largest circle represents 20 individuals who share that haplotype.

Pairwise population fixation (Φ_{ST}) values revealed two locations significantly differentiated from the rest of the archipelago: Johnston Atoll and Hawaiʻi West (Table 3). Given these results, a post hoc AMOVA was conducted to look for regional differences between Johnston Atoll, Hawaiʻi West, and the rest of the archipelago. Significant differences were found among regions, explaining 5.71% of the genetic variation ($\Phi_{CT} = 0.057$, $P < .05$, Table 2).

Pairwise Φ_{ST} values were used to assess whether genetic and geographic distances conformed to the Isolation by Distance model. Only 8% of the relationship was explained ($R^2 = 0.078$) by the IBDWS model, and the associated

Table 2: Analysis of molecular variance results for *Acanthaster planci* populations along the Hawaiian Archipelago and from Johnston Atoll. The regional variance component relative to the total variance is Φ_{CT}. The between-site within region variance component divided by the sum of itself and the within-site variance is Φ_{SC}. Statistical significance ($P < .05$) is indicated by the bold font.

Statistic	df	SS	Var Comp	% Var	Φ_{CT} Φ_{SC}	Significance
NWHIs and MHIs						
Region	1	6.65	0.001	0.03	0.0003	0.38
Sites within regions	10	70.08	0.079	1.66	0.0167	**0.01**
Total	5348	1656.05				
Archipelago and Johnston						
Region	1	22.72	0.255	5.24	0.052	0.075
Sites within regions	11	76.74	0.084	1.73	0.018	**0.000**
Total	381	1773.88				
Archipelago, Johnston, and Hawai‘i West						
Region	2	46.44	0.276	5.71	0.057	**0.013**
Sites within regions	10	53.01	0.027	0.58	0.006	**0.000**
Total	381	1773.88				

Mantel test indicated no significant correlation between genetic and geographic distances ($P = .997$, $r = -0.28$, $n = 78$). When log transformed, the results remained similar ($R^2 = 0.067$, $P = .98$, $r = -0.26$).

4. Discussion

4.1. Connectivity along the Hawaiian Archipelago. Acanthaster planci larvae are planktotrophic and, based on laboratory rearing, have an estimated pelagic larval duration (PLD) of 42 days [50]. Their resilience to temperature and salinity changes [51], and adaptation to limited nutrients [50] enable *A. planci* larvae to survive in a broad range of conditions which is thought to facilitate long-distance dispersal [50–53]. In addition to having resilient larvae, adults are fecund broadcast spawners. Females release up to 10^8 eggs during one spawning season and can spawn for up to 4 years of their approximated 8-year lifespan [26, 54]. The use of PLD as a reliable proxy for dispersal potential has been questioned in several recent meta-analyses of the existing literature [55–58]. In this case, however, the data support the expectations based on life-history traits. The haplotype network (Figure 2), the nonsignificant AMOVA Φ_{CT} between the NWHIs and the MHIs populations ($\Phi_{CT} = 0.003$, $P = .38$), and the lack of significant isolation by distance ($P = .997$) indicate that, with the exception of the Hawai‘i West population, *A. planci* in the Hawaiian Archipelago experience few barriers to gene flow. Furthermore, the shared haplotypes between the 1982 samples with locations throughout the archipelago today suggest long-term mixing of the populations.

The distance traveled during pelagic development is obviously a function of both PLD and of the oceanic currents in which those larvae find themselves [59–62]. Thus, the mechanism for this widespread dispersal is likely the variable currents that flow along the 2500 km archipelago. The prevailing oceanic currents that run along the Hawaiian Archipelago—the west/northwestward flowing North Hawaiian Ridge Current (NHRC), the eastward Hawaiian Lee Countercurrent (HLC), and the Subtropical Countercurrent (SCC)—are conducive to the widespread dispersal of species with long-lived larvae that leave the coastal realm [63, 64]. With the NHRC, recruitment is more likely to move from the MHIs to the NWHIs [65]. However, the SCC has been found, in part, to drive recruitment of spiny lobsters from the NWHIs atolls down the chain [66]. In addition to the prevailing currents, there are wind-driven southwesterly flowing currents moving through the channels of the MHIs [67], and all currents within the archipelago are dominated by eddies and are unstable because of mesoscale and seasonal variability [64, 67, 68].

The temporal and spatial dynamics of all these currents along and within the archipelago provide the mechanism for *A. planci* larvae to disperse widely and haphazardly up and down the chain thereby facilitating mixing. Thus, the isolation of the Hawai‘i West population from the rest of the Hawaiian Archipelago samples, with the exception of Ni‘ihau ($\Phi_{ST} = 0.020$, $P = .064$), is surprising. However, this pattern of isolation has also been seen with anchialine shrimp [69], yellow tang [70], and multiple species of vermetid gastropods [23], where the populations on the west side of Hawai‘i Island were strongly subdivided from the rest of the Big Island, and the other MHIs [71, 72].

The west leeward side of Hawai‘i island is an active area for eddy formation [73]. Two to three times a year anticyclonic eddies form, propagate to the southwest, and approach the westward flowing North Equatorial Current moving away from the Hawaiian Archipelago [74]. These eddies may be limiting larval dispersal from the leeward side of Hawai‘i island to the rest of the chain and from the chain to the west side. Mesoscale and submesoscale circulation may

TABLE 3: Population pairwise Φ_{ST} values (below diagonal) and statistical significance (above diagonal) for *Acanthaster planci* populations along the Hawaiian Archipelago. Bold text indicates significant values: $^{*}P \leq .05$, $^{**}P \leq .01$, and $^{***}P \leq .001$.

	FFSs	HE	HS	HW	JOH	KAU	LAN	MAI	MOL	NII	OAH	1982	PHR
FFSs		0.297	0.771	**0.002****	0.104	0.391	0.492	0.429	0.651	**0.041***	0.258	0.231	0.147
HE	0.009		0.423	**0.002****	**0.002****	0.546	0.685	0.108	0.227	0.161	0.173	0.894	0.407
HS	−0.022	−0.002		**0.001*****	**0.016***	0.746	0.860	0.733	0.915	0.101	0.522	0.365	0.208
HW	**0.107****	**0.070****	**0.064*****		**0.000*****	**0.001*****	**0.002****	**0.000*****	**0.001*****	0.064	**0.040***	**0.001*****	**0.000*****
JOH	0.030	**0.093****	**0.046***	**0.149*****		**0.005****	**0.004****	**0.005****	**0.028***	**0.000*****	**0.005****	**0.001*****	**0.000*****
KAU	−0.002	−0.010	−0.015	**0.087*****	**0.077****		0.926	0.486	0.544	0.079	0.181	0.736	0.818
LAN	−0.007	−0.013	−0.016	**0.061****	**0.068****	−0.022		0.411	0.654	0.184	0.318	0.671	0.655
MAI	−0.006	0.026	−0.013	**0.078*****	**0.064****	−0.006	−0.002		0.697	**0.043***	0.254	0.134	0.184
MOL	−0.020	0.011	−0.019	**0.061*****	**0.042***	−0.009	−0.012	−0.014		0.183	0.803	0.225	0.123
NII	**0.051***	0.015	0.021	0.021	**0.126*****	0.033	0.012	**0.040***	0.013		0.776	0.118	**0.038***
OAH	0.011	0.014	−0.005	**0.023***	**0.066****	0.014	0.004	0.008	−0.014	−0.012		0.122	**0.048***
1982	0.013	−0.017	0.000	**0.085*****	**0.102*****	−0.014	−0.010	0.019	0.009	0.020	0.018		0.449
PHR	0.030	−0.003	0.010	**0.105*****	**0.127*****	−0.018	−0.012	0.014	0.023	**0.047***	0.039*	−0.004	

FFSs: French Frigate Shoals, JOH: Johnston Atoll, MOL: Moloka‘i, OAH: O‘ahu, HE: Hawai‘i East, KAU: Kaua‘i, NII: Niihau, HS: Hawai‘i South, LAN: Lana‘i, PHR: Pearl and Hermes Atoll, HW: Hawai‘i West, MAI: Maui, and HAW 1982: Hawai‘i.

minimize long-distance dispersal of larvae [75]. Eddies and gyres have caused larval retention in some reefs along the Great Barrier Reef [76] and in Guam [77]. Eddy systems capture larvae and advect them to deep oceanic waters where they have a higher likelihood of perishing [75]. The eddies occurring along the west side of Hawai‘i island seem a likely candidate driving the isolation of this population. Despite the significant genetic differentiation, however, gene flow does exist because Hawai‘i West shares haplotypes with every island, including Johnston Atoll, and thus is not completely isolated or self-sustaining.

4.2. Connectivity between Johnston Atoll and the Hawaiian Archipelago. Johnston Atoll is the most geographically isolated population in this study and the closest Indo-West Pacific source of marine species that could have potentially populated the Hawaiian Islands. It has long been postulated that species disperse readily from Johnston Atoll to French Frigate Shoals (FFSs) in the NWHIs. The first indirect evidence came from coral surveys comparing species at Johnston Atoll with the Hawaiian Islands. These surveys found that the most abundant coral at Johnston Atoll, *Acropora cythera,* was prevalent at FFSs but extremely rare elsewhere in the Hawaiian Archipelago [78, 79]. The next indirect evidence was demonstrated using computer simulations that revealed FFSs as being oceanographically connected to Johnston Atoll via the SCC and HLC for larvae with a PLD > 40 days [63]; *A. planci* fit this model. The FFSs population in this study was the only one that was not significantly different from Johnston Atoll ($\Phi_{ST} = 0.029$, $P = .10$). The genetic similarity between FFSs and Johnston Atoll to the exclusion of all other Hawaiian islands supports the FFSs and Johnston Atoll connection. In contrast, gene flow between Johnston Atoll and the remaining Hawaiian Islands is clearly limited (pairwise $\Phi_{ST} = 0.064$–0.13, $P < .05$).

5. Conclusion

Although some genetic structuring was found between Hawai‘i West and the rest of the Hawaiian Archipelago, the absence of *A. planci* genetic population structure along 2500 km of the Hawaiian Archipelago indicates that the dispersal potential of this coral-eating sea star is vast. High dispersal is generally associated with a lack of genetic population structure [80, 81]. The genetic pattern found is driven by the dynamic nature and seasonality of the variable currents and eddies that stretch across the chain. The numerous islands and reefs along the chain provide stepping stones for population expansion. It is likely the larvae released in the MHIs will eventually have progeny in the NWHIs and vise versa.

Understanding *A. planci* dispersal and recruitment mechanisms has become important for reef managers in order to mitigate their populations and monitor their impacts on reef communities. Ecosystem-based management is attractive in this case because in addition to the possible role of anthropogenic activities in initiating outbreaks, these coral-eating sea stars impact more than just the habitat-forming corals on which they prey and can alter entire coral reef ecosystems [26, 82–84]. With coral reef tourism being a multibillion dollar industry, *A. planci* outbreaks could severely impact the economics of island nations. For example, outbreaks on the Great Barrier Reef (GBR), Guam, American Samoa, and Japan have resulted in up to 90% coral mortality in localized areas [85–88]. In the GBR recruitment pathways from mass spawning events have been predicted based on the flow of the East Australian Current [89, 90], and eradication programs have been established to remove *A. planci* populations upstream in order to limit population expansion downstream [91]. The same is true in Japan along the Kurioshio Current [92]. Unlike the GBR and Japan, it will be more difficult to predict potential recruitment pathways in the Hawaiian Archipelago due to the variable currents and high population mixing along the chain.

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Research Article

Genetic Analyses and Simulations of Larval Dispersal Reveal Distinct Populations and Directional Connectivity across the Range of the Hawaiian Grouper (*Epinephelus quernus*)

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Integration of ecological and genetic data to study patterns of biological connectivity can aid in ecosystem-based management. Here we investigated connectivity of the Hawaiian grouper *Epinephelus quernus*, a species of management concern within the Main Hawaiian Islands (MHI), by comparing genetic analyses with simulated larval dispersal patterns across the species range in the Hawaiian Archipelago and Johnston Atoll. Larval simulations revealed higher dispersal from the MHI to the Northwestern Hawaiian Islands (NWHI) than in the opposite direction and evidence for a dispersal corridor between Johnston and the middle of the Hawaiian Archipelago. Genetic analyses using mitochondrial DNA (mtDNA) control region sequences and microsatellites revealed relatively high connectivity across the Hawaiian Archipelago, with the exception of genetically distinct populations and higher mtDNA diversity in the mid-Archipelago. These analyses support the preservation of the mid-archipelago as a source of genetic diversity and a region of connectivity with locations outside the Hawaiian Archipelago. Additionally, our evidence for directional dispersal away from the MHI lends caution to any management decisions that would rely on the NWHI replenishing depleted MHI stocks.

1. Introduction

Growing numbers of studies are integrating ecological and genetic data to investigate population connectivity [1–3]. These techniques have the potential to facilitate ecosystem-based management by increasing our understanding of the interactions between organisms and their environment. For marine species, these techniques may be particularly valuable because population genetic studies of these species are often thought to suffer from low power and therefore to be of limited value for management [4–6]. Studies of marine species commonly reveal weak population genetic structure that is described as "chaotic" due to its apparent unpredictability over space and time [7–10]. However, this weak structure may result from factors other than high genetic connectivity. For example, the presence of large population sizes in the marine environment may prevent genetic divergence due to the slow process by which large populations achieve migration-drift equilibrium [4, 11]. Additionally, violations of the assumptions of commonly used population genetic statistical models are thought to be particularly strong for marine populations; many of these populations have spatial and temporal heterogeneity in abundance and settlement rates which violate the assumptions of constant population sizes and migration rates typical of many population genetic models [5, 12, 13]. These violations are thought to result from the stochastic nature of oceanographic currents as well as cryptic spatial habitat heterogeneity in the sea [14].

Recent studies integrating environmental data with genetic data have proven useful in revealing the ecological drivers underlying the weak and apparently chaotic genetic structure of marine species. For example, genetic analyses indicated weak structure for the subtidal whelk *Kelletia kelletii* across the Santa Barbara Channel of California, but integration of genetic analyses with larval dispersal simulations based on ocean currents revealed that nearly 50 percent of this genetic structure could be accounted for by ocean currents [15]. Additionally, a comparison of genetic and environmental data for *K. kelletii* and two other marine species—kelp bass *Paralabrax clathratus* and California spiny lobster *Panulirus interruptus*—in the Southern California Bight indicated that kelp bed size was an important predictor of genetic structure for all species, with ocean circulation patterns also important for the kelp bass [14]. For each of these studies, the integration of environmental and genetic data provided a greater understanding of the ecological basis of population structure than could be gained from either data source alone. Ultimately these analyses provided a stronger basis from which effective management decisions could be made.

The Hawaiian grouper (*Epinephelus quernus,* Serranidae; recently revised to *Hyporthodus quernus*, Epinephelidae [16, 17]) is a species of management concern within the Hawaiian Archipelago. Endemic to the Hawaiian Archipelago and Johnston Atoll (Figure 1 [18]), *E. quernus* is part of a commercially important bottomfish species complex considered to have experienced long-term decline in the Main Hawaiian Islands (MHI) since the 1950s–1960s due to fishing pressures [19]. In the Northwestern Hawaiian Islands (NWHI), a phasing out the bottomfish fishery began in 2006 and was completed in 2010 as a result of the designation of this region as the Papahānaumokuākea Marine National Monument. Establishment of the Monument led to speculation as to whether dispersal from the protected NWHI to the overfished MHI could replenish depleted MHI stocks. However, several life history traits of *E. quernus* may reduce the likelihood of high connectivity between the NWHI and MHI. Adults appear to be territorial, are found in relatively small groups, swim close to the bottom, have strong habitat preferences for rocky substrate within a depth range of 5–380 m (C.D.K., pers. obs.), and are protogynous [20, 21]. These observations suggest adults may form small stable spawning groups similar to other territorial protogynists. Additionally, the limited biogeographic range of *E. quernus* suggests that this species has overall low dispersal capabilities, although the correlation between dispersal ability and range size is not strong [22]. However in support of the NWHI as a possible source for MHI stocks, the relatively long pelagic larval dispersal (PLD) period of this species may promote connectivity facilitated by larval dispersal between islands. The PLD for this species is estimated at 35–45 days based on an analysis of otoliths from juveniles collected in the NWHI (R. Nichols and E. DeMartini pers. comm.); although this PLD is within the lower range of medium-to large-bodied groupers (range 30–80 days: [23, 24]), it may be long enough to promote connectivity across large geographic distances. The only data available to address this question comes from population genetic analyses using mitochondrial DNA (mtDNA) control region sequences for *E. quernus* samples collected throughout the Hawaiian Archipelago; these analyses found low or nonsignificant genetic divergence between most locations, with the exception of a few genetically distinct locations near the middle of the archipelago [25].

To investigate connectivity across the range of *E. quernus* using both ecological and genetic data, we compared simulated larval dispersal patterns based on oceanographic data with population genetic data. Our simulations utilized existing data on spawning behavior and PLD for *E. quernus*, as well as high-resolution data on ocean currents across the Hawaiian Archipelago and Johnston Atoll. Using data on interannual variability in current patterns over 17 years, we were able to simulate larval dispersal patterns across multiple generations, thus accounting for the cumulative effect of larval migration between intermediary sites over multiple generations [15, 26]. We then compared simulated larval dispersal patterns with the results of genetic structure analyses conducted for *E. quernus* samples collected across the Hawaiian Archipelago. For these analyses, we utilized previously published results from a study of mtDNA control region genetic structure [25], as well as new analyses using microsatellite loci for the same dataset as used in the mtDNA study. We then compared the results of larval dispersal simulations and population genetic analyses to make ecosystem-based management recommendations for *E. quernus* within the Hawaiian Archipelago.

2. Methods

2.1. Larval Simulations. Larval transport simulations were performed using a version of a biased random-walk model as described by Polovina et al. [27]. The following modifications to this approach were made: firstly, surface currents used in this study were five-day interval (from January 1993 through December 2009) 1.0° × 1.0° latitude/longitude resolution gridded flow fields from the Ocean Surface Current Analyses—Real Time (OSCAR) project at NOAA Earth and Space Research, henceforth referred to as OSCAR currents. The bounds of currents used in this study were from 170°E–140°W, 0°–50°N. These surface flow fields are a composite of altimetry-derived geostrophic components and satellite-derived wind components, tuned to 15-m depth drogue trajectories, thus capturing both the large-scale geostrophic motion as well as the surface, wind-driven Ekman transport. This approach is documented in Lagerloef et al. [28]. The OSCAR circulation data was used because it provided a large number of years ($n = 17$) to incorporate interannual and decadal oceanographic variability and allowed the use of as many years of circulation data as possible in a multigenerational simulation model. Secondly, simulations were conducted for both the lower and upper bounds of the

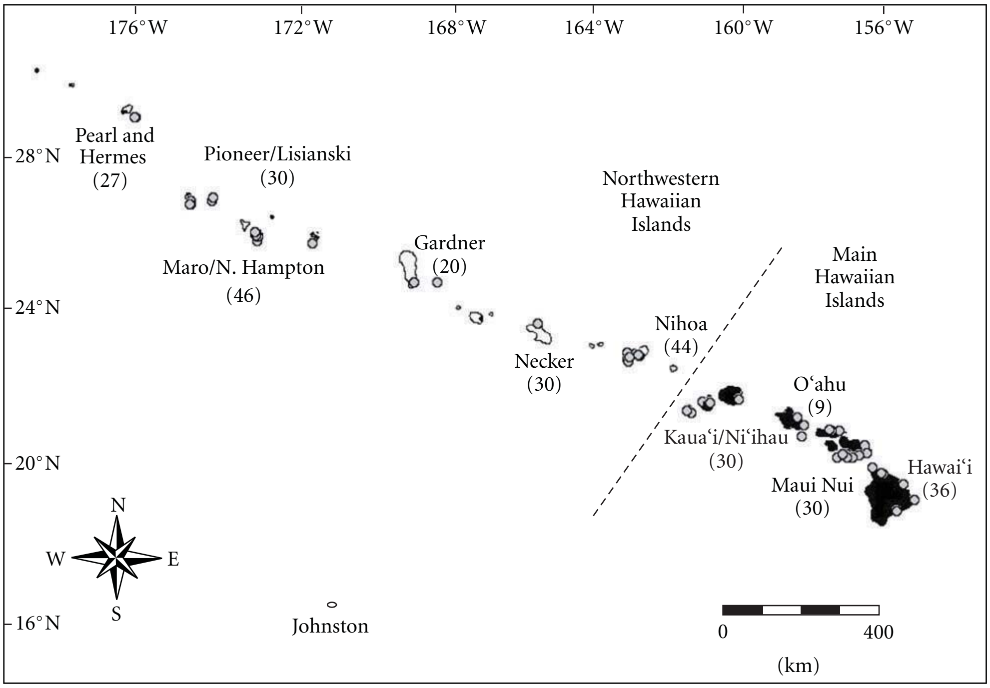

Figure 1: Sample locations and numbers of specimens of *Epinephelus quernus* collected across the Hawaiian Archipelago.

estimated PLD for *E. quernus* (35–45 days, R. Nichols and E. DeMartini pers. comm.). These minimum and maximum PLD values were chosen for analysis due to evidence that these measures are better correlates of F_{ST} than is the average PLD for many marine species [29]. Thirdly, for spawning output, 100,000 larvae were released per year for the 17 years of available OSCAR data, ~85% of which were released during the spawning season of *E. quernus* from February through June, with a peak centered in March. A daily spawning output function was fit with nonlinear regression using a gamma probability distribution coupled with constant (representing both the spawning peak and low level of background spawning activity throughout the year); this was done to emulate the observed spawning patterns of *E. quernus* (R. Nichols and E. DeMartini pers. comm.). Fourthly, release and settlement habitat along the Hawaiian Archipelago was defined using a high-resolution bathymetric database [30]. A total of 959 habitat pixels were grouped to the nearest island, atoll, or bank, resulting in 26 locations in the Hawaiian Archipelago.

The value for eddy diffusivity used in this study was $500\,\text{m}^2\,\text{sec}^{-1}$, the same as that used by Polovina et al. [27]. This value was originally derived by qualitatively tuning the larval transport simulation results to larval lobster catch patterns from a series of midwater trawls. Part of this study involved re-evaluation of this value of eddy diffusivity since the current field used in this study (OSCAR, geostrophic and Ekman transport) is different than the purely altimetric geostrophic currents used by Polovina et al. [27]. Eddy diffusivity was estimated from the trajectories of subsurface drifter buoys (drogued at 15 m depth) which occurred in the spatial domain of this analysis (n = 260 drifter buoys, daily positions = 38921, year = 2006). Drifter buoys are routinely deployed by research vessels and vessels of opportunity as part of a large program to understand global circulation patterns [31]. The drifter buoy dataset used in this analysis is administered by the Global Drifter Program at NOAA, and the data are available at: http://www.aoml.noaa.gov/phod/dac/index.php. Daily drifter buoy positions were merged with the OSCAR data to match the nearest value of currents to the buoy location. The predicted position for the next day was calculated using these currents, and this was compared to the actual position. By assuming that the discrepancy between these two values represents eddy diffusivity, the tabulation of differences can be compared to a tabulation of predicted diffusive steps using the Lagrangian formulation in the transport model. Three values of eddy diffusivity were examined: $100\,\text{m}^2\,\text{sec}^{-1}$, $500\,\text{m}^2\,\text{sec}^{-1}$, and $1000\,\text{m}^2\,\text{sec}^{-1}$.

Multigenerational simulations were conducted by bootstrapping from the 17 available years of forward dispersal probabilities generated from the biased random-walk model and iteratively dispersing propagules for 1000 generations. Simplistic population dynamics (fixed population size with uniform mortality schedule) were assumed with a leveling imposed after each generation, while maintaining and tracking the new source breakdown. This evolving source breakdown incorporated inputs from the new generation added to what was there from the previous generations. The distributions equilibrated after a few hundred generations, and an average result was calculated from the final 100 runs, that is, generation 901–1000. Each island was fully self-seeding at the start of the simulation, that is, at generation 0. This simulation was run five times each for "forward" and "backward" projections to generate settlement probabilities for each island. "Forward" models report the final locations of larvae spawned at a given island, as measured by the percent of successfully settled popagules released from the source site that settled at the receiving site in a multigenerational context. "Backward" models report the natal islands of larvae which recruited successfully to each island, as measured by the percent of successfully settled propagules at the receiving site that originated at the source site in a multigenerational context.

2.2. Genetic Data Collection and Quality Control. A total of 302 individuals were sampled from ten sites from across the Hawaiian Archipelago (Figure 1). Many of the specimens, particularly those from Kaua'i through Pearl and Hermes, were obtained with the help of commercial fishermen operating in Northwestern Hawaiian Islands. Researchers from the Hawai'i Institute of Marine Biology who were conducting habitat surveys provided most of the specimens from the Main Hawaiian Islands, and additional fish were purchased at the Hilo fish auctions to supplement sample size from the island of Hawai'i.

For most individuals, latitude-longitude coordinates were recorded; however, this specific information was not available for 29 out of 36 specimens from the island of Hawai'i that were purchased from the fish auctions. In addition, precise latitude-longitude data were not made available by fishermen for three out of 44 samples from Nihoa, 12 out of 20 from Gardner, two out of 46 samples from Maro/N. Hampton, and nine out of 30 specimens from Pioneer/Lisianski. For these individuals, the only locality information provided was the banks off the coasts of particular islands.

DNA was extracted using Qiagen DNeasy tissue extraction kits, and each individual was amplified using PCR for ten microsatellite loci. Five loci were among those isolated from *E. quernus* [32]; and the remaining five were developed for other epinephelids in the genus *Mycteroperca* [33, Zatcoff & Chapman, unpublished data] (Table 1). Several individuals were chosen at random and sequenced for each of the ten loci to confirm presence and characteristics of the repeat motifs. Once confirmed, 10 μL PCR reactions were performed on all samples using annealing temperatures shown in Table 1. Microsatellite fragments were then visualized on a CEQ 2000XL capillary system (Beckman Coulter). Allele sizes were scored and recorded for each locus and each individual using the CEQ 8000 Genetic Analysis System software 8.0 (Beckman Coulter). Deviations from Hardy-Weinberg Equilibrium were tested for each sampling location individually and for the total sample for all loci using ARLEQUIN 3.11 [34]. Each locus was also tested for null alleles, large allele dropout, and scoring errors using MICROCHECKER 2.2.0.3 [35]. Evidence for selection was examined for each locus using LOSITAN [36].

2.3. Genetic Diversity and Population Structure. Microsatellite diversity was examined by calculating observed and expected heterozygosities for each microsatellite locus, and each sampling site using the program ARLEQUIN 3.11. Allele richness was calculated using FSTAT [37]. Population genetic structure was investigated by calculating pairwise F_{ST} values across sampling sites using ARLEQUIN 3.11. Significance of pairwise comparisons was determined using 16,000 random permutations.

Table 1: Repeat motifs, annealing temperatures, number of alleles per locus, and size range for ten microsatellite loci.

Locus	Repeat motif	Annealing temp (°C)	Number of alleles	Size range (bp)
CA-2	$(CA)_N$	55.0	8	253–273
CA-3	$(CA)_N$	45.0	14	301–329
CA-4	$(CA)_N CG(CA)_N$	50.0	26	95–161
CA-6	$(CA)_N$	50.0	10	290–310
CA-7	$(CA)_N$	40.0	10	214–236
Mbo29	$(CA)_N$	64.3	13	137–167
Mbo61	$(CA)_N$	61.2	19	162–204
Mbo66	$(CA)_N$	60.0	9	101–125
Mbo67	$(CA)_N$	60.0	15	317–347
Gag010	$(GT)_N CA(GT)_N$	51.6	26	110–176

Population genetic structure across the Hawaiian Archipelago was further investigated using mtDNA control region sequences gathered from a previous study which utilized the same sample set as the study presented here [25]. Genealogical relationships between mtDNA haplotypes across the Hawaiian Archipelago were investigated by creating median-joining networks of mtDNA haplotypes using NETWORK [38]. Results from genetic analyses were qualitatively compared with results from larval dispersal modeling. Genetic structure was predicted to occur in regions with high larval retention or regions with asymmetric directional larval dispersal.

3. Results

3.1. Eddy Diffusivity. The tabulation of drifter buoy diffusive daily steps was plotted with predicted diffusive steps at eddy diffusivity values of $100\,m^2\,sec^{-1}$, $500\,m^2\,sec^{-1}$, and $1000\,m^2\,sec^{-1}$. The results indicate that the value of $500\,m^2\,sec^{-1}$ best characterizes the daily diffusive spatial steps of the drifter buoys (Figure 2). The value of $100\,m^2\,sec^{-1}$ predicted a narrower distribution of diffusion than that observed from the drifter buoy trajectories, while the value of $1000\,m^2\,sec^{-1}$ predicted a much wider distribution of diffusion.

3.2. Simulated Larval Dispersal. Modeling of larval connectivity revealed similar patterns for 35- and 45-day PLDs (Figures 3 and 4), although as expected the 35-day PLD showed overall lower levels of connectivity between locations. Within the Hawaiian Archipelago, the highest levels of connectivity generally occurred between adjacent locations. However, forward and backward models for both PLDs indicated very little dispersal from the NWHI to the MHI (lower left

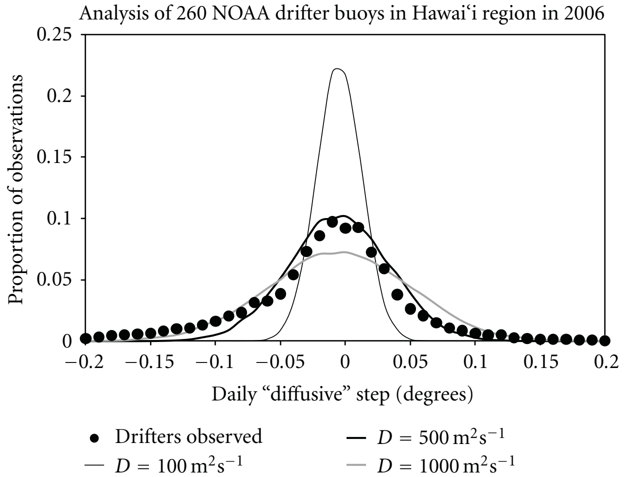

Figure 2: Daily diffusive spatial steps aggregated across latitude and longitude observed from 260 NOAA drifter buoys in 2006 (symbols) and predicted from diffusivity values of $100\,\mathrm{m^2\,s^{-1}}$ (thin line), $500\,\mathrm{m^2\,s^{-1}}$ (thick black line), and $1000\,\mathrm{m^2\,s^{-1}}$ (thick gray line). Lower values of diffusivity cause particles to disperse less about the mean flow field trajectory, whereas high values of diffusivity cause particles to disperse widely about the mean flow field trajectory.

quadrant of each graph), in contrast to relatively high dispersal from the MHI to the NWHI (upper right quadrant of each graph). Additionally, most sites throughout the Hawaiian Archipelago exhibited particularly high dispersal toward Gardner, and to a lesser extent, toward Necker and Ni‘ihau (Figures 3 and 4). Retention of natal larvae was also high at Gardner (Figures 3(a) and 4(a)).

For the 45-day PLD model, both forward and backward models indicated some connectivity between Johnston and the Hawaiian Archipelago (rightmost column of Figure 4(a); bottom row of Figure 4(b)), although as expected, dispersal between these two locations was lower than local retention (Figure 4). Both forward and backward models indicated higher connectivity between Johnston and Gardner than between Johnston and any other location in the Hawaiian Archipelago (Figure 4). Connectivity was also fairly high between Johnston and Necker (Figure 4). For the 35-day PLD model, there was no evidence of connectivity between Johnston and the Hawaiian Archipelago (Figure 3).

3.3. Microsatellite Quality Control. Microsatellite locus CA-4 showed evidence of null alleles for four out of ten sampling sites ($P < .05$) and deviated from Hardy-Weinberg equilibrium for six out of ten sampling sites. Microsatellite locus Gag010 showed evidence of null alleles for three out of ten sampling sites and deviated from Hardy-Weinberg equilibrium for four out of ten sampling sites. Tests for selection also indicated that locus Gag010 had a 99 percent probability of being under positive selection. To investigate the influence of CA-4 and Gag010 on analysis results, all analyses were conducted both with and without these two loci. The results differed little between analyses, and we report here the results without CA-4 and Gag010. No other loci showed evidence of null alleles, selection, or deviation from Hardy-Weinberg equilibrium.

3.4. Genetic Diversity and Population Structure. Observed and expected heterozygosity values, average number of alleles, and allele richness for microsatellite loci were similar across the Hawaiian Archipelago (Table 2). For mtDNA control region sequences, genetic diversity was higher in the NWHI than in the MHI, with the highest value occurring at Gardner (Table 2).

Genetic structure analyses using microsatellite data revealed significant pairwise F_{ST} values for six out of 45 pairwise comparisons ($0.00794 < F_{\mathrm{ST}} < 0.0133$; $P < .05$) (Table 3). Each significant pairwise comparison included at least one sampling location in the mid-archipelago (Pioneer/Lisianski through Nihoa). For mtDNA analyses, 11 out of 45 pairwise comparisons were statistically significant ($0.0295 < \Phi_{\mathrm{ST}} < 0.0649$; $P < .05$), with each of these significant comparisons also including at least one sampling location in the mid-archipelago (Table 3).

Eight shortest mtDNA haplotype networks were found, but each network was similar in structure. One of the shortest networks was randomly chosen to report here (Figure 5). The network revealed that many haplotypes were shared across the archipelago, and most haplotypes were only one or two base pairs different from other haplotypes. The most common haplotype was found at all sampling locations except Gardner, and this haplotype was only one base pair different from many other haplotypes. However, several haplotypes or haplotype groups were at least six to eight base pairs different from any other haplotypes; most of these divergent haplotypes were found in the NWHI, although some were also found at the island of Hawai‘i (also known as the Big Island) and Maui. Notably, four of the most divergent haplotypes occurred at Gardner despite the relatively small sample size at this location ($N = 20$).

4. Discussion

Both genetic analyses and larval modeling revealed relatively high connectivity across the Hawaiian Archipelago for *E. quernus*. Limited population structure appears to be a common feature for most marine fish species studied in the Hawaiian Archipelago thus far. For example, no genetic structure was found throughout the Hawaiian Archipelago for bigscale soldierfish *Myripristis berndti* [39] or surgeonfish *Acanthurus nigrofuscus* [40], and genetic divergence was found for only one sampling location (Kure Atoll) within the archipelago for damselfish *Stegastes fasciolatus* [41]. Other species have exhibited low but significant genetic structure across the archipelago, including two surgeonfish: *Ctenochaetus strigosus* (average pairwise $\Phi_{\mathrm{ST}} = 0.001$) and *Zebrasoma flavescens* (average pairwise $\Phi_{\mathrm{ST}} = 0.003$) [40]. As a counter example, however, the damselfish *Dascyllus albisella* had strong population genetic structure across the archipelago, with pairwise Φ_{ST} values ranging as high as 0.718 [41]. The strong structure for *D. albisella* was proposed

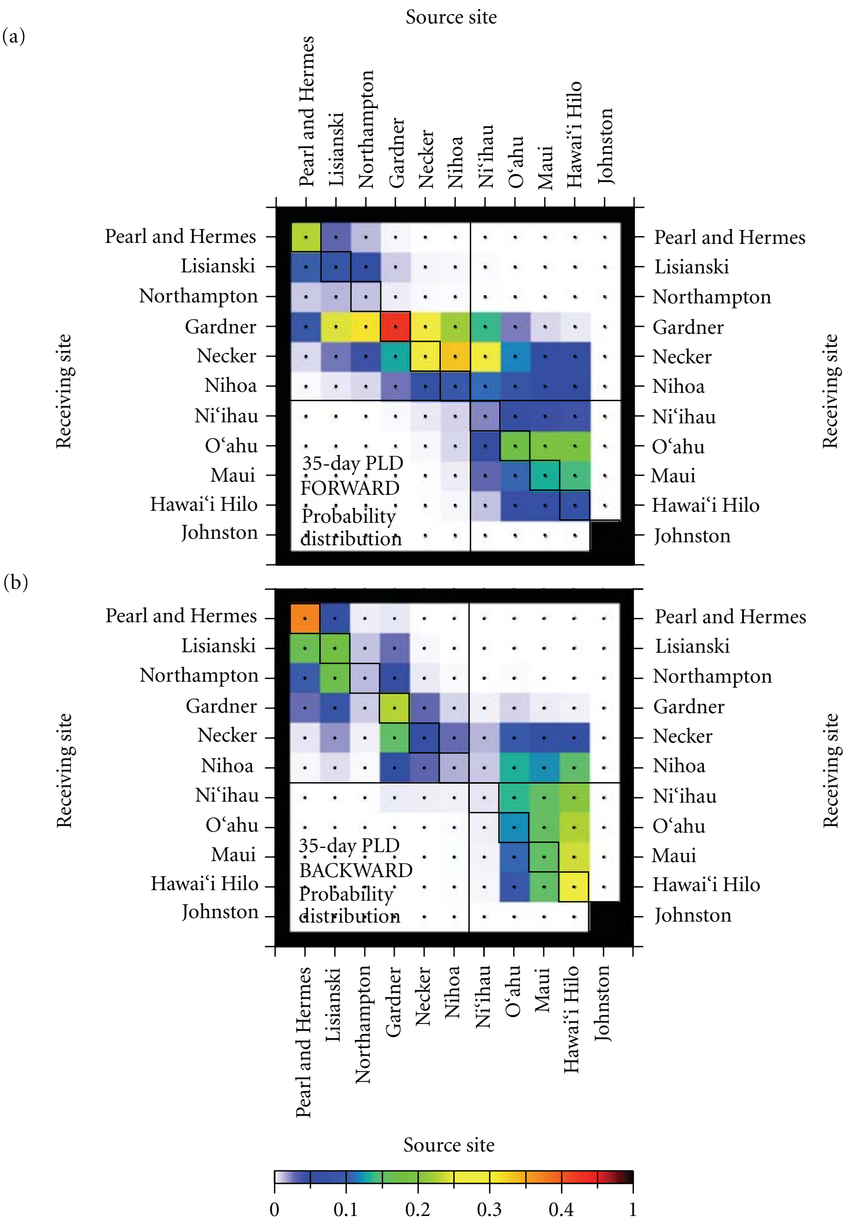

Figure 3: (a) Forward and (b) backward projections of multigenerational settlement probabilities for a 35-day PLD. Values are an average of five runs of the 1,000-generation model. For example, (a) about 30% of successfully settled propagules released from Northampton settled at Gardner and (b) about 2% of successfully settled propagules at Gardner originated at Northampton. The horizontal and vertical lines separate Main Hawaiian Islands and Northwestern Hawaiian Islands, and the diagonal shows self-seeding.

to result from the interaction of species-specific biological factors (spawning seasonality and habitat preferences) with environmental factors (seasonal ocean current patterns) [41].

Given evidence for a benthic adult lifestyle and a 35–45 day pelagic larval dispersal period for *E. quernus*, connectivity across the archipelago for this species is likely driven by larval dispersal rather than adult migration. Therefore oceanographic current patterns are expected to have a strong influence on dispersal patterns for this species [42]. Our larval dispersal simulations based on oceanographic currents across the Hawaiian Archipelago and Johnston Atoll provide evidence that dispersal within the archipelago may be dominated by dispersal from the MHI toward the NWHI and that dispersal in the opposite direction is probably low. Evidence for directional dispersal from the MHI to the NWHI has been observed for other marine species as well. For example, a previous study simulating larval dispersal for corals with a PLD of 60 days using a two-dimensional Eulerian advection-diffusion model also found predominantly northwesterly connectivity across the Hawaiian Archipelago [42, 43]. Additionally, population genetic analyses indicated higher gene flow from the MHI to the NWHI than in the opposite direction for both limpets

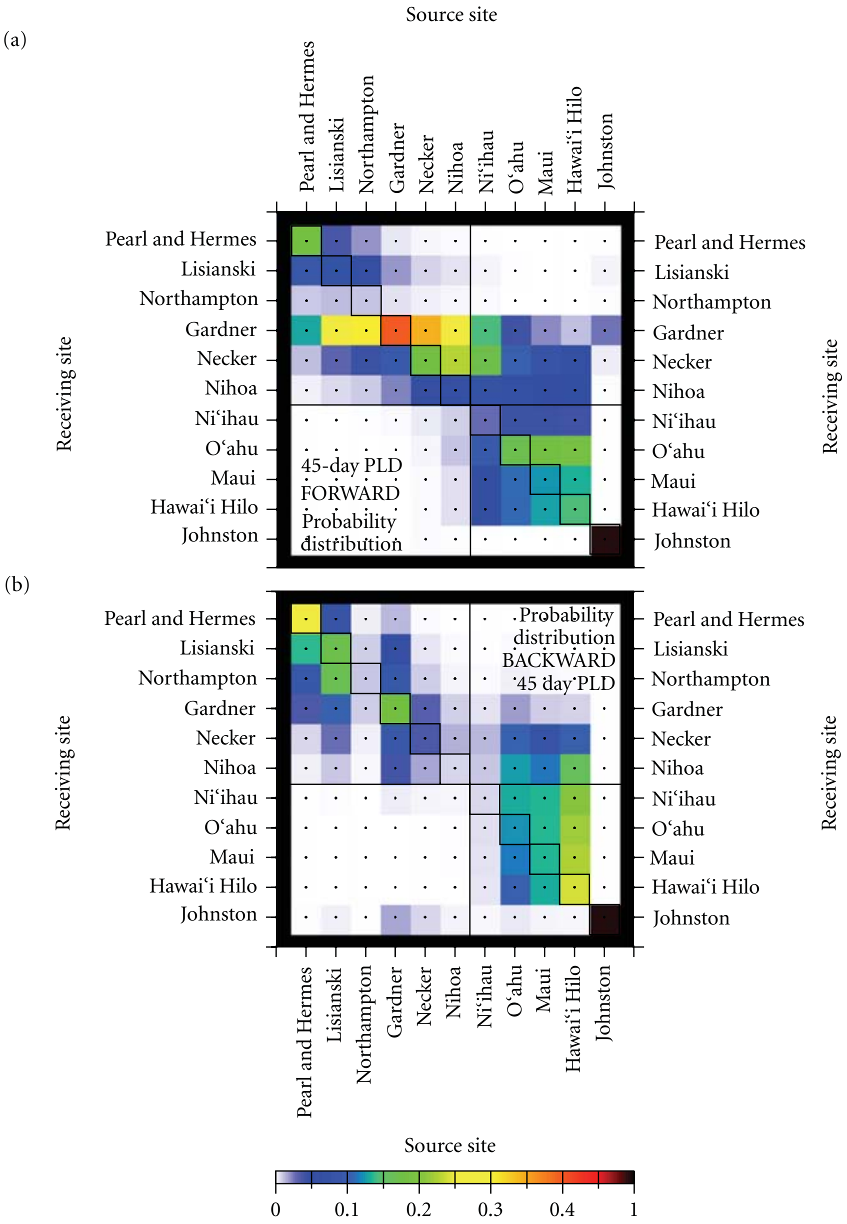

Figure 4: (a) Forward and (b) backward projections of multigenerational settlement probabilities for a 45-day PLD. Values are an average of five runs of the 1,000-generation model. The horizontal and vertical lines separate Main Hawaiian Islands and Northwestern Hawaiian Islands, and the diagonal shows self-seeding.

(*Cellana* spp. [44]) and sea cucumbers (*Holothuria atra* [45]). This directional dispersal provides evidence that the North Hawaiian Ridge Current (NHRC) exerts a strong influence on larval movements for *E. quernus*; the NHRC flows northwest along the MHI [46] and was also proposed to influence genetic structure in this species by Rivera et al. [25]. The evidence for directional dispersal revealed by our larval modeling analyses does not support the proposition that the protected NWHI could act as a source to replenish the depleted MHI bottomfish fishery.

Both genetic analyses and larval modeling also revealed unusual patterns of connectivity for two sites near the middle of the archipelago: Gardner and Necker. Population genetic analyses revealed genetic distinctions between these two sites versus many other sites in the archipelago, and the highest mtDNA diversity value occurred at Gardner. Examination of the mtDNA haplotype network revealed that the high diversity at Gardner resulted from the presence of a large proportion of highly divergent haplotypes and the absence of the haplotype found most often in the rest of the archipelago. The presence of divergent haplotypes at Gardner may result from recent connectivity with a source outside of the Hawaiian Archipelago; this source would most likely be Johnston Atoll, because this is the only location outside of the Hawaiian Archipelago where this species has been reported. Unfortunately, *E. quernus*

Table 2: Number of specimens (N) collected from each location and diversity statistics for microsatellites and mitochondrial DNA (mtDNA) control region: H_o: observed heterozygosity; H_e: expected heterozygosity; k: average number of alleles; π: nucleotide diversity. MtDNA data is from Rivera et al. [25].

Location	Microsatellites					mtDNA
	N	H_o	H_e	k	Allele richness	π
Pearl & Hermes	27	0.758	0.717	7.5	5.23	3.407
Pioneer/Lisianski	30	0.723	0.728	7.9	5.37	6.956
Maro/N. Hampton	46	0.688	0.707	8.6	5.26	7.156
Gardner	20	0.695	0.680	7.1	5.34	8.489
Necker	30	0.634	0.703	7.9	5.32	5.515
Nihoa	44	0.689	0.720	8.3	5.40	5.701
Kauaʻi/Niʻihau	30	0.718	0.722	6.9	5.21	3.161
Oʻahu	9	0.767	0.730	5.6	5.57	3.444
Maui Nui	30	0.700	0.700	8.8	5.53	4.749
Hawaiʻi	36	0.696	0.704	7.9	5.26	6.084

Table 3: Pairwise F_{ST} values for 8 microsatellite loci (below diagonal) and pairwise Φ_{ST} values for mtDNA control region sequences (above diagonal) for *E. quernus* between locations in the Hawaiian Archipelago. MtDNA data is from Rivera et al. [25]. Bolded numbers indicate significant values: $^*P < .05$, $^{**}P < .01$.

	Pearl & Hermes	Pioneer	Maro	Gardner	Necker	Nihoa	Kauaʻi	Oʻahu	Maui Nui	Hawaiʻi
Pearl & Hermes		**0.023***	0.013	**0.065****	**0.045****	0.006	−0.015	−0.006	−0.002	0.017
Pioneer/Lisianski	−0.008		0.004	0.004	0.002	0.005	0.017	−0.022	0.004	−0.003
Maro/N Hampton	−0.010	−0.001		0.014	**0.014***	−0.003	−0.001	−0.022	0.001	−0.002
Gardner	−0.015	−0.012	0.000		−0.001	**0.025***	**0.043****	0.013	**0.037***	**0.005***
Necker	0.000	**0.009***	**0.012****	0.005		**0.020***	**0.034****	−0.001	**0.030***	0.001
Nihoa	−0.003	**0.013****	**0.008***	**0.012***	−0.001		−0.007	−0.023	−0.002	0.005
Kauaʻi/Niʻihau	−0.015	−0.002	0.004	−0.006	−0.001	0.004		−0.027	−0.008	0.009
Oʻahu	−0.011	−0.003	−0.009	−0.006	−0.003	−0.011	−0.002		−0.036	−0.020
Maui Nui	−0.008	**0.008***	−0.006	−0.003	0.003	−0.002	0.002	−0.022		0.008
Hawaiʻi	−0.007	−0.003	−0.004	−0.017	−0.008	−0.006	−0.013	−0.015	−0.009	

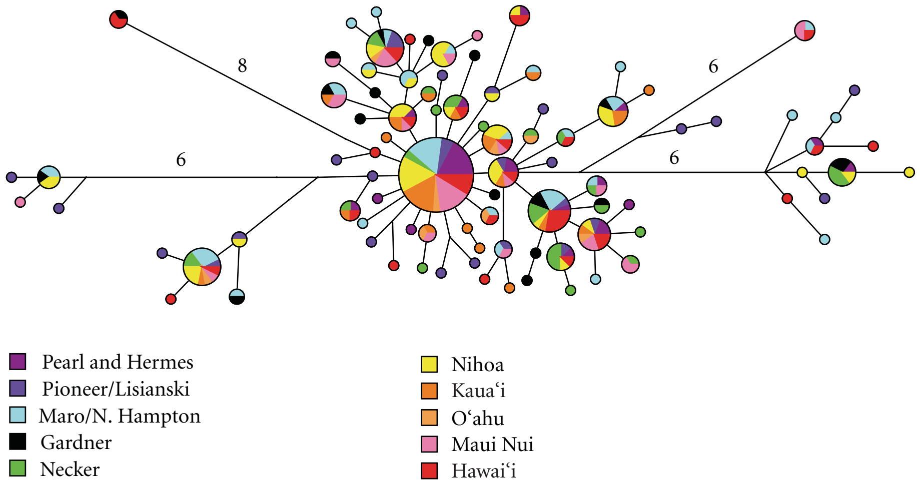

Figure 5: Median-joining network of mtDNA control region haplotypes obtained from [25]. Circle diameters are proportional to the frequency of the haplotype, and lines are proportional to the number of mutations separating haplotypes. Lines that represent greater than two mutations are labeled.

samples were not available from Johnston Atoll for this study, and we could not evaluate this hypothesis. Alternatively, the divergent haplotypes at Gardner may be remnants from an ancestral population, and their presence may be evidence that the ancestral population for the Hawaiian Archipelago occurred at Gardner, as suggested by Rivera et al. [25]. Other studies [44, 45] have highlighted unusual patterns of genetic diversity in the central NWHI (Gardner, French Frigate Shoals and/or Necker) indicating that this finding is not a spurious result. Whether these divergent haplotypes are a result of recent connectivity or ancestral haplotypes, both of these scenarios provide evidence that the central NWHI, in the area of Gardner/French Frigate Shoals/Necker, may be an important source of genetic diversity for the Hawaiian Archipelago.

Larval modeling indicated that most sites in the archipelago had unusually high connectivity with Gardner and to a lesser extent Necker and Nihoa, with all models indicating dispersal from most sites toward these three locations. For the 45-day PLD model, both forward and backward models also revealed higher levels of connectivity between Johnston Atoll and Gardner/Necker than between Johnston Atoll and any other locations within the Hawaiian Archipelago; again in these cases, the level of connectivity was higher for Gardner than for Necker. These analyses provide evidence that the genetic divergence of Gardner and Necker may result from the accumulation of genetic material through connectivity with multiple sources across the Hawaiian Archipelago as well as with Johnston. A connection between Johnston and the middle of the Hawaiian Archipelago near Gardner has been proposed for other marine species as well based on biogeographic or genetic data, including corals within the genus *Acropora* [47], the crown-of-thorns seastar *Acanthaster planci* [48], and vermetid snails [49]. A previous study simulating larval dispersal patterns based on ocean current data also found evidence for a dispersal corridor between Johnston and the middle of the Hawaiian Archipelago near Gardner for species with a PLD greater than 40 days, facilitated by the subtropical countercurrent and the Hawaiian Lee countercurrent [50]. Similarly, a study simulating larval dispersal for corals with a PLD of 60 days also found higher connectivity between Johnston versus the mid-archipelago (Maro, Gardner, and Necker) than Johnston versus other sites within Hawai‘i [42, 43]. Our study provides further evidence that the middle of the Hawaiian Archipelago is a region of connectivity with locations outside of the archipelago.

5. Conclusions

Our comparative analyses of genetic and oceanographic data indicated fairly high connectivity across the Hawaiian Archipelago for *E. quernus*, driven primarily by directional dispersal from the MHI to the NWHI. The mid-archipelago around Gardner and Necker was found to harbor higher genetic diversity than the rest of the archipelago, possibly due to connectivity between this region and Johnston Atoll. Our evidence for low levels of directional dispersal from the NWHI to the MHI lends caution to any management efforts that would rely on the NWHI replenishing depleted stocks in the MHI. Additionally, our analyses highlight the importance of the central NWHI from Gardner to Necker and support preserving the mid-archipelago as a source of genetic diversity for this species. Overall these analyses illustrate the benefits that can be gained for ecosystem-based management by integrating both environmental and genetic data for studies of biological connectivity.

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Research Article

Gateways to Hawai‘i: Genetic Population Structure of the Tropical Sea Cucumber *Holothuria atra*

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Holothuria atra is one of the most common and widest ranging tropical, coral reef sea cucumbers in the world, and here we examine population genetic structure based on mitochondrial COI to aid in determining the appropriate scale for coral reef management. Based on SAMOVA, AMOVA and BARRIER analyses, we show that despite its large range, *H. atra* has hierarchical, fine-scale population structure driven primarily by between-archipelago barriers, but with significant differences between sites within an archipelago as well. Migrate analyses along with haplotype networks and patterns of haplotype diversity suggest that Hawai‘i and Kingman reef are important centers of the genetic diversity in the region rather than an evolutionary dead-end for migrants from the Indo-Pacific. Finally we show that for *H. atra* Kingman Reef is the most likely stepping stone between Hawai‘i and the rest of the Pacific, not Japan or Johnston Atoll as previously presumed. Based on our data, Johnston Atoll can instead be seen as an outpost of the Northwestern Hawaiian Islands rather than a gateway to the Hawaiian Archipelago.

1. Introduction

Echinoderms play a major role in structuring many marine ecosystems, and many are described as “keystone species” because of their profound influence on benthic community structure (e.g., [1–3], reviewed by Uthicke et al. [4]). In addition to their important ecosystem functions, many echinoderm species are also the focus of artisanal or commercial fishing efforts, particularly the sea urchins and sea cucumbers [5–7]. The influence of echinoderm harvest on a wide range of other commercial fisheries, such as abalone, lobster, kelp, and kelp-associated fin fish, has long stimulated discussions of multispecies approaches to managing their exploitation (e.g., [5], reviewed by Purcell [7]). Delineation of the appropriate spatial scales for management zones within a spatial management network requires a detailed understanding of dispersal pathways and population connectivity (reviewed by Hedgecock et al. [8], Thorrold et al. [9], Fogarty and Botsford [10]).

Understanding connectivity in the sea is complicated by the fact that many marine organisms share a biphasic life cycle typified by an adult form that is relatively sedentary and a larval form that can potentially disperse across large expanses of open ocean [11–15]. For example, in the sea urchin genus *Tripneustes*, some well-known biogeographic barriers, such the Isthmus of Panama or the long stretch of deep water in the western Atlantic, are important barriers to dispersal whereas others, such as the Eastern Pacific Barrier, show no evidence for limiting dispersal [16]. However, the geographic limits of such dispersal are uncertain because it is virtually impossible with current technology to directly track these microscopic juveniles during the pelagic phase (reviewed by Levin [17]) making indirect methods of quantifying larval dispersal particularly attractive (reviewed by Hedgecock et al. [8], Grosberg and Cunningham [18], Selkoe et al. [19], and Hellberg [20]). Proxies for dispersal, such as pelagic larval duration (PLD) and geographic range, have generally been used as rules of thumb in the absence of a detailed understanding of connectivity for most marine species. Unfortunately, intuitive expectations of larval dispersal potential as a function of PLD and range size are not upheld in recent meta-analyses of the existing literature [21–26, 88]. Realized dispersal distance is typically less than potential dispersal distance because of the presence of biophysical or biogeographical barriers [27–31]. Barriers that limit dispersal between marine populations include obvious geographical features such as land masses like the Isthmus of Panama [32], but also more subtle factors such as currents and oceanographic regimes [33–37]. The correlation between geographic distance and the probability of larval exchange among sites is low in many marine systems (e.g., [38]), and thus quantitative estimates of connectivity are an important prerequisite for delineating the appropriate scale over which marine populations ought to be managed.

The Hawaiian Archipelago lies at the periphery of the tropical Central Pacific and is the most isolated island chain in the world, making it biogeographically partitioned from the rest of the Pacific Islands (reviewed by Ziegler [39]). This isolation results in one of the highest proportions of endemism in the world (e.g., [40–42]; reviewed by Ziegler [39], Eldredge and Evenhuis [43]). Though there are many examples of pan-pacific coral reef organisms in Hawai‘i, the isolation of the Hawaiian Archipelago is thought to limit larval exchange sufficiently that colonization is rare [44]. For example, Kay [45] estimated that Western Pacific marine species successfully colonize the Hawaiian Archipelago about once every 13,000 years. Unlike the terrestrial fauna, however, the Hawaiian marine fauna contains a large proportion of endemics that are differentiated but not diversified from their Indo-West Pacific roots [39, 46–48]. Johnston Atoll is believed to be a stepping stone into Hawai‘i, and simulations of larval dispersal suggest that larvae from Johnston atoll can reach French Frigate Shoals or Kaua‘i along two separate larval corridors [49, 50].

The lollyfish, *Holothuria atra*, is one of the most common shallow-water tropical sea cucumbers in the Indo-Pacific, spanning from Madagascar to French Polynesia [51, 52]. *H. atra* performs vital ecosystem services on coral reefs for which there is an active fishery in many regions of the Pacific [7, 53, 54]. Echinoderms are described as a boom-bust phylum in which populations go through marked natural population cycles [4], an attribute that can compound problems in a harvested population but may hasten repopulation in previously impacted areas. As such, there is a call for ecosystem-based management of sea cucumber harvests [7]. Furthermore, the boom-bust nature of echinoderms has important implications for connectivity in evolutionary time frames, where biological attributes can drive population structure to a greater extent than oceanographic processes as hypothesized in the *Tripneustes* sea urchins [16]. Together these characteristics make *H. atra* an ideal organism to examine levels of connectivity and historical population dynamics to inform management and to test hypotheses about Hawai‘i's connection with other archipelagos in the Central Pacific. Here, we assess the inferred range of dispersal for *H. atra* in Hawai‘i and the Central Pacific by investigating its mitochondrial genetic population structure in an attempt to delineate the appropriate scales for management.

2. Methods

2.1. Sampling, PCR, and Sequencing. Holothuria atra was sampled from five archipelagos (Hawaiian Islands, Line Islands, Marshal Islands, Bonin Islands, and Ryukyu Islands) at a total of 19 sites (Figure 1). Sampling in the Northwest Hawaiian Islands and the Line Islands took place on research cruises aboard the NOAA *R.V. Hi‘ialakai*. All other samples were collected on shore dives or while snorkeling. Sampling took place between spring 2006 and fall 2009. Samples were obtained nonlethally through muscle-tissue biopsy and preserved in either 95% ethanol or DMSO salt buffer and archived at the Hawai‘i Institute of Marine Biology at room temperature. Skillings and Toonen [55] made an extended discussion of sampling and preservation protocol. No asexual morphs—distinguished by transverse scarring, smaller body size, and their location in lagoonal habitats—were found during sampling expeditions, and no reports are known indicating the presence of the asexual stage of *H. atra* in the sampled locations. The asexual morph of *H. atra* appears to be located only in the Southern and West Pacific (e.g., [52, 56, 57]).

Total genomic DNA was extracted using DNeasy Blood and Tissue Kits (QIAGEN) following the manufacturer's instructions. Polymerase chain reaction (PCR) was used to amplify a 423-base pair fragment of the mitochondrial *cytochrome c oxidase subunit I* gene (COI) using custom primers created with Primer3 [58] targeting *Holothuria* spp.: GenHol2L (5′-AACCAAATGGTTCTTGCTTACC-3′) and GenHol2R (5′-TTCTGATTAATCCCACCATCC-3′). PCR was performed using 15 μL reactions containing 1 μL of diluted DNA extract (one part template DNA to 199 parts nanopure water), 1 μL each of 0.2 μM forward and reverse primers, 0.6 μL of 0.5 μM BSA, 7.5 μL of (Bioline) Biomix Red diluted as per manufacturer's instructions, and 3.9 μL of nanopure water. PCR was done on Icycler thermocyclers (Bio-Rad Laboratories) with an initial denaturation at 95°C for 7 min followed by 35 cycles of a denaturing step at 95°C for 1 min, annealing at 50°C for 1 min, and extension at 72°C for 1 min. A final extension at 72°C was held for 7 min before refrigeration. PCR product (8 μL) was treated with 0.7 μL of *Exonuclease I* combined with 0.7 μL of calf intestinal alkaline phosphatase (Exo-CIAP) and incubated at 37°C for 30 minutes and with a final inactivation step at 85°C for 10 minutes. The treated PCR product was sequenced using an ABI Prism automatic sequencer at the Hawai‘i Institute of Marine Biology's EPSCoR sequencing facility. All samples were sequenced in the forward direction; uncertain sequences and all unique haplotypes were also sequenced in the reverse direction for confirmation. Sequences were compiled and trimmed using Sequencher 4.8 and aligned using ClustalW implemented in Bioedit 7.0.5 [59, 60].

2.2. Data Analysis. A statistical parsimony network of mitochondrial haplotypes was constructed by creating a reduced median network that was then used to make a median joining network; both procedures implemented in Network 4.516 (http://www.fluxus-engineering.com/; [61, 62]). The network was drawn using Network Publisher 1.1.0.7 (http://www.fluxus-engineering.com/).

Nei's average pairwise genetic difference (π) [63] and haplotype diversity (h) were calculated in DnaSP 4.1 [64]. The effective number of alleles was calculated by hand following Jost [65]. Tajima's D [66] and Fu's F_S [67] were calculated in ARLEQUIN v.3.1 with 10,000 simulations to establish confidence intervals.

To assess levels of genetic differentiation between sites, we calculated pairwise Φ_{ST} values using Arlequin 3.1 [68] and pairwise D_{est_chao} values by hand following Jost [65]. Φ_{ST} is a fixation index incorporating genetic distance that ranges from 0 to 1, where a zero indicates identical haplotypic composition and a one signifies alternate fixation of alleles and a complete lack of gene flow. D_{est_chao} is an index of genetic differentiation, which does not account for genetic distance among haplotypes but also ranges from 0 to 1 (note that both Φ_{ST} and D_{est_chao} can be slightly negative due to bias correction for sampling error). In the case of D_{est_chao}, a zero also indicates identical haplotypic composition, but unlike Φ_{ST}, a one simply indicates that no haplotypes are shared between the populations. The primary difference in interpretation is that in the absence of gene flow Φ_{ST} values can be significantly less than one, while this is not the case for D_{est_chao}, which is argued to be an advantage of this latter statistic [65]. To correct the critical P value for statistical significance in pairwise comparisons, the familywise false discovery rate (FDR) correction found in [69] was implemented. Analysis of molecular variance (AMOVA) was used for hierarchical analysis of the partitioning of COI diversity among sites within archipelagic regions and among archipelagic regions using Arlequin 3.1. SAMOVA 1.0 was used to identify groups of samples that maximize the proportion of total genetic variance due to differences between regions [70]. The most important genetic barriers were ranked using BARRIER 2.2 [71]. BARRIER uses Monmonier's maximum-difference algorithm to compare a matrix of difference values, such as pairwise Φ_{ST} values, with a matrix of geographic distances in order to identify the strongest barriers within the matrix. We compared barriers created using each Φ_{ST} and D_{est_chao} distance matrix. AMOVAs were performed using groupings determined by SAMOVA and BARRIER for hypothesis testing to compare genetic groupings to the archipelagic groupings. The pairwise Φ_{ST} and AMOVA analyses were conducted using a distance matrix with 50,000 permutations and the Tamura-Nei mutational model [72] with gamma = 0.0164. The mutational model HKY+G was selected using AIC in MODELTEST 3.7; the model hierarchy was used to select the closest available model when the best-fit model could not be implemented by the chosen program, as in the case of ARLEQUIN [73]. Regardless, the inferences are robust to the mutational model, and our conclusions are not altered regardless of which model is chosen (data not shown).

MRBAYES 3.1 was used to construct a Bayesian estimation of a phylogeny containing all *H. atra* haplotypes from this study along with all *Holothuria* and *Actinopyga* COI haplotypes available from GenBank as of February 2010 [74]. Two independent runs with identical conditions were completed and averaged. A general time reversible (GTR) simple nucleotide model with a gamma-shaped rate variation of 0.0164 was used; Markov chain length = 4 × 3,000,000 sampled every 100 generations with a 10% burn-in. The GTR nucleotide model was chosen as it is the most general and neutral nucleotide model available in MrBayes 3.1 and corresponds most closely to the Tamura-Nei model [75]. The sea cucumber *Actinopyga agassizi* was set as the outgroup. Program defaults were used for all other settings. MrBayes was used to summarize all of the trees produced into a single consensus tree.

RAxML 7.0 [76] implemented through CIPRES Web Portal v.1.15 [77] was used to construct the highest scoring maximum likelihood-based estimation of a phylogeny containing all haplotypes used in the Bayesian analysis and run 10,000 bootstrap simulations to assess branch support. A GTR nucleotide model that uses four discrete gamma rates set by the program was used for the analysis; program defaults were used for all other settings.

Bayesian coalescent-based calculations of migration rate among regions (N_eM) and the region mutation parameter (θ) were conducted using MIGRATE 3.1.3 [78]. Three independent runs of a Bayesian MCMC search strategy were completed and averaged by MIGRATE. A nucleotide model with a transition-to-transversion ratio of 6.1584 : 1 and three regions of substitution rates with a gamma-shaped rate variation of 0.016 was used; Markov chain length = 1,000,000 sampled every 20 generations with a 10% burn-in. Program defaults were used for all other settings. The transition-to-transversion ratio was calculated using Modeltest 3.7. Two replicate MIGRATE analyses were run using different population groupings. Preliminary analyses that split the data by sampling location returned flat posterior probabilities, presumably from having too many parameters to estimate. The software's author advocates using the minimal number of sensible regions in order to reach convergence (Peter Beerli, pers. comm.). The first analysis used regions separated along the most important breaks identified by the program BARRIER. Archipelagos were used as regions for the second analysis with the Hawaiian Archipelago further divided between the main Hawaiian Islands and the Northwestern Hawaiian Islands plus Johnston Atoll and Kingman Reef separated from the Line Islands; this grouping was chosen based on BARRIER and pairwise analyses. Values for the migration rate among regions (M) and region mutation parameters (θ) were taken from the highest peaks in the posterior probability distribution curves. The posterior probability distributions were examined to determine the validity of each estimated parameter.

3. Results

A total of 385 individuals, 55 haplotypes, and 37 private haplotypes are sampled in this study (Table 1). Of the 18 haplotypes shared across sampling sites, 10 are found in multiple archipelagos (Figure 2). However, no haplotypes are shared between the most distant regions: Hawai‘i and Japan.

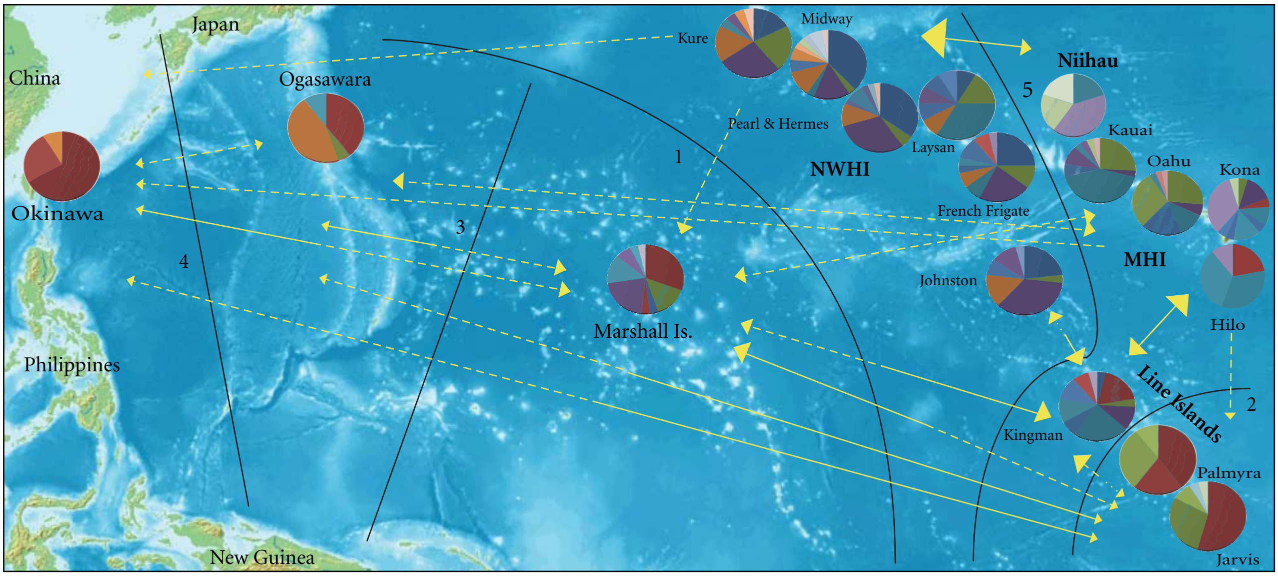

Figure 1: Map of the northern Central and West Pacific. Pie charts represent haplotype frequencies overlaid on sites. To avoid overlap, the Marshall Islands sites, Kwajalein and Majuro, have been combined. Black lines are major gene flow constraints drawn by BARRIER, numbered from strongest to weakest. Yellow arrows represent directional migration rates estimated by MIGRATE. Effective migration rate estimates (N_eM) with modes between 0.01 and 0.49 are represented by small arrows, rates between 0.5 and 0.99 are represented by medium arrows, and rates over 1.0 are represented by large arrows. Solid lines represent migrate posterior probability distributions, where the 50% credibility set does not include zero. Dashed lines represent migration posterior probability distributions, where the 50% credibility set includes zero, but the distribution peak is greater than zero. Migration parameters with a posterior distribution peak of zero are not shown.

Because many population genetic estimates are relatively insensitive to weak selection [79], loci which do not show significant deviations from neutral expectations should provide reliable inferences about population structure [80]. None of the site-by-site Tajima's D values were significant, and only Laysan deviated from expectation using Fu's F_s; thus, there is no evidence to indicate that nonneutral processes are responsible for the pattern of COI haplotype diversity presented here.

To ensure there was no misidentification of the samples included here, we performed a phylogenetic reconstruction of our samples with those available in GenBank. We confirmed that the samples included here are monophyletic and there are no reciprocally monophyletic groups among the *H. atra* haplotypes included in our population genetic analyses (Appendix A).

Haplotype diversity, as a function of longitude, increases from west to east across the Pacific Ocean (Table 1, $R^2 = 0.80$, $P < 0.05$). Japanese sites exhibit the lowest haplotype diversity ($h = 0.51$–0.66) and effective number of haplotypes ($H_E = 2.0$–2.9); the centrally located Line Islands ($h = 0.65$–0.90, $H_E = 2.9$–9.7) and Marshall Islands ($h = 0.75$–0.76, $H_E = 4.0$–4.1) exhibit mid to high levels of diversity; the Hawaiian sites exhibit the highest diversity ($h = 0.75$–0.90, $H_E = 4$–10). Nucleotide diversity does not appear to be correlated with haplotype diversity because nucleotide diversity is lower in the Hawaiian Archipelago than in all other locations except for Okinawa (Table 1). This pattern can be visualized in the haplotype network, where sites exhibiting high nucleotide diversity harbor disparate haplotypes separated by a relatively large number of mutations (Figure 2).

Four AMOVAs were run on the *H. atra* COI haplotype data (Table 2). In each AMOVA, a different method was employed to group the population samples into regions. Under the first geographic hypothesis, sites were grouped into five regions by archipelago, with Johnston Atoll included with Hawai‘i. In order to assess the subdivision of the Hawaiian Archipelago into the NWHI and the MHI, this grouping hypothesis was compared to a second geographic hypothesis, where population samples were grouped into six regions; Hawaiian sites were divided into the MHI and the NWHI + Johnston and four regions comprised of the four remaining archipelagos. Both grouping hypotheses (geographic hypothesis one and two) exhibited similar partitioning of variation among groups (32.1% versus 30.9%) and among populations within groups (8.9% versus 5.5%). In both cases, there was stronger partitioning among the groups of samples ($\Phi_{CT} = 0.32$, $\Phi_{CT} = 0.31$; $P < 0.0001$) than among the simples nested within the groupings ($\Phi_{SC} = 0.13$, $\Phi_{SC} = 0.07$; $P < 0.0001$).

The two geographic hypotheses were compared to six-region groupings identified by SAMOVA and BARRIER; BARRIER selected the same dominant barriers using both the Φ_{ST} and $D_{\text{est\_chao}}$ distance matrices (Table 2 and Figure 1). Six regions were chosen for a direct comparison to the archipelagic geographic hypothesis that included Hawai‘i divided into two main regions. These groupings partitioned variance similarly to the geographic hypotheses with the SAMOVA grouping minimizing among-population within-group variance with more among-group variance explained (Table 2). The grouping of population samples using BARRIER and SAMOVA had slightly greater levels of genetic

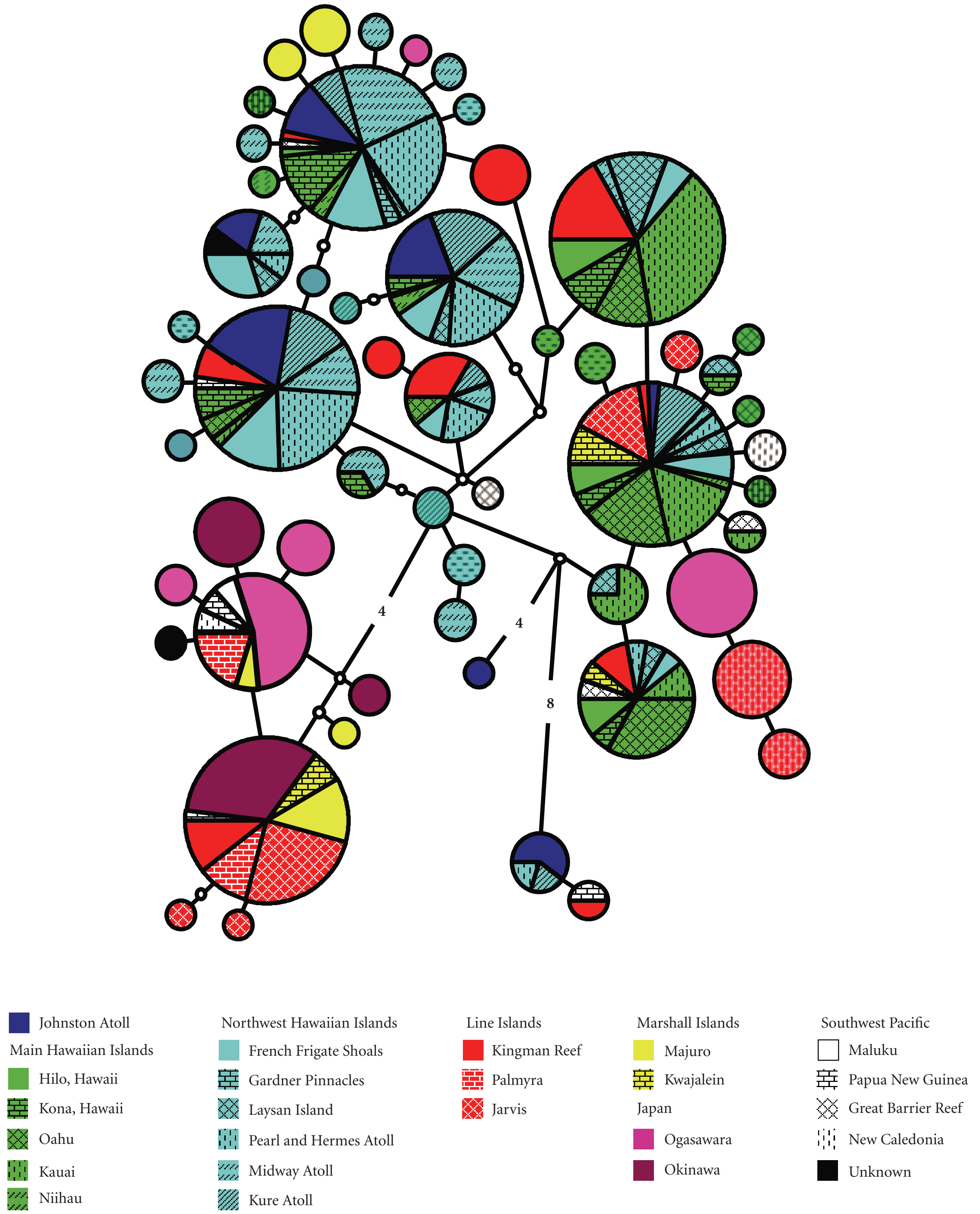

Figure 2: Haplotype network for *Holothuria atra*. Each circle represents a unique haplotype connected by a line to those that differ by one base pair. Nodes on lines indicate a missing haplotype, and numbers represent multiple missing haplotypes. Each haplotype is color coded by site, and circle size is proportional to frequency. The smallest circles represent one occurrence of a halotype.

Table 1: N is the Sample size, H is the total number of haplotypes, H_u is the number of unique haplotypes at site, π is the nucleotide diversity, h is the haplotype diversity, and A_E is the effective number of alleles in COI.

Region	Site	N	H	H_u	$\pi \pm$ SD	$h \pm$ SD	A_E	Tajima's D	Fu's F_s
Main Hawaiian Islands	Hilo	9	4	0	0.0041 ± 0.0030	0.81 ± 0.08	5.3	−0.27	0.08
	Kona	21	10	2	0.0078 ± 0.0046	0.87 ± 0.06	7.5	−0.57	−2.21
	Oahu	24	7	2	0.0052 ± 0.0033	0.79 ± 0.05	4.7	−0.88	−0.58
	Kauai	30	8	2	0.0033 ± 0.0023	0.75 ± 0.06	4.0	−1.21	−2.61
	Niihau	5	4	1	0.0071 ± 0.0052	0.90 ± 0.16	10.0	−0.75	−0.33
Northwest Hawaiian Islands	French Frigate	28	10	2	0.0082 ± 0.0048	0.88 ± 0.04	8.3	−0.14	−1.12
	Gardner	2	1	0	N/A	N/A	N/A	N/A	N/A
	Laysan	12	8	0	0.0064 ± 0.0041	0.89 ± 0.08	9.1	−1.06	**− 2.91**
	Pearl & Hermes	37	10	2	0.0086 ± 0.0049	0.79 ± 0.05	4.8	−1.26	−0.23
	Midway	35	14	6	0.0084 ± 0.0048	0.84 ± 0.05	6.2	−0.64	−3.61
	Kure	23	8	2	0.0096 ± 0.0055	0.85 ± 0.04	6.9	−0.92	0.47
Johnston	Johnston	26	7	1	0.0131 ± 0.0073	0.81 ± 0.05	5.3	−0.28	2.96
Line Islands	Kingman	27	10	3	0.0142 ± 0.0078	0.90 ± 0.03	9.7	−0.39	0.81
	Palmyra	16	4	2	0.0155 ± 0.0087	0.76 ± 0.06	4.1	2.59	6.13
	Jarvis	23	5	3	0.0126 ± 0.0070	0.65 ± 0.08	2.9	1.8	4.84
Marshall Islands	Majuro	14	5	3	0.0139 ± 0.0079	0.76 ± 0.08	4.1	2.22	3.32
	Kwajalein	9	4	1	0.0126 ± 0.0076	0.75 ± 0.11	4.0	1.49	2.81
Bonin Islands	Ogasawara	20	4	3	0.013 ± 0.0073	0.66 ± 0.06	2.9	2.25	6.15
Ryukyu Islands	Okinawa	24	3	2	0.0028 ± 0.0021	0.51 ± 0.09	2.0	0.26	1.82
Overall		385	55	37	0.0088 ± 0.0045	0.92 ± 0.08	12.5	0.12 ± 1.28	0.83 ± 2.91

differentiation among groups of samples ($\Phi_{CT} = 0.33$, $\Phi_{CT} = 0.37$; $P < 0.0001$) and lower levels of differentiation among samples nested within groups ($\Phi_{SC} = 0.07$, $\Phi_{SC} = 0.03$; $P < 0.0001$). Overall, the four AMOVAs exhibited similar levels of partitioning of variance, and all tests were significant ($P < 0.0001$).

There is a strong pattern of restricted gene flow between sites among the population samples of *H. atra*. Pairwise comparisons for both Φ_{ST} and D_{est_chao} reveal significant differences between sites located in different archipelagos in almost all cases, where sample sizes are 10 or greater (Table 3). The exceptions are between the Line Islands and the Marshall Islands, where one of six pairwise Φ_{ST} comparisons is statistically significant; between the Line Islands and the Bonin Islands, one of three Φ_{ST} comparisons is statistically significant; between the Hawaiian Islands and Kingman Reef, where only four of twelve pairwise Φ_{ST} comparisons were statistically significant.

Some significant differences were also detected among samples within archipelagos. In the Main Hawaiian Islands (MHI), O'ahu and Kaua'i are significantly different than the Kona sample from the Big Island of Hawai'i. Despite small sample sizes, Ni'ihau is also partitioned from the adjacent island of Kaua'i as well as O'ahu, but not the Big Island. Within the Northwestern Hawaiian Islands (NWHI), only Laysan is significantly partitioned from the other sampling sites, including Johnston Atoll. Overall, 42% of pairwise comparisons between the MHI and the NWHI + Johnston were significant, compared to 30% of the comparisons within the MHI and 19% of the comparisons within the NWHI + Johnston. The samples from both the Line Islands (LI) and the Marshall Islands (MI) were significantly partitioned within their respective archipelagos when using D_{est_chao}; there was not significant partitioning between MI sites when using Φ_{ST}.

The results from the MIGRATE runs show similar patterns of gene flow between regions (Table 4, Figure 1). Effective migration rates (N_eM) between regions are low. There is less than one migrant per generation, the rule-of-thumb number below which population cohesion starts to break down, between most regions [81]. The exceptions include the one-way migration from the Main Hawaiian Islands into the Northwest Hawaiian Islands and Johnston Atoll and the one-way migration from Kingman Reef to the Main Hawaiian Islands (Table 4). The high effective migration rate from the NWHI to the MHI in the first analysis splits almost evenly between Kingman Reef and the MHI when these two regions are separated in the second analysis (Table 4). Overall, higher effective migration rates are observed leaving the Hawaiian regions then going into them (Table 4, Figure 1). Though effective migration rates are a product of migration and effective population size, the effective migration rates larger than 1 migrant per generation are driven primarily by migration and not effective population size (Appendices A and B). This pattern is indicative of recent migration rather than ancestral polymorphisms and high effective population sizes. Posterior probability distributions for all values were in the form of unimodal curves. A full description of N_e and M values for both analyses can be found in Appendices B and C.

TABLE 2: Pairwise comparisons by site. $\mathrm{D}_{\mathrm{est\_chao}}$ values are contained in the lower left half of the table, and Φ_{st} values are in the upper right half of the table. Bolded values signify significant differences after correction using the procedure outlined in Benjamini 2008.

Region	Site	Main Hawaiian Islands					Northwest Hawaiian Islands						Johnston	Line Islands			Marshall Islands		Bonin Iss.	Ryukyu Iss.
		Hilo	Kona	Oahu	Kauai	Niihau	Fr. Frigate	Gardner	Laysan	Pearl &Hermes	Midway	Kure		Kingman	Palmyra	Jarvis	Majuro	Kwajalein	Ogasawara	Okinawa
Main Hawaiian Islands	Hilo	—	0.101	−0.039	−0.029	**0.234**	**0.209**	0.463	−0.059	**0.253**	**0.243**	**0.185**	**0.204**	0.084	**0.303**	**0.399**	**0.416**	0.159	**0.335**	**0.864**
	Kona	0.225	—	**0.127**	**0.203**	−0.047	−0.006	−0.044	0.049	0.026	0.016	0.009	0.046	0.056	**0.327**	**0.401**	**0.361**	**0.203**	**0.345**	**0.786**
	Oahu	−0.167	**0.515**	—	0.049	**0.261**	**0.221**	**0.399**	0.018	**0.258**	**0.263**	**0.193**	**0.231**	**0.117**	**0.351**	**0.431**	**0.468**	**0.181**	**0.368**	**0.826**
	Kauai	−0.109	**0.499**	0.172	—	**0.377**	**0.305**	**0.568**	0.001	**0.341**	**0.335**	**0.278**	**0.309**	**0.183**	**0.456**	**0.524**	**0.573**	**0.333**	**0.473**	**0.873**
	Niihau	0.245	−0.388	0.516	**0.698**	—	−0.011	−0.224	0.091	0.006	−0.045	−0.005	0.007	0.024	0.266	0.359	0.269	0.178	0.301	**0.847**
Northwest Hawaiian Islands	Fr. Frigate	0.392	−0.105	**0.518**	**0.629**	−0.239	—	−0.039	**0.145**	−0.014	−0.012	0.001	0.015	**0.084**	**0.358**	**0.421**	**0.367**	**0.256**	**0.371**	**0.767**
	Gardner	0.814	0.412	**1**	**1**	0.273	0.553	—	0.23924	−0.021	−0.091	0.033	−0.045	0.011	0.258	**0.375**	0.215	0.199	**0.315**	**0.889**
	Laysan	−0.294	0.138	0.122	−0.13	0.191	0.286	0.849	—	**0.194**	**0.173**	**0.124**	**0.156**	0.068	**0.306**	**0.396**	**0.398**	0.167	**0.334**	**0.832**
	Pearl & Hermes	**0.689**	0.008	**0.744**	**0.888**	−0.11	−0.033	0.42	**0.674**	—	−0.012	−0.013	−0.005	**0.089**	**0.365**	**0.419**	**0.358**	**0.269**	**0.372**	**0.739**
	Midway	**0.661**	−0.08	**0.846**	**0.88**	−0.356	−0.026	0.36	**0.555**	−0.018	—	0.004	0.0177	0.091	**0.365**	**0.421**	**0.349**	**0.271**	**0.373**	**0.747**
	Kure	0.461	0.111	**0.41**	**0.666**	−0.201	−0.03	0.697	**0.483**	0.0349	0.16	—	−0.013	0.042	**0.304**	**0.369**	**0.329**	**0.197**	**0.316**	**0.739**
	Johnston	**0.799**	0.144	**0.782**	**0.901**	0.0909	−0.012	0.611	**0.694**	−0.041	0.093	−0.022	—	0.071	**0.297**	**0.358**	**0.294**	**0.205**	**0.308**	**0.682**
Line Islands	Kingman	0.279	**0.432**	**0.467**	**0.354**	**0.781**	**0.463**	**0.933**	0.142	**0.643**	**0.695**	**0.612**	**0.666**	—	**0.145**	**0.183**	**0.153**	0.019	**0.152**	**0.571**
	Palmyra	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0.664**	–	0.065	0.109	0.031	0.009	**0.451**
	Jarvis	**0.626**	**0.88**	**0.591**	**0.73**	**0.728**	**0.86**	**1**	**0.776**	**0.941**	**0.966**	**0.732**	**0.956**	**0.521**	**0.447**	—	0.041	0.046	0.064	**0.289**
Marshall Islands	Majuro	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0.539**	**0.391**	**0.241**	—	0.099	0.107	**0.386**
	Kwajalein	0.222	**0.752**	0.155	**0.499**	0.492	**0.72**	1	0.532	**0.883**	**0.938**	**0.512**	**0.922**	**0.51**	**0.576**	−0.034	**0.419**	—	0.044	**0.619**
Bonin Islands	Ogasawara	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0.743**	**1**	**0.902**	**1**	—	**0.428**
Ryukyu Islands	Okinawa	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0.585**	**0.433**	**0.172**	**0.222**	**0.402**	**1**	—

Familywise false discovery rate corrected P-values: $D_{\mathrm{est\_chao}}$ $P \leq .036$; Φ_{st} $P \leq .023$.

Table 3: Analysis of molecular variance (AMOVA) for different population groupings. Beginning at the top, groupings are as follows: (1) by archipelago, (2) by archipelago with Hawaii divided between the Northwest Hawaiian Islands (NWHI) and the Main Hawaiian Islands (MHI), (3) six groups chosen by BARRIER and (4) six groups chosen by SAMOVA.

Population groupings	Source of variation	% of Variation	Φ statistics
Okinawa; Ogasawara; Marshall Islands; Hawaiian Archipelago + Johnston Atoll; Line Islands	AG	32.14	$\Phi_{CT} = 0.321^*$
	AP(G)	8.9	$\Phi_{SC} = 0.131^*$
	WP	58.96	
Okinawa; Ogasawara; Marshall Islands; MHI; NWHI + Johnston Atoll; Line Islands	AG	30.94	$\Phi_{CT} = 0.309^*$
	AP(G)	5.47	$\Phi_{SC} = 0.0793^*$
	WP	63.58	
Okinawa; Ogasawara; Marshall Islands; MHI + Kingman; NWHI + Johnston Atoll; Palmyra + Jarvis	AG	32.59	$\Phi_{CT} = 0.326^*$
	AP(G)	4.48	$\Phi_{SC} = 0.066^*$
	WP	62.93	
Okinawa; Ogasawara + Kwajalein + Palmyra; Jarvis + Majuro; Hilo + Oahu + Kauai; All Others	AG	37.35	$\Phi_{CT} = 0.373^*$
	AP(G)	2.02	$\Phi_{SC} = 0.032^*$
	WP	60.63	

AG = Among groups, AP(G) = Among populations within Groups, WP = Within populations. $^*P < 0.0001$.

Table 4: Pairwise population migration rate estimates (N_eM) based on a Bayesian MCMC simulation. Kingman Reef is grouped with the Main Hawaiian Islands in the upper table and treated as a seprate population in the lower table. The value of M calculated by MIGRATE was multiplied by the θ, as calculated by MIGRATE, of the destination population to estimate migration. The estimates of migration are separated by direction; the columns are source populations, and the the rows are sink populations.

Region	Line Islands	MHI+King	NWHI+J	Okinawa	Ogasawara	Marshall Islands	
Line Islands	—	0.13125	0.00375	0.15375	0.16875	0.13875	
MHI+Kingman	0.02375	—	3.01625	0.02375	0.02375	0.45125	
NWHI+Johnston	0.03125	4.34375	—	0.03125	0.03125	0.03125	
Okinawa	0.04625	0.00875	0.02875	—	0.04375	0.04375	
Ogasawara	0.04625	0.01375	0.00125	0.04875	—	0.02875	
Marshall Islands	0.46125	0.55125	0.19125	0.43875	0.39375	—	
	Line Islands	MHI	NWHI+J	Okinawa	Ogasawara	Marshall Islands	Kingman
Line Islands	—	0.04375	0.01125	0.05125	0.05125	0.04875	0.03125
MH Iss.	0.01625	—	0.95875	0.01625	0.27625	0.30875	1.02375
NWHI+Johnston	0.02625	4.96125	—	0.02625	0.02625	0.02625	0.49875
Okinawa	0.04625	0.05125	0.02875	—	0.04375	0.04875	0.04125
Ogasawara	0.04375	0.02625	0.03125	0.04375	—	0.04875	0.02875
Marshall Islands	0.46125	0.43875	0.41625	0.46125	0.39375	—	0.41625
Kingman Reef	0.69375	0.84375	0.80625	0.88125	0.01875	0.73125	—

4. Discussion

In this survey of population genetic structure, we elucidate patterns of connectivity throughout the north-central range of the sea cucumber *Holothuria atra* with a focus on the Hawaiian Archipelago. The Hawaiian Archipelago is highly isolated and also contains one of the highest proportions of endemism in the world (e.g., [40–42]; reviewed by Ziegler [39], Eldredge and Evenhuis [43]). Though there are many pan-pacific marine organisms in Hawai‘i, the isolation of the archipelago is thought to limit larval exchange such that colonization is rare but sufficient to maintain species cohesion among these taxa. The Hawaiian marine fauna contains a large proportion of endemics that are differentiated but not diversified from its Indo-West Pacific roots [39, 46–48]. In this scenario, Hawai‘i is seen primarily as a dead end, an isolated land mass that does not contribute in a significant way to the overall diversity of the tropical pacific. Counter to the island biogeography hypotheses of Hawaiian diversity, Jokiel and Martinelli [44] proposed the Vortex model of speciation, wherein the stunning biodiversity of the Coral Triangle is a result of centrifugal accumulation of species from the peripheral habitats around the Pacific. Though these two models primarily make predictions about speciation-level processes and do not speak directly to gene flow within a species, they do make opposite claims about the dominant direction of gene flow and dispersal. *H. atra* has a broad species range, extending from the Western Indian Ocean to the Eastern Pacific Ocean, which suggests the capacity for long-distance dispersal; however, populations showed significant population structuring within archipelagos, sometimes across very short oceanic distances. Even so, hierarchical genetic population structure in *H. atra* gives insight into the phylogeography of the north-central tropical Pacific. Our data test between the divergent hypotheses of whether peripheral archipelagos act as a source of genetic diversity in the Pacific and the likely colonization routes, into and out of, the extremely isolated Hawaiian Archipelago.

4.1. Biogeography and Range Size. If a large species range is a consequence of high dispersal potential, then *H. atra* should have little pronounced population structure, especially across small scales [11, 15, 82]. Indeed, this is the case for many species in the central West Pacific [16, 83–86]. Despite a species range which stretches from the Western Red Sea to the eastern Central Pacific in which *H. atra* is found in almost all shallow tropical habitats, we did not find support for extensive dispersal. The majority of sites from which we sampled *H. atra* were genetically distinct, with some sites less than 75 km apart being among the most distinct in our study (Table 3). These contrasting patterns highlight the dangers of making predictions about population connectivity and diversity based solely on the location and size of a species' range.

The larval life history of *H. atra* is not known exactly, but they require at least 18–25 days to reach competency to settle and are capable of traversing long oceanic distances with sufficient frequency to maintain species cohesion across a very broad geographic range [87]. The obvious question becomes why then is population subdivision found on such small geographic scales (e.g., Kingman Reef and Palmyra Atoll are only 67 km apart)? Counter to intuition, the geographic distance among sites is a poor predictor of the ease with which larvae can disperse among locations; the "oceanographic distance" experienced by larvae between sites is uncorrelated with geographic separation between them [36, 38]. Likewise, recent meta-analyses indicate the relationship between the length of pelagic larval development and dispersal ability is not as tight as has been generally assumed [23–26, 88]. Finally, a broad meta-analysis by Lester et al. [21] indicates that the intuitive relationship between range size and larval dispersal potential is poorly correlated overall but can play an important role in some taxa. Toonen et al. in this issue also show a number of breaks in the Hawaiian Archipelago that are shared by several species and are unexplained solely by appeal to one metric such as range size or larval dispersal potential. Although the mechanism of isolation across small scales remains unknown, our data clearly indicate that *H. atra* is not one of those species for which range size predicts relative dispersal ability.

4.2. Population Structure in the Hawaiian Archipelago and Johnston Atoll. Our mtDNA examination of *Holothuria atra* reveals significant genetic population structure across the surveyed portion of the range. There are two interesting patterns to this structure. Excluding Laysan Island, there are no significant pairwise differences between any other islands in the NWHI (spanning nearly 2000 km), suggesting that the NWHI, excluding Laysan, comprises a single large population. In contrast, there is significant structuring within the MHI (roughly 600 km) and between the NWHI and the MHI. This finding suggests that factors beyond merely geographic distance influence population partitioning.

Johnston Atoll, the nearest neighboring land mass, roughly 860 km south of French Frigate Shoals, is genetically distinct from most of the MHI and Laysan and genetically similar to all of the NWHI except Laysan. It has been suggested that Johnston Atoll acts as a stepping stone into the Hawaiian Islands [89]. Kobayashi [49, 50] used computer simulations to predict two larval transport corridors from Johnston Atoll to the Hawaiian Archipelago: one corridor stretching from Johnston to French Frigate Shoals in the NWHI and one from Johnston to Oʻahu in the MHI. Our data support the predicted larval transport corridor between Johnston Atoll and French Frigate Shoals, but not the corridor predicted between Kauaʻi and Johnston. Additionally, based on our data, Kingman Reef may also be an important stepping stone into and out of Hawaiʻi. The BARRIER analysis shows the division between the NWHIs, including Johnston Atoll, and the MHI to be the strongest barrier to gene flow within the Archipelago (Figure 1). Migration across this barrier is heavily one sided, where migration from the MHI into the NWHI dominates. The effectively one-way migration rates into the NWHI and Johnston Atoll coupled with the strong genetic similarity between Johnston Atoll and the NWHI suggest Johnston Atoll is an isolated outpost of the Northwest Hawaiian Islands, providing support for a vortex model [44] rather than the stepping stone entry into Hawaiʻi [89] for *H. atra*. These data indicate that Johnston Atoll exchanges migrants with Hawaiʻi far more often than its nearest neighbors to the south, and the same can be said for Kingman Reef. This result is particularly surprising because in the case of Kingman Reef, *H. atra* sampled there show greater similarity to populations in Hawaiʻi (roughly 1700 km southwest of Honolulu) than they do to those sampled at Palmyra Atoll, only 67 km away.

4.3. Phylogeographic Relationships between Archipelagos. Counter to conventional wisdom that Hawaiʻi is a passive recipient of rare dispersal from the diverse Pacific, the weight of available evidence, including pairwise Φ_{ST} values, mtDNA phylogeny, BARRIER divisions, and clustering within the haplotype network, provides substantial evidence for the opposite pattern in *H. atra;* Johnston Atoll is an outpost of Hawaiian diversity, and Kingman Reef acts as the primary stepping stone between the Hawaiian Archipelago and the rest of the Pacific. As far as we are aware, this is the first time empirical evidence has been provided for such a pathway. Higher haplotypic diversity in Hawaiʻi and the Line Islands relative to the other archipelagos supports a scenario in which population sizes are far greater, or Hawaiʻi and/or Kingman Reef are the ancestral population in the region. Likewise, the dominant haplotypes found in the Japanese Archipelagos are relatively distantly related and appear derived (Figure 2), suggesting that the western portion of the surveyed range was colonized in at least two separate events (or one of them has gone extinct in Hawaiʻi and Kingman), one of which did not make it all the way to Okinawa.

Excluding the dense sampling within the Hawaiian Archipelago, virtually all pairwise comparisons between sites are significantly different from each other (Table 3). The few comparisons that were not significant between sites have relatively high pairwise values but low sample sizes, a likely statistical limitation also noted by Bird et al. [90]. Hierarchical population structuring was detected with AMOVA using either D_{est} or Φ_{ST} values; sampling sites within archipelagos are significantly different from each other but are more similar within than between archipelagos. Four of the five most substantial restrictions to gene flow uncovered in this study (and the top ranked by BARRIER) were those between archipelagos; the one exception to this trend being Kingman Reef which is included with the Hawaiian rather than the Line Islands (Figure 1). The AMOVA run using the regions selected by BARRIER was only minimally different than the AMOVA run using regions divided by archipelagos; grouping Kingman Reef with the MHI, as per BARRIER, did explain 1.5% more of the overall variance.

In addition to the distinct archipelagic groupings in the haplotype network (Figure 2), several other patterns are noteworthy here. First, the NWHI and Johnston Atoll haplotypes are clustered together and interspersed whereas the MHI haplotypes are clustered together. Also, the Japanese haplotypes occur in two divergent areas of the network. The Line Island and Marshall Island haplotypes are interdispersed throughout the network, suggesting that these island groups are either mixing or transition zones. Nearly every locality haplotype (those found in only one sampling location) branch off in a starburst pattern from the major haplotypes found primarily in the same archipelago. This pattern is an indication that regional populations have been separated long enough for new haplotypes to arise, and that these new haplotypes are not being spread to other archipelagos by long-distance dispersal. Uniformly low migration rates between archipelagos estimated with MIGRATE support this isolation scenario.

5. Conclusion

Many echinoderm species are the focus of artisanal or commercial fishing efforts, and managing these fisheries requires a detailed understanding of dispersal pathways and population connectivity within a spatial management network. The Hawaiian Archipelago lies at the periphery of the tropical Central Pacific and is the most isolated island chain in the world; the question remains as to why some species maintain connectivity and species cohesion between the Hawaiian Islands and the rest of the Pacific, why some species diverge and become Hawaiian endemics, and why other species with similar inferred dispersal ability fail to colonize the Hawaiian Archipelago at all.

The genetic diversity of COI in *H. atra* across the studied portion of the range presents a complex pattern, but it is not inscrutable. Based on AMOVA, SAMOVA, and BARRIER analyses, it can be seen that population structuring is hierarchical; there are significant differences between sites, but the primary degree of population structure is archipelago by archipelago. Our analyses taken together suggest that the Hawaiian Archipelago and Kingman reef are ancestral populations in the region with migration moving out of these periphery archipelagos toward a less diverse central Pacific rather than the reverse. This pattern is inconsistent with the hypothesis that Hawai‘i is a dead end for rare migrants from the Indo-Pacific. Instead, the weight of the evidence shows that these peripheral populations are not sinks, but important centers for the generation of genetic diversity feeding back towards the West Pacific. Specifically for *H. atra*, our data suggest that the pathway between Hawai‘i and the rest of the Pacific is primarily out through Kingman Reef and the Line Islands and not in through Japan, the Marshall Islands, or the closest neighbor to the Hawaiian Archipelago, Johnston Atoll. We show that, at least for *H. atra*, Johnston Atoll is in fact an outpost of the Northwestern Hawaiian Islands and not a primary gateway for colonization of the Archipelago.

Considerable evidence is accumulating that it is indefensible to make predictions of connectivity based solely on proxies such as ecological or phylogenetic similarity, pelagic larval duration, or species range sizes [21, 23–25, 90]. The fine-scale structuring of populations in *H. atra* suggests that place-based management approaches, as exemplified by ecosystem-based management, are ideal for responding to the complex relationships between genetically distinct populations. *Holothuria atra* must be managed on a local scale; migration between archipelagos, and often between islands, does not occur in ecologically relevant time frames.

Appendices

A.

Phylogenetic tree of sampled *Holothuria atra* haplotypes and *Holothuria* and *Actinopyga* haplotypes retrieved from GenBank. The maximum likelihood tree is shown; Bayesian analysis produced a tree with almost identical topology. The first of the numbers beside branches corresponds to bootstrap support calculated from the maximum likelihood analysis; the second number, seperated by a /, corresponds to the posterior probability estimated during the Bayesian analysis. Only support values with 50% majority rule or 0.50 posterior probability are included. *Actinopyga agassizi* is the outgroup. All non-*H. atra* nodes were collapsed. GenBank accession numbers are included for uncollapsed taxa (see Figure 3).

B.

M and θ posterior probability distributions were calculated by MIGRATE using a Bayesian MCMC simulation. Population key: 1 = Kingman Reef; 2 = Line Islands; 3 = Main Hawaiian Islands; 4 = Northwestern Hawaiian Islands and Johnston Atoll; 5 = Okinawa; 6 = Ogasawara; 7 = Marshall Islands (see Table 5).

Table 5

Parameter	2.50%	25.00%	Mode	75.00%	97.50%	Median	Mean
$\theta1$	0	0.0015	0.00375	0.0055	0.0115	0.00525	0.00518
$\theta2$	0	0	0.00025	0.0015	0.0035	0.00175	0.00114
$\theta3$	0	0.0015	0.00325	0.0045	0.007	0.00375	0.00345
$\theta4$	0.001	0.0035	0.00525	0.007	0.0105	0.00625	0.00586
$\theta5$	0	0	0.00025	0.0015	0.003	0.00175	0.00095
$\theta6$	0	0	0.00025	0.001	0.003	0.00125	0.00085
$\theta7$	0	0.0005	0.00225	0.0045	0.011	0.00375	0.00417
M2–>1	0	0	185	350	1150	345	426.5
M3–>1	0	90	225	560	1430	495	580.3
M4–>1	0	80	215	580	1460	525	609.3
M5–>1	0	110	235	530	1310	455	536.8
M6–>1	0	0	5	160	580	165	204.9
M7–>1	0	10	195	350	1110	335	417.3
M1–>2	0	0	125	260	1010	265	347.2
M3–>2	0	0	175	280	1000	285	363.1
M4–>2	0	0	45	220	860	225	293.6
M5–>2	0	20	205	490	1500	475	575.1
M6–>2	0	70	205	580	1500	525	612.6
M7–>2	0	0	195	360	1350	365	481.7
M1–>3	10	140	315	580	1490	515	609.7
M2–>3	0	0	5	160	620	165	208.8
M4–>3	0	150	295	660	1490	565	644.1
M5–>3	0	0	5	100	370	105	126.2
M6–>3	0	10	85	210	600	195	227.9
M7–>3	0	0	95	220	920	225	299.9
M1–>4	0	0	95	220	910	225	299.7
M2–>4	0	0	5	100	350	105	123.3
M3–>4	350	640	945	1340	1950	1085	1094.5
M5–>4	0	0	5	70	280	75	93.9
M6–>4	0	0	5	80	280	85	96.6
M7–>4	0	0	5	140	470	145	170.4
M1–>5	0	0	165	280	1050	285	371.1
M2–>5	0	0	185	350	1290	355	457.5
M3–>5	0	60	205	440	1260	385	480.6
M4–>5	0	0	115	260	960	265	344
M6–>5	0	0	175	300	1200	305	412.1
M7–>5	0	20	195	380	1200	355	444.4
M1–>6	0	0	115	270	1020	275	358
M2–>6	0	0	175	340	1240	345	440.7
M3–>6	0	0	105	250	910	255	322.7
M4–>6	0	0	125	250	950	255	330.6
M5–>6	0	0	175	310	1020	305	377.4
M7–>6	0	20	195	370	1170	345	434.6
M1–>7	0	0	185	320	1040	315	387.3
M2–>7	0	30	205	570	1580	535	637.2
M3–>7	0	40	195	440	1280	405	496.2
M4–>7	0	0	185	300	1040	305	385.1
M5–>7	0	0	205	580	1640	575	671.4
M6–>7	0	10	175	280	960	275	344

Table 6

Parameter	2.50%	25.00%	Mode	75.00%	97.50%	Median	Mean
$\theta 1$	0	0	0.0008	0.0015	0.0035	0.00175	0.00125
$\theta 2$	0.001	0.003	0.0048	0.0065	0.01	0.00575	0.00532
$\theta 3$	0.002	0.0045	0.0063	0.0085	0.012	0.00725	0.00709
$\theta 4$	0	0	0.0003	0.0015	0.003	0.00175	0.00099
$\theta 5$	0	0	0.0003	0.0015	0.004	0.00175	0.00127
$\theta 6$	0	0.0005	0.0023	0.004	0.0105	0.00375	0.00399
M2–>1	0	0	175	270	1000	275	356
M3–>1	0	0	5	210	840	215	286.9
M4–>1	0	10	205	530	1570	515	616.5
M5–>1	0	80	225	550	1410	485	573.5
M6–>1	0	0	185	340	1260	345	447.1
M1–>2	0	0	5	210	750	215	265.9
M3–>2	160	390	635	950	1700	805	858.6
M4–>2	0	0	5	120	420	125	150.1
M5–>2	0	0	5	80	310	85	106.6
M6–>2	0	0	95	230	790	235	294.7
M1–>3	0	0	5	80	320	85	108.3
M2–>3	210	460	695	1030	1750	885	926.5
M4–>3	0	0	5	60	210	65	70
M5–>3	0	0	5	100	290	105	111.2
M6–>3	0	0	5	100	360	105	123.9
M1–>4	0	0	185	390	1440	395	511.3
M2–>4	0	0	35	230	860	235	298.3
M3–>4	0	0	115	240	880	245	315.2
M5–>4	0	0	175	320	1170	325	417
M6–>4	0	0	175	330	1280	335	447.2
M1–>5	0	0	185	330	1190	325	422.7
M2–>5	0	0	55	230	930	235	316
M3–>5	0	0	5	190	700	195	243.8
M4–>5	0	40	195	380	1160	345	430.6
M6–>5	0	0	115	250	940	255	328.9
M1–>6	0	10	205	550	1640	535	650.1
M2–>6	0	120	245	570	1410	505	584.5
M3–>6	0	0	85	230	880	235	307.3
M4–>6	0	0	195	470	1510	475	581
M5–>6	0	0	175	270	940	275	345.8

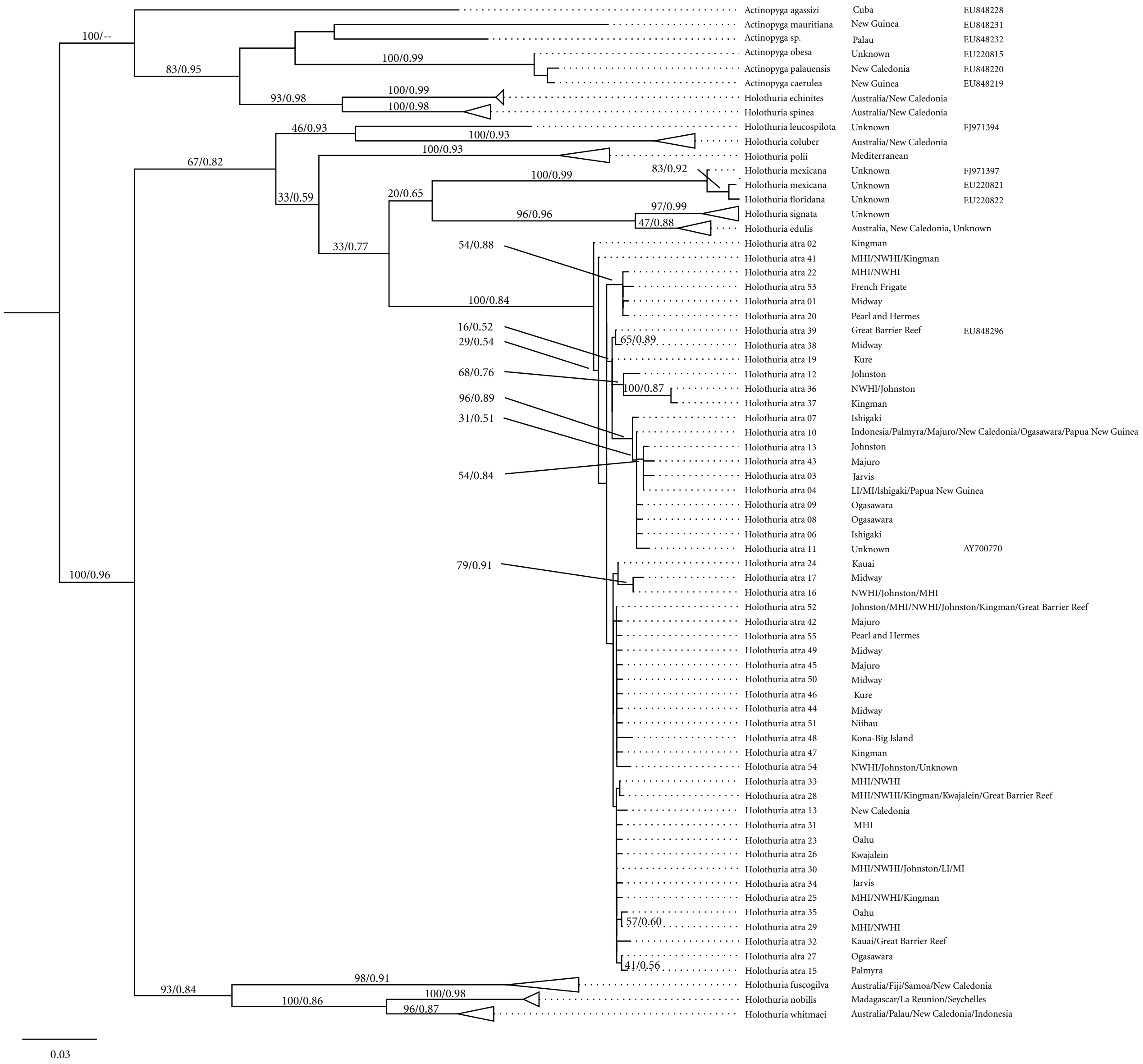

Figure 3

C.

M and θ posterior probability distributions were calculated by MIGRATE using a Bayesian MCMC simulation. Population key: 1 = Line Islands; 2 = Main Hawaiian Islands + Kingman; 3 = Northwestern Hawaiian Islands + Johnston; 4 = Okinawa; 5 = Ogasawara; 6 = Marshall Islands (see Table 6).

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Research Article

Phylogeography of the Pacific Blueline Surgeonfish, *Acanthurus nigroris*, Reveals High Genetic Connectivity and a Cryptic Endemic Species in the Hawaiian Archipelago

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Understanding genetic connectivity is fundamental to the design of marine protected areas in the service of ecosystem-scale management. Here we evaluate such trends for a Pacific surgeonfish (*Acanthurus nigroris*; $N = 544$) at two spatial scales: (1) within the Hawaiian archipelago, and (2) across the entire species range from the central to southwest Pacific. The mtDNA cytochrome *b* data reveal genetic divergence ($d = 0.041$) between Hawaii and the rest of the Pacific range indicating a cryptic species pair, with one taxon endemic to Hawaii. Johnston Atoll, 1400 km SW of Hawaii, also has the Hawaiian species but is distinct from most Hawaiian locations in population genetic comparisons, indicating the limits of gene flow for this widespread reef species. No consistent population genetic differences were observed among Hawaiian sites or among the other Pacific island sites. We also detected a modest bias in gene flow from the southeast towards the northwest islands of the Hawaiian Archipelago, indicating that the Papahānaumokuākea Marine National Monument may be a recipient, rather than a source of propagules to replenish reef resources.

1. Introduction

Reef fishes have been subject to a number of genetic studies in the interest of understanding the dynamics of population connectivity and phylogeography [1–3]. Early molecular studies indicated that many fishes are genetically homogeneous across wide geographic scales owing to their potential for dispersal over substantial distances during the pelagic larval stages [4–7]. This traditional view has begun to shift, however, with increased genetic surveys and the advent of novel techniques (e.g., [8, 9]). Recent research has shown population genetic structure in marine fishes on the scale of tens to a few hundred kilometers (see [10–13]), challenging the prediction of vast panmictic populations based on potential dispersal during planktonic development [14–16]. Although it is clear that larval dispersal ability remains a predictor of population structure in some cases (e.g., [17]), mounting empirical evidence suggests that other factors such as biogeographic barriers [18], contemporary oceanographic patterns [19], larval behavior [12, 20], local adaptation [21], and the ecological requirements of each species [16, 22] may all play greater roles in shaping population connectivity (for review, see [23]).

Contemporary population genetic structure can also be reflective of historical episodes of isolation rather than recent patterns of connectivity. Factors such as population fragmentation, extinction and recolonization, and range expansion have the potential to influence genetic signatures in reef fish that persist for many generations ([24]). One example is the rapid sea level changes driven by glaciation cycles during the Pleistocene [25, 26]. Lowering of the sea by up to a 120 m below present levels during the Last Glacial

Maximum (∼19 000 BP; [27]) exposed coral reef, altered the direction of sea surface currents, and even isolated entire oceans basins (e.g., formation of the Indo-Pacific Barrier; [28]). Such periodic changes in habitat availability have the potential to alter the range of reef fish species while producing cycles of population isolation, secondary contact, and subsequent merging or speciation [4, 11]. Repeated geological-climactic events in the Indo-West Pacific have also been invoked to explain geminate species pairs distributed in the Indian and Pacific Oceans, which display similar geographic (and genetic) boundaries [4, 18].

The study of genetic connectivity (i.e., gene flow) is particularly relevant in defining spatially explicit management regimes for reef fishes, like Marine Protected Areas (MPAs). The degree of interpopulation connectivity among geographic areas, or specific location of genetic breaks, sets the scale at which management strategies for marine species need to be applied to ensure that local extirpation is overcome by continued demographic exchange [3]. In order to promote species persistence and abundance, MPAs must be simultaneously self-sustaining and adequately linked via dispersal to other areas outside of the reserve boundaries (spillover effect; [29]). In the absence of genetic connectivity, isolated populations within a species can be identified by random changes in neutral genetic variation that accumulate over long periods of time [30].

Genetic management strategies are highly relevant to the unique ecosystems of the Pacific Islands. The Hawaiian archipelago is of particular interest given that it represents an isolated island chain and is characterized by some of the highest levels of tropical marine endemism in the world (i.e., 25% for shore fishes, [31]; 20% for molluscan fauna, [32]; 25% for algae, [33]). Endemism in other centrally located archipelagos in the Pacific is usually less than 2%, with one notable exception, the Marquesas Islands (12% for fishes; [34]). The Hawaiian Island chain, which includes both the geologically young Main Hawaiian Islands (MHI; 0.5 to 4.7 million years (my) old and the much older Northwestern Hawaiian Islands (NWHI; 7.3 to 29.8 my; [35]), extends 2600 km across the Central North Pacific (area = 341,360 km^2). The MHI start from the southeastern island of Hawaii (Big Island) through all eight inhabited Windward Islands ending at Kauai. The NWHI consist of 10 uninhabited islands extending from Nihoa to Kure Atoll (see Figure 1). Despite the large size of the archipelago, individual islands lie in close proximity to each other (mean separation 150 km), indicating that genetic connectivity may be high within Hawaii even with the overall isolation of the island chain (e.g., [36–39]).

The most immediate concern of marine resource managers in Hawaii is the extent of demographic linkages between the NWHI, which was declared a marine monument in June 2006 (the Papahānaumokuākea Marine National Monument) but mostly closed to fishing for decades, and the heavily fished MHI [40]. For example, if the MHI and the NWHI fish populations are connected, then stocks spanning the entire Hawaiian archipelago should be managed as a single unit. On the other hand, if NWHI populations are isolated from the MHI, management as separate units would be more appropriate. Although these islands clearly vary in terms of their level of fishing pressure, differences in oceanography and ecology further complicate the issue [40]. As one example, the NWHI are low lying atolls with modest freshwater runoff, whereas the MHI are high, mountainous islands with much greater runoff; this has the potential to influence sediment load over the surrounding coral reefs. Given that the objectives of a well-designed MPA should include fisheries enhancement [41] and the conservation of unique biodiversity [42], phylogeographic surveys assessing reef fish connectivity within the Hawaiian archipelago, as well as between Hawaii and other Pacific islands, are clearly mandated.

Here we focus on the Pacific Blueline Surgeonfish (*Acanthurus nigroris*), which provides an opportunity to examine the role of contemporary and historical factors in shaping present day patterns of genetic connectivity in the Pacific. *A. nigroris* is usually found in schools from a few to several hundred individuals and feeds primarily on plankton or filamentous algae [43]. This habitat generalist occupies lagoons, seaward reefs, mixed coral and rubble, and sand (depth range: 1 to 90 m; [43]) across the central and western Pacific and likely lives up to 25 years [44]. This colorful fish is also not fished or targeted by the aquarium trade [45]. Long-distance dispersal in *A. nigroris* presumably occurs during the pelagic larval stage that lasts approximately 55 to 60 days, based on estimates from related surgeonfish [46, 47]. Despite this potential for high levels of gene flow, slight morphological differences (fin rays and gill raker counts) in this species have been detected among Pacific populations, indicating that some regions may have been isolated on an evolutionary timescale [48].

In this study, we obtained samples from across much of the known distribution of *A. nigroris* in order to assess genetic structure using mtDNA sequence data (see Figure 1). Such sampling efforts also afforded a rare opportunity to consider genetic connectivity among sites in the Pacific Ocean and thus identify putative management units. Our objective is, therefore, to address the following questions: (1) Is there evidence of genetic structure within the Hawaiian archipelago (i.e., MHI versus NWHI) that would guide ecosystem-level management? (2) Is there genetic structure among other sampled Pacific populations? and (3) Is there evidence of recent or ongoing genetic exchange across the large stretches of open ocean separating Hawaii from the rest of the Central Pacific?

2. Methods

2.1. Collections. A total of 544 tissue samples of *A. nigroris* were collected with pole spears while scuba diving or snorkeling at 20 locations across the Hawaiian Archipelago (14 sampling sites in the NWHI and MHI), Johnston Atoll, and the Central Pacific (5 sampling sites: American Samoa, Line Islands, Marshall Islands, Society Islands, and Tokelau Islands) between 2004 and 2009 (see Figure 1). Specimens collected from the uninhabited NWHI were obtained on the NOAA Ship Hi'ialakai as part of an initiative to document and monitor resources in the Papahānaumokuākea Marine

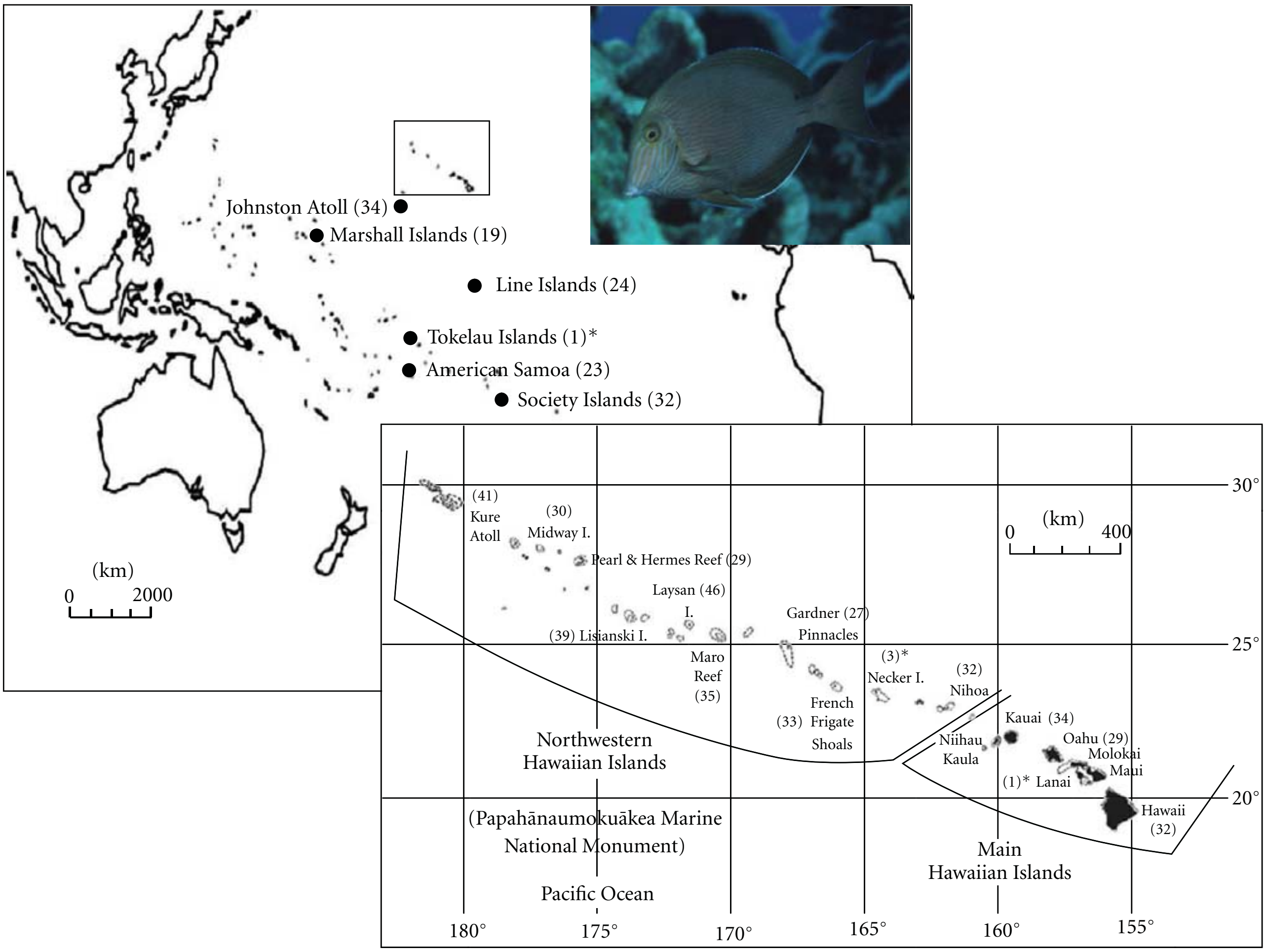


Figure 1: Scaled maps indicating the collection sites and sample sizes for *Acanthurus nigroris* in the Pacific Ocean. Locations marked with an asterisk were omitted from most population genetic analyses owing to low sample sizes (i.e., $N < 6$ in all cases) but were included when all (or only "Pacific") populations were pooled together, as well as in subsequent statistical parsimony networks. Map of the Hawaiian archipelago is courtesy of NOAA. Note that the boundaries of the Papahānaumokuākea Marine National Monument include only the Northwestern Hawaiian Islands (Photo credit: Jack Randall).

National Monument; all other samples were obtained during research expeditions by authors and colleagues. Tissue was stored in 70% ethanol or in a saturated salt-DMSO buffer at room temperature (25°C) until DNA extraction.

2.2. DNA Extraction, PCR, and Sequencing. Total genomic DNA was extracted from each tissue sample using a "Hot-SHOT" protocol [49] and subsequently stored at −20°C. A 797 base pair (bp) segment of the mtDNA cytochrome *b* (cyt *b*) gene was amplified using heavy-strand (5′-GTG-ACTTGAAAAACCACCGTTG-3′; [50]) and light-strand primers (5′-AATAGGAAGTATCATTCGGGTTTGATG-3′; [51]). Polymerase chain reaction (PCR) mixes were prepared following manufacturer's instructions using BioMixRED (Bioline Ltd., London, UK), 0.26 μM of each primer, and 5–50 ng template DNA in 15 μl total volume. Thermal cycling reactions used the following parameters: initial denaturing step at 95°C for 10 minutes, then 35 cycles of amplification (30 seconds of denaturing at 94°C, 45 seconds of annealing at 63°C, and 45 seconds of extension at 72°C), followed by a final extension at 72°C for 10 min.

PCR products were cleaned of excess oligonucleotides and unincorporated primers by incubating with exonuclease I and shrimp alkaline phosphatase (ExoSAP; USB, Cleveland, OH, USA) at 37°C for 60 min, followed by deactivation at 85°C for 15 min. All samples were then sequenced in the forward direction (and reverse direction for rare or questionable haplotypes, $N = 3$) with fluorescently labeled dye terminators following manufacturer's protocols (BigDye, Applied Biosystems Inc., Foster City, CA, USA) and analyzed using an ABI 3130XL Genetic Analyzer (Applied Biosystems) at the Hawaii Institute of Marine Biology EPSCoR Sequencing Facility. The sequences were aligned, edited, and trimmed to a common length using Geneious Pro *vers.* 4.8.4 DNA analysis software [52]. Variable sites were visually checked to ensure accuracy, and unique mtDNA cyt *b* haplotypes were deposited in GenBank (accession numbers: HM242298 to HM242393). jModelTest *vers.* 1.0.1 ([53]; but also see [54]) was used to determine the best nucleotide substitution model under Akaike information criterion (*AIC*); the Tamura-Nei model [55], with no gamma parameter, was here selected.

2.3. Population Genetic Analyses. ARLEQUIN vers. 3.1 software [56] was used to calculate haplotype (*h*) and nucleotide diversity (π) for cyt *b* sequences (as per [57]), as well as to test for genetic connectivity on several geographic scales: (1) within the Hawaiian archipelago, (2) among all other Central Pacific island groups (hereafter denoted "Pacific"), and (3) between Hawaiian and Pacific populations considered here. To test for genetic partitioning between regions, among populations within regions, and between all populations, we used Analysis of Molecular Variance (AMOVA; [58]); nonparametric permutation procedures ($N = 99999$ iterations) were used to construct null distributions and test the significance of variance components for each hierarchical comparison. Population pairwise Φ_{ST} statistics (a molecular analog of F_{ST} that includes information on mitochondrial haplotype frequency and genetic distance) were generated to identify genetic partitioning; significance was tested by permutation and *P* values adjusted according to the modified false discovery rate method (as per [59]). Genetic structure was also assessed with methods that do not make *a priori* assumptions about group identity (Spatial Analysis of Molecular Variance, *SAMOVA* 1.0; [60]) in order to confirm genetic patterns apparent with AMOVA. SAMOVA mitigates bias in group designation by implementing a simulated annealing process ($N = 100$ permutations) to randomly partitioned mtDNA sequences into *K* groups. We tested $K = 2$ to $K = 20$, and the configuration with the largest among group differentiation (Φ_{CT}) was retained. Moreover, pairwise genetic differences between populations (or regions) were calculated by dividing the average number of corrected nucleotides that differ between samples (as per [55]) by the total number of base pairs in that sequence (i.e., corrected sequence divergence, *d*).

Deviations from neutrality were assessed with Tajima's *D* [61] and Fu's *Fs* [62] for each population using *ARLEQUIN*; significance was tested with 99999 permutations. Negative (and significant) Tajima's *D* and Fu's *Fs* values indicate an abundance of rare haplotypes or recent mutations in nonrecombining sequences such as mtDNA, a signature of population expansion or background selection. As neutrality tests are sensitive to deviations from panmixia, we estimated these statistics both on the full data set and independently within each region identified as genetically distinct by SAMOVA (i.e., all Hawaiian Islands including Johnston Atoll versus all other Pacific islands). Samples collected from Johnston Atoll were initially grouped with Hawaiian samples given the pronounced overlap of inshore fish fauna between these two regions [63]. Moreover, three sites had low sample sizes (Necker Island, $N = 3$; Lanai, $N = 1$; Tokelau Islands, $N = 1$) and were, therefore, omitted from most population genetic analyses, although these specimens were included in parsimony networks and when all populations (or exclusively Hawaiian or Pacific populations) were pooled together.

Evolutionary relationships were estimated by constructing unrooted parsimony-based haplotype networks with the program *NETWORK vers.* 4.5.1.0 (http://www.fluxus-engineering.com/network_terms.htm). The haplotype network was generated using a median joining algorithm and default settings (as per [64]), and each haplotype divided into representative populations as reflected by the pie diagrams.

2.4. Coalescence Analyses. The historical demography of *A. nigroris* was analyzed by calculating mismatch distributions (the distribution of observed differences between haplotypes; [65]) and Harpending's raggedness index [66] with *ARLEQUIN*. We estimated such metrics for cyt *b* sequences from four different datasets: (1) all MHI populations ($N = 92$ individuals), (2) all NWHI populations ($N = 315$ individuals), (3) the entire Hawaiian archipelago (including Johnston Atoll, $N = 441$ individuals), and (4) all remaining Pacific populations ($N = 98$ individuals, excluding Tokelau). Populations that have been stable over time exhibit bimodal or multimodal mismatch distributions, whereas unimodal distributions or nonsignificant raggedness scores suggest recent (and rapid) population expansion (see [65]). All four datasets were also fitted with the population parameter τ in order to estimate the time to coalescence (as per [66, 67]). Time to coalescence (or population age) was calculated using the equation $\tau = 2\mu t$, where *t* is the age of the population in generations and μ is the mutation rate per generation for the sequence (μ = number of base pairs $\cdot$ divergence rate within a lineage $\cdot$ generation time in years). A range of mutation rate estimates were taken from previous work in fish (1% to 2%, based on 2% per million years between lineages or 1% within lineages, [5]; 1.55% per million years within lineages or 1.55×10^{-8} mutations per site per year, [68]), and while generation time is unknown for *A. nigroris*, we conditionally used 5 years based on estimates in a related surgeonfish (*Acanthurus nigrofuscus,* [44]). Although absolute values of time to coalescence should be interpreted with caution here owing to the approximation of mutation rate and generation time, comparisons between populations within this dataset provide useful estimates of within-species variation.

To further explore genetic connectivity of *A. nigroris* within the Pacific Ocean, we estimated coalescence-based migration rates (*Nm*, where *N* is the effective female population size and *m* is migration rate) with the program *MIGRATE vers.* 3.1.2 [69]. Estimates of gene flow generated in *MIGRATE* are not constrained by the assumption that a single ancestral population has split into two daughter populations [70] and appear to be robust to some common biases [71]. Although these approaches are sometimes sensitive to the presence of unsampled (i.e., ghost) populations [72], collecting *A. nigroris* from almost all of the Hawaiian islands as well as pooling the remaining Pacific samples for analysis likely reduced these effects. *MIGRATE* was therefore run: (1) among the MHI ($N = 92$ individuals), NWHI ($N = 278$ individuals), and Johnston Atoll ($N = 34$ individuals), (2) among all remaining Pacific populations ($N = 98$ individuals), and (3) between Hawaiian and Pacific populations by pooling all sampled individuals from each region (Hawaii, including Johnston Atoll, $N = 445$; Central Pacific, $N = 99$).

Estimates of migration rates based on coalescence theory provide not only an indication of the level of migration and population size, but also the directionality of gene flow in most cases. The maximum-likelihood (ML) approach implemented in *MIGRATE,* however, can sometimes provide unrealistic migration rate estimates and inflated confidence intervals (see [71, 73]). We therefore employed the recommended Bayesian inference search strategy of a single, replicated, 500,000 step chain with the first 20% discarded as burn in [74]. Each run was replicated ten times to ensure that the parameter space was widely sampled, and we took the average of all runs to calculate migration rates, thus accounting for variability between runs. Starting parameters for θ (theta) and M were estimated from F_{ST} [75], and initial runs were conducted with default exponential priors and an unrestricted migration model; posterior distributions for θ and M were used to inform priors for the final set of replicated runs. Only runs that produced normally distributed, unimodal posterior θ distributions were considered here.

Estimates of the number of migrants per generation were calculated by multiplying final estimates (mean 2.5%, and 97.5% quantile) of θ and M [76]. Given that we employed a single locus and make a number of simplifying assumptions regarding population history, we also regard these estimates as informative primarily for comparisons among populations *within* this dataset; comparisons with other species should be conducted with caution.

3. Results

3.1. Molecular Characteristics. We resolved 797 bp of mtDNA (cyt *b*) from 544 *A. nigroris* sampled at 20 locations across the Pacific Ocean (see Figure 1 and Table 1). There were no shared haplotypes between Hawaiian populations (including Johnston Atoll) and the remaining Pacific islands. In the Hawaiian samples, we observed 38 haplotypes (35 transitions, 1 transversion, and no indels). The most common and second most common haplotypes were detected at every site, and overall, the number of unique haplotypes per site was low. In the remaining Pacific islands, 58 haplotypes were observed (66 transitions, 3 transversion, and no indels), and while there were multiple haplotypes common to many of the sites, the majority of haplotypes were observed exclusively at single locations. Indeed, haplotype diversity was twice as high and nucleotide diversity almost an order of magnitude higher within Pacific sites ($h = 0.97$, $\pi = 0.0061$) compared to Hawaiian sites ($h = 0.52$, $\pi = 0.00080$; Table 1), despite a much greater sampling effort in the latter ($N = 441$ in Hawaii versus $N = 98$ in the Pacific). Note that the three sites that had low sample sizes (Necker Island, $N = 3$; Lanai, $N = 1$; Tokelau Islands, $N = 1$) shared common haplotypes with either Hawaiian or Pacific samples, thus justifying their inclusion in pooled analyses.

Negative and significant Tajima's D (or Fu's Fs) values in 7 out of the 13 (or 9 out of 13) Hawaiian samples (Tajima's $D = -1.99$ to -0.46; Fu's $Fs = -7.018$ to -0.73) and in 3 out of the 4 (or 4 out of 4) remaining Pacific samples (Tajima's $D = -1.64$ to -1.31; Fu's $Fs = -17.76$ to -7.54; Table 1) indicate past population expansion or selection within each region. These results were similar when both the Hawaiian and Pacific regions were analyzed separately (data not shown), indicating that our neutrality statistic estimates were robust to deviations from panmixia (see below).

3.2. Population Genetic Analyses. Grouping samples into Hawaiian (including Johnston Atoll) and the remaining Pacific locations with AMOVA revealed that most of the variability in mtDNA was explained by a significant break between these two regions ($\Phi_{\mathrm{CT}} = 0.96$, $P < 0.001$; see Table 2). Moreover, variance explained by the among-populations-within-regions variance component ($\Phi_{\mathrm{SC}} = 0.014$, $P = 0.035$) was an order of magnitude smaller than that between regions. This pattern held even when Johnston Atoll was excluded from AMOVA analysis altogether ($\Phi_{\mathrm{CT}} = 0.96$, $P < 0.001$; $\Phi_{\mathrm{SC}} = 0.010$, $P = 0.088$; $\Phi_{\mathrm{ST}} = 0.96$, $P < 0.001$), and so the overall patterns were therefore not driven by its inclusion in the Hawaiian group. SAMOVA further confirms these genetic partitions (i.e., $K = 2$ maximally differentiated groupings) with all Hawaiian populations (including Johnston Atoll) being significantly different from the remaining Pacific populations ($\Phi_{\mathrm{CT}} = 0.96$, $P < 0.001$).

Population pairwise tests provide insight into particular geographic regions or sites, where genetic partitioning is considerable, modest, or absent (Table 3). We found no significant genetic differentiation among sites within the Pacific (pairwise Φ_{ST} range: -0.0063 to 0.027), but comparisons among sampling locations in the Hawaiian archipelago revealed some genetic structure (pairwise Φ_{ST} range: -0.0015 to 0.19). Samples from Johnston Atoll were significantly different from all other Hawaiian locations except for French Frigate Shoals ($P = 0.043$), Kauai ($P = 0.049$), and Kure ($P = 0.24$). Removal of Johnston Atoll from the analysis eliminated significant (albeit marginal) genetic structuring within the Hawaiian archipelago (AMOVA with Johnston Atoll: $\Phi_{\mathrm{ST}} = 0.019$, $P = 0.011$; AMOVA without Johnston Atoll: $\Phi_{\mathrm{ST}} = 0.011$, $P = 0.073$).

A haplotype network based on statistical parsimony supports the genetic (and geographic) partitioning of *A. nigroris* into two clusters corresponding to the Hawaiian archipelago (including Johnston Atoll) and the remaining Pacific sampling sites (Figure 2). The characteristic "star phylogeny" for the two dominant Hawaiian haplotypes is consistent with low partitioning among samples [77], as well as a more recent population expansion of *A. nigroris* within Hawaii. Numerous low frequency haplotypes, on the other hand, were observed for the Pacific populations. We also found that the average corrected sequence divergence between Hawaiian and Pacific haplotypes was large ($d = 4.12\%$, based on 25 mutational steps), consistent with a long period of separation between the two lineages. Genetic divergence within each region, on the other hand, was much lower (Hawaii, average $d = 0.10\%$; Pacific, $d = 0.60\%$).

3.3. Coalescence Analyses. In order to resolve the relative timing of *A. nigroris* lineage divergence between Hawaii and the rest of the Pacific, as well as to infer putative population expansion events, we estimated pairwise mismatch distributions and coalescence times for individuals from:

Table 1: Sample size and molecular diversity indices for the studied *Acanthurus nigroris*.

Collection locality	N	H_N	H_U	Haplotype diversity (h ± SD)	Nucleotide diversity (π ± SD)	Tajima's D	Fu's Fs
Hawaiian Archipelago							
French Frigate Shoals	33	6	1	0.42 ± 0.10	0.00064 ± 0.00062	**−1.57**[a]	**−3.74**
Gardner Pinnacles	27	4	0	0.57 ± 0.061	0.00080 ± 0.00072	−0.46	−0.76
Hawaii (i.e., Big Island)	32	10	3	0.66 ± 0.085	0.0012 ± 0.00094	**−1.93**	**−7.018**
Johnston Atoll	34	4	1	0.22 ± 0.093	0.00037 ± 0.00044	**−1.75**	**−2.37**
Kauai	34	3	1	0.27 ± 0.092	0.00040 ± 0.00047	−0.69	−0.73
Kure Atoll	41	6	1	0.31 ± 0.093	0.00054 ± 0.00056	**−1.84**	**−4.059**
Laysan Island	46	9	5	0.58 ± 0.069	0.00086 ± 0.00074	**−1.74**	**−6.43**
Lisianski Island	39	8	3	0.58 ± 0.082	0.0010 ± 0.00083	**−1.99**	**−4.45**
Maro Reef	35	7	2	0.62 ± 0.064	0.00095 ± 0.00080	−1.34	**−3.57**
Midway Island	30	6	3	0.58 ± 0.080	0.00097 ± 0.00081	−1.41	**−2.47**
Nihoa	32	9	4	0.63 ± 0.091	0.00086 ± 0.00075	**−1.97**	**−7.35**
Oahu	29	5	1	0.54 ± 0.093	0.00082 ± 0.00073	−0.94	−1.81
Pearl and Hermes Reef	29	5	0	0.64 ± 0.057	0.00096 ± 0.00081	−0.66	−1.39
All of Hawaii[b]	441	38	25	0.52 ± 0.025	0.00080 ± 0.00069	**−2.38**	**-3.4×10^{38}**
Pacific							
American Samoa	23	16	7	0.94 ± 0.034	0.0054 ± 0.0031	**−1.61**	**−7.95**
Line Islands	24	16	10	0.95 ± 0.029	0.0053 ± 0.0031	−1.31	**−7.54**
Marshall Islands	19	19	15	1.00 ± 0.017	0.0065 ± 0.0037	**−1.64**	**−17.76**
Society Islands	32	25	15	0.98 ± 0.012	0.0073 ± 0.0040	**−1.53**	**−16.56**
All of Pacific[b]	98	58	47	0.97 ± 0.0081	0.0061 ± 0.0033	**−2.069**	**−25.54**

Abbreviations are as follows: N: sample size; H_N : number of haplotypes; H_U: number of unique haplotypes.

[a] Numbers in bold are significant, $P < 0.05$.

[b] Samples from Necker Island ($N = 3$), Lanai ($N = 1$), and the Tokelau Islands ($N = 1$) were omitted from these analyses.

Table 2: Genetic structuring (Analysis of Molecular Variance, AMOVA) of *Acanthurus nigroris* sampled at sites throughout the Pacific based on 797 bp of mtDNA cyt *b* sequence data ($N = 539$). All Hawaiian populations (including Johnston Atoll) and the remaining Pacific populations were divided into two separate groups to assess the relationship between these regions. Φ_{CT}: region variance component relative to total variance; Φ_{SC}: between population within region variance component divided by the sum of itself and within population variance; Φ_{ST}: sum of the variance due to region and population within region divided by the total variance.

Source	*d.f.*	*SS*	*Variance components*	*% variation*	Φ_{CT} Φ_{SC}	*P value*	Φ_{ST}	*P value*
Among regions (Hawaii versus Pacific)	1	2543.54	15.86	95.74	**0.96**[a]	< 0.001	**0.96**	< 0.001
Among populations (within regions)	15	15.11	0.0097	0.06	**0.014**	0.035		
Within populations	522	363.35	0.70	4.2				

[a] Numbers in bold are significant, $P < 0.05$.

(1) all MHI populations, (2) all NWHI populations, (3) the entire Hawaiian archipelago (including Johnston Atoll), and (4) the remaining Pacific populations (Figure 3). For all MHI populations, the unimodal mismatch distribution did not show a significant deviation from the simulated sudden demographic expansion null model (Harpending's raggedness index, $r = 0.11$, $P = 0.35$, Figure 3a); all other datasets, on the other hand, deviated from such a model despite being unimodally distributed (NWHI: Harpending's raggedness index, $r = 0.12$, $P = 0.005$, Figure 3b); Hawaiian archipelago: Harpending's raggedness index, $r = 0.11$, $P = 0.016$, Figure 3c; Pacific: Harpending's raggedness index, $r = 0.026$, $P = 0.004$, Figure 3d). Using the range of mutation rates (see Methods) and the population parameter τ, we identified markedly different coalescence dates in Hawaiian and Pacific populations (MHI: 20,953 to 41,905 years, $\tau = 0.67$; NWHI: 23,771 to 47,541 years, $\tau = 0.76$; Hawaiian archipelago: 22,178 to 44,356 years, $\tau = 0.71$; Pacific: 163,210 to 326,419 years, $\tau = 5.20$). Notably the coalescent estimates here reflect only the most recent population expansion in each region and not separation times between Hawaiian and Pacific *A. nigroris* (see above).

Our population genetic analyses were further supported by estimates of bidirectional, effective migration rates (Nm)

Table 3: Matrix of population pairwise Φ_{ST} values (below diagonal) and associated P values (above diagonal) based on 797 bp of mtDNA cyt *b* sequence data from *Acanthurus nigroris* sampled at sites across the Pacific ($N = 539$).

Location	Kure	Midway	P and H	Lisianski	Laysan	Maro	Gardner	FFR	Nihoa	Kauai	Oahu	Hawaii	JOH	AS	LI	MI	SI
Kure	—	0.016	0.00058	0.15	0.041	0.0035	0.0024	0.54	0.085	0.33	0.083	0.040	0.24	<0.001	<0.001	<0.001	<0.001
Midway	**0.071**[a]	—	0.44	0.54	0.51	0.69	0.70	0.20	0.44	0.15	0.52	0.94	0.0013	<0.001	<0.001	<0.001	<0.001
P and H	**0.14**	−0.0091	—	0.15	0.22	0.75	0.88	0.021	0.13	0.020	0.26	0.46	0.00047	<0.001	<0.001	<0.001	<0.001
Lisianski	0.013	−0.0078	0.021	—	0.95	0.18	0.15	0.92	0.99	0.69	0.81	0.95	0.023	<0.001	<0.001	<0.001	<0.001
Laysan	0.035	0.077	0.010	−0.014	—	0.28	0.26	0.42	0.88	0.40	0.88	0.93	0.0074	<0.001	<0.001	<0.001	<0.001
Maro	**0.10**	−0.016	−0.018	0.010	0.0050	—	0.99	0.091	0.24	0.091	0.37	0.45	0.0011	<0.001	<0.001	<0.001	<0.001
Gardner	**0.14**	−0.017	−0.026	0.018	0.0059	−0.026	—	0.063	0.21	0.052	0.34	0.40	0.00064	<0.001	<0.001	<0.001	<0.001
FFR	−0.0055	0.014	**0.064**	−0.014	−0.0040	0.037	0.059	—	0.68	0.77	0.50	0.46	0.043	<0.001	<0.001	<0.001	<0.001
Nihoa	0.021	−0.0052	0.023	−0.014	−0.013	0.0070	0.012	−0.012	—	0.60	0.84	0.88	0.023	<0.001	<0.001	<0.001	<0.001
Kauai	0.0024	0.024	**0.080**	−0.010	−0.0015	0.049	0.077	−0.019	−0.013	—	0.24	0.29	0.049	<0.001	<0.001	<0.001	<0.001
Oahu	0.034	−0.011	0.0093	−0.015	−0.017	−0.0038	0.0016	−0.0068	−0.016	0.0040	—	0.98	0.011	<0.001	<0.001	<0.001	<0.001
Hawaii	0.034	−0.018	−0.0050	−0.015	−0.015	−0.0067	−0.0047	−0.0055	−0.015	−0.0010	−0.022	—	0.012	<0.001	<0.001	<0.001	<0.001
JOH	0.0055	**0.12**	**0.18**	**0.043**	**0.080**	**0.15**	**0.19**	0.029	**0.043**	0.035	**0.078**	**0.060**	—	<0.001	<0.001	<0.001	<0.001
AS	**0.95**	**0.93**	**0.94**	**0.94**	**0.95**	**0.94**	**0.93**	**0.94**	**0.94**	**0.94**	**0.94**	**0.93**	**0.95**	—	0.095	0.54	0.10
LI	**0.95**	**0.93**	**0.93**	**0.94**	**0.94**	**0.94**	**0.93**	**0.94**	**0.94**	**0.94**	**0.93**	**0.93**	**0.94**	0.027	—	0.38	0.26
MI	**0.94**	**0.93**	**0.93**	**0.93**	**0.94**	**0.93**	**0.93**	**0.93**	**0.93**	**0.94**	**0.93**	**0.93**	**0.94**	−0.0063	0.00096	—	0.41
SI	**0.92**	**0.91**	**0.90**	**0.91**	**0.92**	**0.91**	**0.90**	**0.91**	**0.91**	**0.92**	**0.91**	**0.90**	**0.92**	0.020	0.0064	0.00040	—

AS: American Samoa; FFR: French Frigate Shoals; JOH: Johnston Atoll; LI: Line Islands; MI: Marshall Islands; P and H: Pearl and Hermes Reef; SI: Society Islands.

[a] Significant Φ_{ST} values (adjusted $P < 0.025$; as per [59]) are indicated in bold.

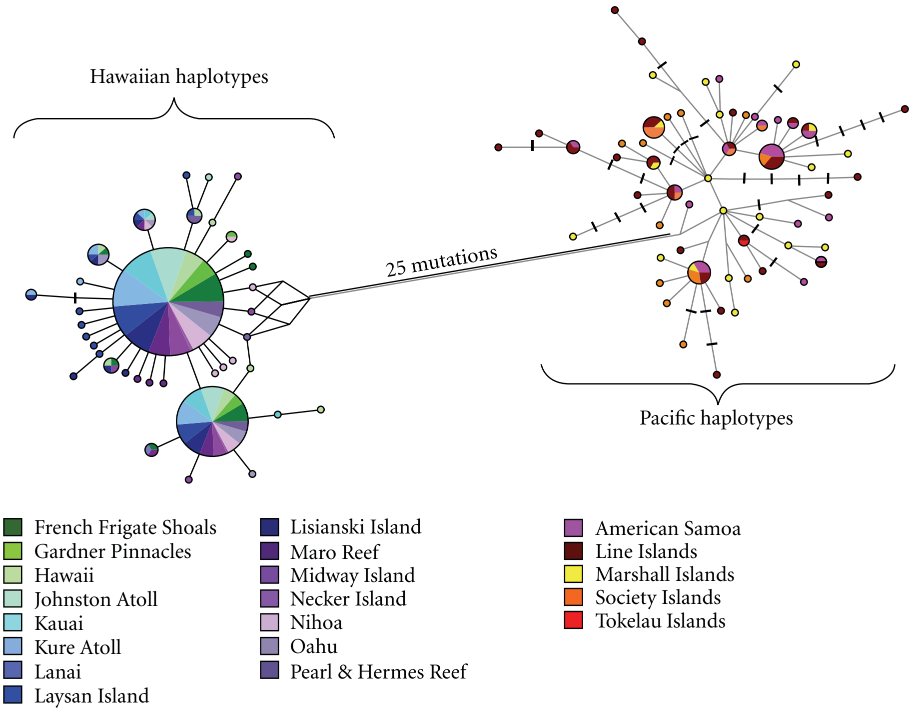


FIGURE 2: Median-joining statistical parsimony network based on 797 bp of mitochondrial cyt *b* sequence data ($N = 544$) from *Acanthurus nigroris* sampled across the Pacific. Each circle represents a haplotype, and its size is proportional to its total frequency. Branches represent a single nucleotide change and black crossbars indicate unsampled haplotypes; colors denote collection location as indicated by the embedded key. It should be noted that there were no shared haplotypes between Hawaiian (including Johnston Atoll) and the remaining Pacific populations, which form two distinct clades separated by 25 mutational steps (corrected sequence divergence, $d = 4.12\%$; [55]).

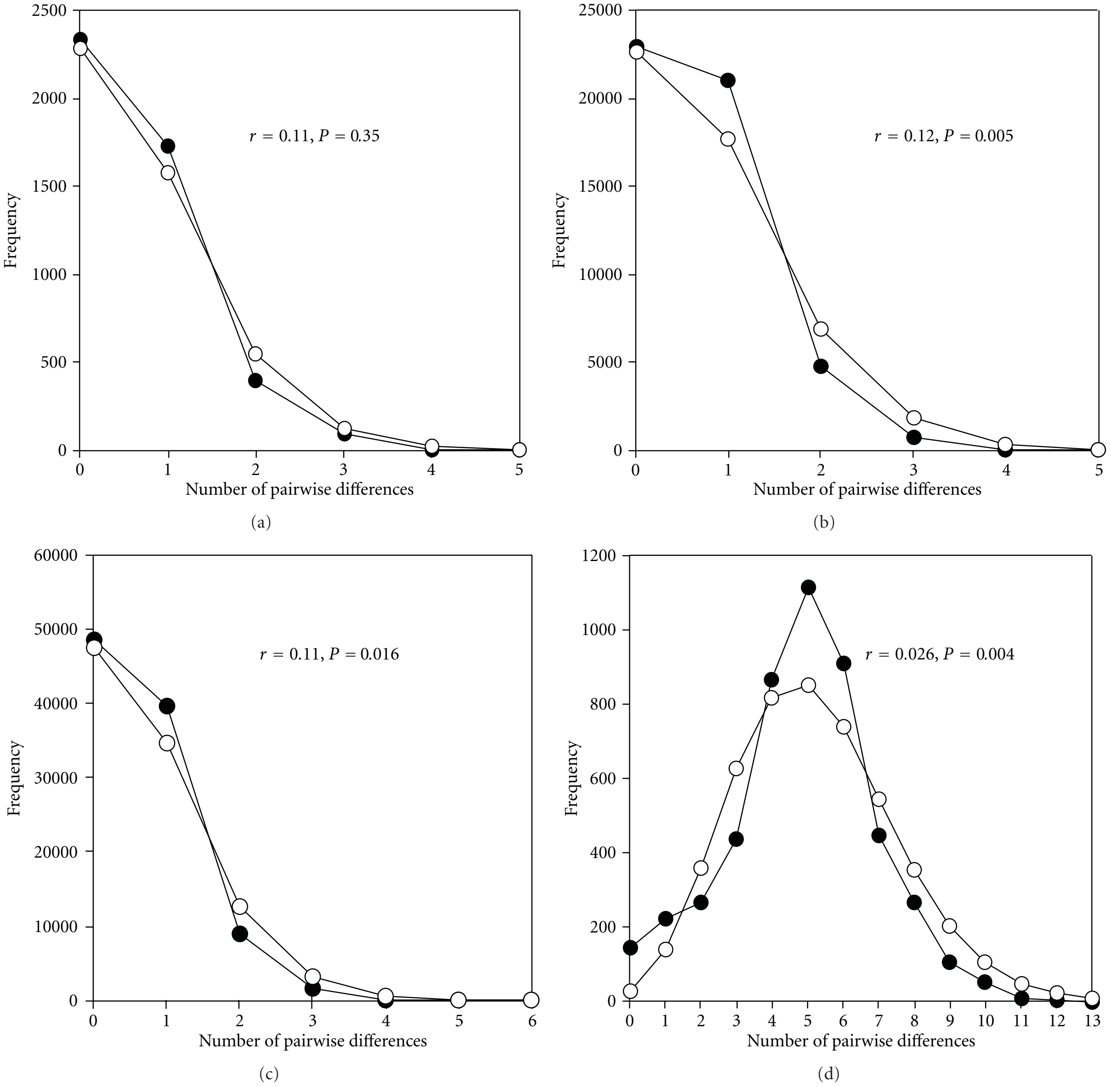
with Bayesian methods. Migration was by far the greatest within the Pacific and Hawaiian regions and not surprisingly low between regions (Table 4). Indeed, based on a genetic distance of 25 mutational steps, the number of estimated migrants from the Hawaiian archipelago to the rest of the Pacific (and vice versa) approaches zero. Within Hawaii in particular, there was a modest bias in migration from the MHI to the NWHI ($Nm = 35.19$, 95% CI = 0–162) versus from the NWHI to the MHI ($Nm = 22.99$, 95% CI = 0–132). Moreover, the number of migrants per generation moving from Hawaii to Johnston Atoll (from MHI: $Nm = 3.69$, 95% CI = 0–26.01; from NWHI: $Nm = 3.22$, 95% CI = 0–24.65) was more than an order of magnitude lower than migration from Johnston to Hawaii (to MHI: $Nm = 62.11$, 95% CI = 4.79–197; to NWHI: $Nm = 62.56$, 95% CI = 3.83–190), indicating that gene flow is biased towards rather than away from the Hawaiian archipelago. The posterior distributions for all parameters were also consistent over multiple runs, thus indicating sufficient convergence to interpret values [78].

4. Discussion

All genetic analyses outlined above support the conclusion that Hawaiian *A. nigroris* represents an ancient evolutionary separation from those sampled elsewhere in the Pacific Ocean. Genetic distance among these distinct groups is comparable to or greater than comparisons among other congeneric pairs of reef fishes [79–82], which indicates independence between regions. On the other hand, we found that with few exceptions, there were high levels of genetic connectivity within Hawaii as well as among all other sampled Pacific island populations. Johnston Atoll also has a significant population genetic distinction from many, but not all Hawaiian samples (see Table 3), with implications for the colonization of Hawaiian reefs.

4.1. Gene Flow in Hawaii. One objective in this study was to characterize genetic structure within the Hawaiian archipelago (2600 km from Kure Atoll to the island of Hawaii); throughout this region, we found little evidence for population genetic differentiation of *A. nigroris*. The existence of haplotypes shared across vast distances in Hawaii indicates that populations from each of these separate islands either freely exchange propagules or have done so in the recent past.

We are particularly interested in whether fish sampled in the MHI are connected to those in the NWHI, the largest marine conservation area under US jurisdiction. Based on our genetic results here, we cannot exclude this possibility. Although the short-term success of the NWHI monument in protecting regional biodiversity depends on enforcement within the reserve itself, long-term persistence of these reef fish populations also requires connectivity with other sites. The high genetic connectivity of *A. nigroris* detected within the Hawaiian archipelago indicates that movement of



(a) (b) (c) (d)

Figure 3: Mismatch distributions of mitochondrial cyt *b* sequence data from *Acanthurus nigroris* from (a) all Main Hawaiian Island (MHI) populations ($N = 92$ individuals), (b) all Northwest Hawaiian Island (NWHI) populations ($N = 315$ individuals), (c) the entire Hawaiian archipelago (including Johnston Atoll, $N = 441$ individuals), and (d) all remaining Pacific populations ($N = 98$ individuals). Observed and simulated pairwise differences calculated in *ARLEQUIN vers.* 3.1 are represented by lines drawn through black and open circles, respectively. Harpending's raggedness index (r) and associated P values are shown for each dataset.

fish larvae from the NWHI may supply adjacent fisheries, although high exploitation rates in the MHI could erode any such beneficial effects. High human population density, along with the immediate effects of urbanization (i.e., increased sediment, nutrients, and pollutants) and unregulated fishing, have depleted MHI fish fauna [40, 83]. Total fish biomass of large apex predators, a common indicator of healthy coral reef ecosystems, is also more than an order of magnitude higher in the uninhabited NWHI [40], as well as elsewhere in the Pacific [83–85].

If the lack of genetic structure observed throughout the Hawaiian archipelago is the result of life-history traits that differentially affect larval dispersal in reef fishes, comparisons among published genetic surveys might help resolve why some species appear to exchange propagules over long distances and others do not (Table 5). Here we show that 6 out of the 14 species surveyed throughout Hawaii display clear genetic breaks between sites in the NWHI versus MHI, but that there is no obvious correlation between genetic structure and pelagic larval duration (PLD), reproductive strategy,

Table 4: Strength and direction of gene flow for *Acanthurus nigroris:* (1) between the MHI ($N = 92$ individuals), NWHI ($N = 278$ individuals), and Johnston Atoll ($N = 34$ individuals), (2) among all remaining Pacific populations ($N = 98$), and (3) between Hawaiian and Pacific populations by pooling all sampled individuals (Hawaii, $N = 445$; Pacific, $N = 99$). Values are reported as the mean effective number of migrants (Nm) per generation taken from ten independent runs.

		Number of immigrants per generation into receiving population		
	Comparison	2.5% percentile	Mean	97.5% percentile
Among regions (Hawaii versus Pacific)	Hawaii into Pacific	0	0.71	3.19
	Pacific into Hawaii	0	0.34	1.63
Among populations[a] (within Hawaii)	MHI into NWHI	0	35.19	162.00
	NWHI into MHI	0	22.99	132.00
	MHI into JOH	0	3.69	26.04
	JOH into MHI	4.79	62.11	197.00
	NWHI into JOH	0	3.22	24.65
	JOH into NWHI	3.83	62.56	190.00
Among populations[a] (within Pacific)	AS into LI	0	11.94	54.80
	AS into MI	0	20.87	63.20
	AS into SI	0	22.91	66.00
	LI into AS	0	13.76	54.40
	MI into AS	0	7.14	37.60
	SI into AS	0	10.58	50.40
	LI into MI	0	16.17	53.60
	LI into SI	0	18.33	56.80
	MI into LI	0	6.40	35.60
	SI into LI	0	8.38	48.40
	MI into SI	0	9.18	39.60
	SI into MI	0	14.62	53.20

AS: American Samoa; JOH: Johnston Atoll; LI: Line Islands; MHI: Main Hawaiian Islands; MI: Marshall Islands; NWHI: Northwest Hawaiian Islands; SI: Society Islands.

[a] Samples from Necker Island ($N = 3$), Lanai ($N = 1$), and the Tokelau Islands ($N = 1$) were omitted from these analyses.

or habitat preference. Furthermore, there is no agreement among even closely related surgeonfish species with similar life-history characteristics. Indeed, one species (*Ctenochaetus strigosus*) shows genetic structure within Hawaii, whereas mtDNA of the other surgeonfish species considered, including *A. nigroris*, do not (*Acanthurus nigrofuscus* and *Zebrasoma flavescens* [38]; see [39]). Clearly connectivity between the MHI and NWHI needs to be evaluated on a case-by-case basis, incorporating the relevant facets of life history and ecology where possible (e.g., [86]); other factors not considered here (i.e., timing of reproduction, larval behavior, and ecological requirements) warrant further investigation. Indeed, several recent reports have drawn links between reef fish ecology and dispersal, phylogeography, and speciation [16, 86–89].

The estimates of gene flow generated here and elsewhere are useful in the design of marine reserves. Such gene flow estimates based on F (or Φ) statistics, however, are subject to several caveats [90]. Rare dispersal may be sufficient to ensure genetic homogeneity over evolutionary time scales, and so AMOVA analyses cannot distinguish whether genetic similarity among sampling sites is due to ongoing gene flow or incomplete lineage sorting (i.e., recent isolation). In some cases, supplementation with physical tagging can solve this problem [12, 29], but such treatments are outside the scope of this study. We instead turn to Bayesian estimation of migration rates using coalescent procedures in MIGRATE [69], which clearly show elevated migration within the Hawaiian and Pacific regions in comparison to that between regions (Table 4). MIGRATE results also support an emerging trend for northwestward flow of larvae from the depleted reefs of the MHI into the healthy NWHI (i.e., existing MPA acts as a sink rather than a source; [91, 92]). Although *MIGRATE*-based estimates of gene flow based on a single molecular marker should be treated with caution, we are here interested in relative differences between regions and not absolute values. Therefore, these findings, along with complimentary data based on multi-disciplinary research in other taxa (e.g., genetics, mark-recapture, and oceanographic modeling), should be considered by managers in the design of future marine reserves in the MHI.

4.2. Johnston Atoll and the Colonization of Hawaii. Another objective in this study was to test for recent or ongoing genetic exchange between Hawaii and the rest of the Central Pacific. Indeed, the Hawaiian archipelago is separated from

Table 5: Surveys of intraspecific genetic structure (Φ_{ST} or F_{ST}) in reef fishes sampled within the entire Hawaiian archipelago (i.e., Main Hawaiian Islands and Northwest Hawaiian Islands). Species common (and scientific) name, marker type (and mtDNA gene or number of nuclear loci), genetic structure, ecological differences (pelagic larval duration, PLD; Habitat type) between the study species, and references are listed here.

Species	Marker type	Genetic structure?	Genetic break	Global (or pairwise) Φ_{ST} or F_{ST}	P value	PLD (days)	Reproduction	Habitat type	Reference
Bigscale soldierfish (*Myripristis berndti*)	mtDNA (Cyt *b*)	No	N/a	0.00040	> 0.05	55	N/a	Subtidal reef flats to outer reef slopes	Craig et al. [36]
Blueline surgeonfish (*Acanthurus nigroris*)	mtDNA (Cyt *b*)	No	N/a	0.011	0.073	55 to 60	Group, broadcast spawning	Reef and rubble (1 to 90 m)	This study
Blue-striped butterflyfish (*Chaetodon fremblii*)	mtDNA (Cyt *b*)	No	N/a	−0.014	0.41	N/a	Pair, broadcast spawning	Shallow reef	Craig et al. [37]
Brown surgeonfish (*Acanthurus nigrofuscus*)	mtDNA (Cyt *b*)	No	N/a	−0.0060	> 0.05	55 to 60	Broadcast spawning	Reef and rubble	Eble et al. [38]
Hawaiian gregory (*Stegastes fasciolatus*)	Allozymes (8)	No	N/a	0.0010 to 0.0050	N/a	25	Demersal eggs	Reef and rock	Shaklee and Samollow [129]
Hawaiian gregory (*Stegastes fasciolatus*)	mtDNA (control)	Yes	NWHI versus MHI	0.093 to 0.10	< 0.05	25	Demersal eggs	Reef and rock	Ramon et al. [130]
Hawaiian grouper (*Epinephelus quernus*)	mtDNA (control)	Yes	NWHI versus MHI	−0.007 to 0.043	0.01	40	Group, broadcast spawning	Reef and rubble	Rivera et al. [131]
Milletseed butterflyfish (*Chaetodon miliaris*)	mtDNA (Cyt *b*)	No	N/a	−0.0050	0.66	N/a	Group, broadcast spawning	Shallow reef	Craig et al. [37]
Milkfish (*Chanos chanos*)	Allozymes (9)	Yes	Oahu versus Hawaii	0.000080 to 0.0041	N/a	14 to 21	Group, broadcast spawning	Shallow reef/ estuarine (1 to 30 m)	Winans [87]
Pebbled butterflyfish (*Chaetodon multicinctus*)	mtDNA (Cyt *b*)	No	N/a	−0.0080	0.82	N/a	Pair, broadcast spawning	Shallow reef	Craig et al. [37]
Pink snapper (*Pristipomoides filamentosus*)	Allozymes (5)	No	N/a	0.0010 to 0.011	N/a	60 to 120	Group, broadcast spawning	Reef and rock (180 to 270 m)	Shaklee and Samollow [129]
Spotted surgeonfish (*Ctenochaetus strigosus*)	mtDNA (Cyt *b*)	Yes	P and H and Maro versus rest of islands	0.034 to 0.074	0.041 to 0.008	55 to 60	Group/pair, broadcast spawning	Shallow reef	Eble et al. [38]
Undulated moray (*Gymnothorax undulatus*)	mtDNA (Cyt *b* and COI)	Yes	Maro versus Hawaii and Oahu	0.060 to 0.10	< 0.05	Up to 730	Pair mating	Reef and rock (1 to 100 m)	Reece et al. [88]
White-spotted damselfish (*Dascyllus albisella*)	mtDNA (control)	Yes	NWHI versus MHI	0.033 to 0.72	< 0.05	27	Pair, broadcast spawning	Shallow reef	Ramon et al. [130]

Table 5: Continued.

Species	Marker type	Genetic structure?	Genetic break	Global (or pairwise) Φ_{ST} or F_{ST}	*P* value	PLD (days)	Reproduction	Habitat type	Reference
Yellow-edged moray (*Gymnothorax flavimarginatus*)	mtDNA (Cyt *b* and COI)	No	N/a	−0.070 to 0.030	> 0.05	Up to 730	Pair mating	Reef and rock (1 to 100 m)	Reece et al. [88]
Yellow tang (*Zebrasoma flavescens*)	mtDNA (Cyt *b*)	Yes	Hawaii	0.077 to 0.17	0.034 to 0.001	55 to 60	Group, broadcast spawning	Reef and rubble (1 to 80 m)	Eble et al. [38]
Yellow tang (*Zebrasoma flavescens*)	Microsatellite (14)	Yes	Multiple	−0.010 to 0.042	< 0.001	55 to 60	Group, broadcast spawning	Reef and rubble (1 to 80 m)	Eble et al. [132]

Abbreviations: MHI: Main Hawaiian Islands; NWHI: Northwest Hawaiian Islands; P and H: Pearl and Hermes Reef.

other Central Pacific archipelagos by a minimum deep water gap of *ca.* 1400 km. The Line Islands directly south of Hawaii represent the closest archipelago, and so this island chain has been suggested as a source of colonizing fishes. Gosline [63] proposed that at low sea level stands associated with glaciations periods, the North Equatorial Current (and Countercurrent) may have been deflected by the Line Islands, providing greater opportunities for colonization into Hawaii. Johnston Atoll has also been forwarded as a key gateway (i.e., stepping stone) for larvae dispersing into Hawaii given its intermediate location (minimum distance of 865 km) and east/west prevailing current system [63, 93]. In support of this possibility, our *MIGRATE* analysis indicates an order of magnitude greater gene flow from Johnston to Hawaii, rather than in the opposite direction (Table 4). Subtle (but overlapping) meristic differences between fish collected from Johnston versus all Hawaiian locations [48], however, along with concordant population-level isolation observed in this study, indicate that Johnston may simply serve as the southernmost outpost of Hawaiian *A. nigroris* [94]. Indeed, Johnston is genetically divergent from most (i.e., 9 out of 12 comparisons significantly different; pairwise Φ_{ST} range: 0.043 to 0.19) but not all Hawaiian sampling sites (pairwise Φ_{ST} range: 0.0055 to 0.029).

The transport of larval fishes from the West Pacific via the Kuroshio extension of the North Pacific Equatorial Current has also been suggested as an alternative dispersal corridor into Hawaii [94, 95]. This possibility is supported by the discovery of some West Pacific fishes in the NWHI, including the Japanese angelfish (*Centropyge interruptus*; [96, 97]) and the splendid perch (*Grammatonotus macrophthalmus*; [98]). Indeed, 4.6% (57 species) of the Hawaiian fish fauna have ranges restricted to the Western North Pacific and Hawaiian Islands [98]. Using phylogenetic methods, Craig et al. [37] also showed that two endemic Hawaiian butterflyfish (*Chaetodon fremblii* and *Chaetodon miliaris*) groups with ancestral species in the West Pacific. We feel that this alternative colonization pathway is unlikely for *A. nigroris,* however, because this species is absent from the Pacific region west of Micronesia (i.e., China, Indonesia, Japan, Philippines, and Taiwan). Hence a South Pacific origin, as proposed by Gosline [63], seems more likely in this case. That said, our analysis is based on extant populations only, with the observed phylogenetic separation of Hawaiian and Pacific fish being too old to provide clues; the conclusion of a southern colonization pathway into Hawaii must therefore be regarded as provisional.

4.3. Endemism in Hawaii.

The possibility of an endemic surgeonfish species in Hawaii is not surprising given that this Pacific archipelago supports many endemic reef fishes (25%; [31]). Although nuclear loci were not considered here, high levels of mtDNA differentiation between Hawaiian and Pacific *A. nigroris* (Table 2) is concordant with differences in morphology. More than half a century ago, Randall [48] noted variation in dorsal fin rays (Hawaii, range =23 to 26; Pacific, range =24 to 27) and anal soft rays (Hawaii, range =22 to 24; Pacific, range =22 to 25), as well as nonoverlapping gill raker counts (Hawaii, range =26 to 31; Pacific, range =21 to 25) between regions, although this morphological difference was not used to distinguish species at that time due to identical coloration. With the new genetic information provided here, a reclassification of this species is proposed in a companion paper, which includes a Hawaiian endemic (*A. nigroris*) and a widespread Pacific form (resurrected *A. nigros*; [99]). Given that other members of the genus *Acanthurus* show no genetic differentiation between Hawaii and elsewhere in the Pacific [39], what then might explain the apparent isolation of *A. nigroris*?

Several factors may contribute to the generation of endemic shore fishes. One conventional possibility is allopatric speciation, in this case by marine barriers that differentially impact larval dispersal [100]. Larvae must travel vast distances to either colonize or disperse outside the Hawaiian archipelago [94]. While some species may readily overcome these large stretches of open ocean, rare colonization events by a few individuals, coupled with natural selection (i.e., local adaptation, which may inhibit further gene flow; [101]) or the genetic consequences of variance in reproductive success (sweepstakes recruitment; [102]), could prompt rapid speciation [103]. Mesoscale eddy formation, upwelling zones, and sustained wind patterns may then enhance the local retention of fish larvae at oceanic islands and thus promote isolation between incipient species.

Several studies have highlighted the genetic distinctiveness of Hawaiian fishes relative to other locations in the Pacific Ocean ([104–107] but see [39]). This is in contrast to reef fish populations within the Hawaiian archipelago that exchange propagules across the relatively short distances between neighboring reefs. High genetic connectivity between adjacent reefs may also explain the lack of adaptive radiation among Hawaiian fishes [108]. For example, few closely related marine species (i.e., sister taxa) cooccur in Hawaii [109, 110], and so most Hawaiian endemics are paired with widespread Indo-Pacific taxa in phylogenetic analyses (e.g., [37]).

The alternative hypothesis of speciation along ecological boundaries has been applied to explain the extremely high biodiversity on coral reefs [16, 82, 111]. While natural selection for habitat preference and other life-history traits is undoubtedly influencing the evolutionary pathways of Hawaiian fauna, we feel that ecological components are probably not driving speciation within *A. nigroris*. The evidence from comparisons of Johnston Atoll and Hawaiian locations indicate that 865 kilometers is near the limit of larval dispersal for this species. Indeed, the closest Hawaiian island, French Frigate Shoals, shares two common haplotypes with Johnston and is not genetically different, a pattern also apparent in other reef fishes [100]. The nearest alternate sites for dispersal and colonization are found in the Northern Line Islands (Kingman Reef and Palmyra Atoll), a minimal distance of 1385 km (see [93]). That said, our sample of *A. nigroris* from the Line Islands has been isolated from the Hawaiian population for approximately 2 my based on conventional mutation rates. Although divergence time estimates from single-locus data should be interpreted with caution (see [112]), our approximation is consistent with phylogenetic studies of closely related reef fishes that diverged in the last one to five million years (e.g., [113]). Our approximation is also consistent with the emerging trend for most Hawaiian marine biota to be much younger than the formation of the Hawaiian archipelago itself [35, 37]. Thus, the observed genetic pattern for *A. nigroris* in Hawaii likely reflects a long history of rare colonization and peripatric isolation resulting in divergence from ancestral Pacific populations.

Regardless of the process that generates endemic species, there are many unrecognized reef fishes awaiting discovery. As we have shown here, genetic tools are instrumental in identifying unique evolutionary significant units (ESUs, *sensu* [114]), which provide a phylogenetic framework for specifying taxa with highly restricted gene flow at the level of the species. Genetic methods have uncovered cryptic evolutionary lineages in other reef fish families in Hawaii (*Canthigaster coronata,* [115]; *Cirrhitops fasciatus,* [116]; *Halichoeres ornatissimus,* [117]), in addition to elsewhere in the Indo-Pacific (*Discotrema monogrammum* and *Discotrema chrinophylum*, [118]; *Amphiprion melanopus*, *Cirrhilabrus punctatus*, *Labroides dimidiatus*, and *Pomacentrus moluccensis*, [119]; *Chaetodontoplus poliourus*, [120]; *Pictichromis dinar*, [121]; *Scarus ghobban*, [122]) and Eastern Pacific (*Epinephelus quinquefasciatus,* [123]). In the tropical Atlantic Ocean, 8 out of 15 surveyed reef fishes showed cryptic evolutionary partitions [124]. Cryptic species are aptly named because they often develop barriers to fertilization despite a lack of accompanying divergence in other aspects of morphology or ecology (for review see [125]). This therefore stresses the importance of conducting range-wide genetic surveys for existing species to identify marine biodiversity that may have been overlooked (e.g., [126]).

In conclusion, we identified genetic isolation and independent evolutionary trajectories of Hawaiian and Pacific *A. nigroris*, despite high connectivity within each region. The Pacific Blueline Surgeonfish can readily traverse the tens to hundreds of kilometers between reef habitats in the Hawaiian Archipelago (average distance =150 kilometers) and the hundreds of kilometers between reef habitats elsewhere in the Pacific (maximum distance =800 kilometers; [127]). This species appears to rarely disperse between Johnston Atoll and the Hawaiian Archipelago (average distance =1250 kilometers), and there is effectively no migration between the Hawaiian Islands and other locations in the Pacific that are *ca.* 1400 km away or more (i.e., Line Islands). While such dispersal is impressive (and daunting from a management perspective), several other groups of reef fishes can even exceed this, including pygmy angelfishes (genus *Centropyge*; [127]), unicornfishes (genus *Naso*; [7]), soldierfishes (genus *Myripristis*; [36]), and moray eels (genus *Gymnothorax*; [88]). The Pacific BlueLine Surgeonfish therefore joins a growing list of reef fishes (Table 5) for which high dispersal is coupled with broad habitat and feeding preferences, as well as a large geographic range. These dispersive species present a special challenge to wildlife managers because they exhibit connectivity on a scale that far exceeds the boundaries of any single jurisdiction. We suggest that genetic connectivity in the less dispersive corals and other reef architects may provide guidelines for regional ecosystem-level management [128], but the more dispersive reef fishes demonstrate the need for international cooperation.

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Research Article

Defining Boundaries for Ecosystem-Based Management: A Multispecies Case Study of Marine Connectivity across the Hawaiian Archipelago

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Determining the geographic scale at which to apply ecosystem-based management (EBM) has proven to be an obstacle for many marine conservation programs. Generalizations based on geographic proximity, taxonomy, or life history characteristics provide little predictive power in determining overall patterns of connectivity, and therefore offer little in terms of delineating boundaries for marine spatial management areas. Here, we provide a case study of 27 taxonomically and ecologically diverse species (including reef fishes, marine mammals, gastropods, echinoderms, cnidarians, crustaceans, and an elasmobranch) that reveal four concordant barriers to dispersal within the Hawaiian Archipelago which are not detected in single-species exemplar studies. We contend that this multispecies approach to determine concordant patterns of connectivity is an objective and logical way in which to define the minimum number of management units and that EBM in the Hawaiian Archipelago requires at least five spatially managed regions.

1. Introduction

Global catches of commercially fished species have declined by up to 90% under classic single-species fisheries models [1–3]. The high-profile failures of fisheries managed for maximum sustainable yield has led to widespread interest in a shift toward ecosystem-based management (EBM) of marine resources (reviewed by [4]). EBM can be broadly defined as an integrated approach that considers the entire ecosystem, including linkages and the cumulative impacts of all human activities within and as part of the system. As such, EBM is explicitly place-based and adaptive in nature, and therefore particularly attractive for management. In recognition of the need for explicit boundaries in ecosystem-based management, Spalding et al. [5] divided the oceans into 232 ecoregions. However, marine ecosystems are highly complex, with many linkages and feedbacks that occur across multiple scales of space and time in ways that have proven difficult to predict [4]. Existing approaches to EBM in marine systems include spatial control of human activities through the use of marine protected areas (MPAs) and/or ocean zoning, changes in governance, monitoring and evaluation via ecosystem indicators derived from multiple disciplines (e.g., oceanography, ecology, economics, political science, and sociology), risk assessment, and precautionary adaptive management [6]. Successful spatial management requires a complex system of zones, each of which seeks to match resource exploitation with biological productivity, local population levels, and socioeconomic payoffs [7]. Delineation of the appropriate spatial scales for management zones within a specific management network requires a detailed understanding of dispersal pathways and population connectivity (reviewed by [8–10]). Despite the central role of dispersal and connectivity in sustaining marine populations, our understanding of these processes is still largely underdeveloped, and "a strong commitment to understanding patterns of connectivity in marine populations will clearly be necessary to guide the practical design of networks of marine reserves" [10, p.113]. In effect, managers cannot practice EBM if they do not know the boundaries of the corresponding ecosystems.

Understanding connectivity in the sea is complicated by the fact that most marine organisms have a biphasic life cycle with benthic or sedentary adults and dispersing eggs and/or larvae, which may be pelagic for as little as a few minutes to more than a year. Following the pelagic phase, larvae settle onto a patch of suitable habitat, where they may remain throughout their lives, and in cases of sessile organisms such as corals, the act of settlement includes permanent attachment to a single site. Thus, long-distance dispersal is accomplished almost exclusively during the pelagic larval phase, which can potentially span large expanses of open ocean [11–15]. On the other hand, species which lack a pelagic larval phase, such as marine mammals and elasmobranchs, have the potential to range widely throughout the oceans and face few obvious barriers to dispersal. Despite the potential for long-distance movement in most marine species, the geographic limits of such dispersal remain uncertain, because it is virtually impossible to track microscopic juveniles during the pelagic phase (reviewed by [16]), making indirect methods of quantifying larval dispersal particularly attractive (reviewed by [8, 17–19]). Intuitive expectations that larval dispersal is a function of pelagic larval duration (PLD) are not supported by recent meta-analyses ([20–25]). Despite considerable research, the scale of larval dispersal and the boundaries for EBM remain nebulous due to the complex interaction of larval biology, oceanographic regimes, habitat quality and distribution, and the variability of each through time [26].

Delineating management units is further complicated by the fact that single-species studies of genetic connectivity are often contradictory. Analyses of connectivity frequently focus on single-species exemplars which are then extrapolated to the level of the community, but the utility of exemplars in such cases is limited; even among closely related species with similar ecology, life histories, and geographic ranges, the corresponding patterns of connectivity can be very different [27, 28]. In other cases, animals with highly divergent biology can have surprisingly similar patterns of connectivity [26]. Such variability among species appears to be the rule rather than the exception, and has led to a call for multispecies comparisons of connectivity across trophic levels to broadly define the boundaries for management, and to determine shared avenues of exchange among ecosystems. Due to logistical difficulties in completing such comparisons in marine habitat, few such studies exist (e.g., [29–31]). The linear nature of the Hawaiian Archipelago (Figure 1) provides an excellent forum for resolving shared barriers to gene flow across species and trophic levels, with the goal of developing a geographic framework for EBM.

The Hawaiian archipelago stretches more than 2600 km in length and consists of two regions: the Main Hawaiian Islands (MHI) which are high volcanic islands with a heavy human presence and the Northwestern Hawaiian Islands (NWHI) which are a string of tiny islands, atolls, shoals, and banks that are essentially uninhabited. Due to their isolation, the roughly 4,500 square miles of coral reefs in the NWHI are among the healthiest and most extensive remaining in the world [32] with abundant large apex predators, a high proportion of endemic species [33, 34], and few human impacts compared to the MHI [18, 35]. In contrast, coral reefs in the MHI are under considerable anthropogenic pressure from the 1.29 million residents (with over 900,000 of those living on the island of O'ahu) and the more than 7 million tourists that visit the state annually. Coral reefs in many of the urban areas and popular tourist destinations have sustained significant impacts, and many show ongoing declines [35–37]. The primary impacts to coral reefs in the MHI are local and anthropogenic, including coastal development, land-based sources of pollution, overfishing, recreational overuse, and alien species. In contrast, the primary stressors in the NWHI are global in nature, including climate change, ocean acidification, and marine debris [18, 35–37].

On June 15, 2006, the President of the United States signed a proclamation creating the Papahānaumokuākea Marine National Monument (PMNM), encompassing the entire NWHI, at the time the world's largest marine protected area (MPA). The monument designation affords the NWHI the greatest possible marine environmental protection under United States law. The PMNM spans nearly 140,000 square miles and is home to more than 7,000 currently described species including fishes, invertebrates, algae, marine mammals, and birds although many biologists believe that this is a gross underestimate of the true biodiversity in the region [38]. While the full extent of PMNM biodiversity is unknown, about 25% of the known species are found nowhere else on Earth [39–42]. In 2010, the PMNM was inscribed to the UNESCO World Heritage List, the first U.S. site to be designated in over 15 years. The remote PMNM and surrounding waters became the first primarily marine site to be named in the United States, and the first primarily marine location in the world to be designated as a mixed site for both its outstanding natural and cultural value.

Our research group has embarked on a genetic survey of approximately 60 species of reef-associated fishes, gastropods, crustaceans, echinoderms, cnidarians, and marine mammals, designed to address the issue of population connectivity across the Northwestern and Main Hawaiian Islands and linkages of the Hawaiian Archipelago to other locations throughout the Central Pacific. This effort seeks to inform ecosystem-based management of the PMNM and to evaluate the potential for spillover from the protected area of

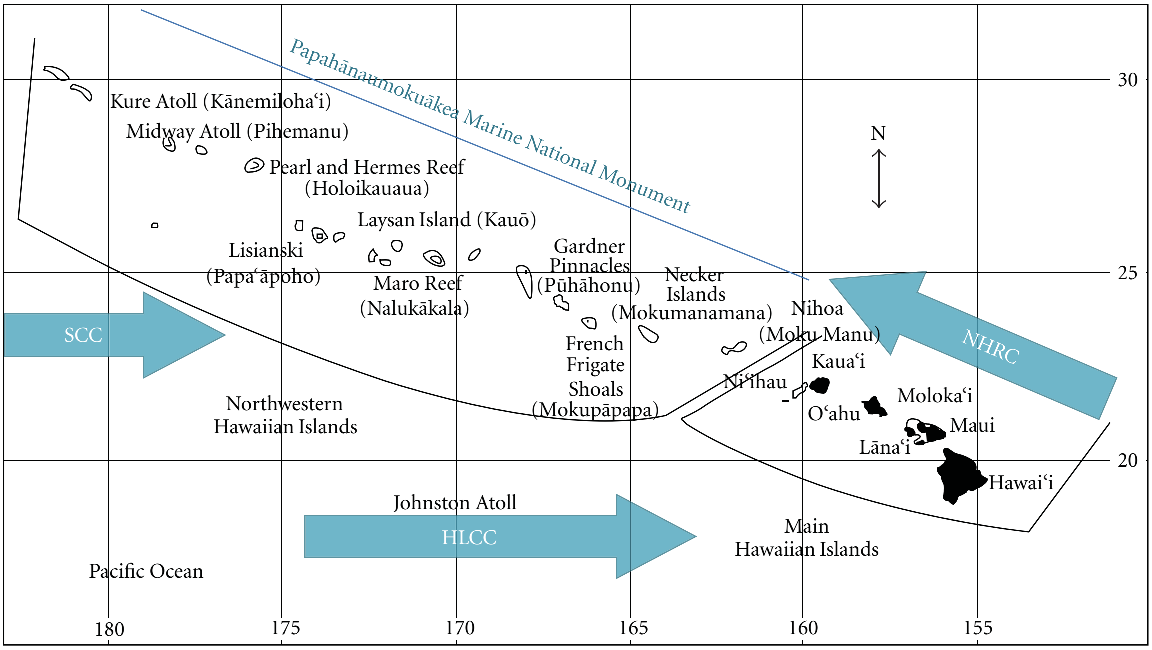

Figure 1: Map of the Hawaiian Archipelago with major currents denoted: the North Hawaiian Ridge Current (NHRC), the Hawaiian Lee Countercurrent (HLCC), and the Subtropical Countercurrent (SCC). The lines around the two regions of the archipelago highlight the islands, atolls, and banks protected within the Papahānaumokuākea Marine National Monument in the Northwestern Hawaiian Islands (NWHI) and the inhabited high islands of Main Hawaiian Islands (MHI) with each of the 15 primary target areas for collection labeled. For purposes of this analysis, the islands of Lāna‘i, Maui & Moloka‘i are treated as a single site within the Maui Nui complex of the MHI. Listed from northwest to southeast, these are: Kure Atoll (Kānemiloha‘i), Midway Atoll (Pihemanu), Pearl and Hermes Reef (Holoikauaua), Lisianski (Papa‘āpoho), Laysan Island (Kauō), Maro Reef (Nalukākala), Gardner Pinnacles (Pūhāhonu), French Frigate Shoals (Mokupāpapa), Necker Island (Mokumanamana), Nihoa (Moku Manu), Ni‘ihau, Kaua‘i, O‘ahu, Maui Nui, and Hawai‘i.

the NWHI to the heavily populated and exploited MHI. Here we take a molecular genetic approach to infer patterns and magnitude of connectivity in a suite of taxonomically diverse reef-associated species and present preliminary results from 27 species, a subset of the 60 or so target species being collected to understand connectivity across the Hawaiian Archipelago and aid in defining the spatial scale over which EBM should be considered. Although EBM is explicitly place-based, and superficially the definition of an ecosystem seems straightforward, the resolution of geographic boundaries is confounded by obscure biological and oceanographic processes in most marine locations that complicates direct application to management (reviewed by [43]). In managing reefs in the Hawaiian Archipelago, what exactly constitutes a coral reef ecosystem? Is it a reef complex, an island or atoll, an arbitrary geographic distance, a series of adjacent islands and atolls, or the entire Archipelago that is the appropriate geographic scale for management? This work seeks to resolve and quantify the direction and magnitude of exchange among reef habitats across a broad taxonomic spectrum, and to use this information to define objective boundaries, as a necessary prerequisite for the implementation of EBM.

2. Methods

2.1. Sample Collection, DNA Extraction, and Amplification. Tissue samples for DNA analyses were collected from approximately 60 species at as many of the 16 primary islands and atolls as possible in the Hawaiian Archipelago, including the remote and tightly regulated NWHI (Figure 1). It is important to note that sampling remote areas of the Pacific is difficult and expensive and requires extensive permitting and voyage planning compared to collections on the mainland; permitted collections are limited to a maximum of 50 individuals per species at each site, and there are only 1 or 2 days per location, during which the researchers are at the mercy of the weather as to whether or not they can even launch dive boats. Thus, we do not have complete coverage for all species, but in addition to the two species available in the published literature (e.g., [44]), we have currently analyzed 25 additional species (total 27, Tables 1 and 2) from many of the islands and atolls across the Hawaiian Archipelago (Figure 1). Details for the sampling protocols, tissue preservation, DNA extraction, and amplification can be found in Iacchei and Toonen [45] and Skillings and Toonen [46]. Briefly, tissue biopsy samples were taken in the field and stored in either 20% dimethyl sulfoxide salt-saturated buffer [47] or >70% ethanol. DNA was extracted using either a commercially available extraction kit (e.g., Qiagen DNeasy), the chloroform extraction protocol described in Concepcion et al. [48] or a modified salting-out protocol [49]. Following extraction, DNA was stored at −20°C. Most studies were conducted with direct sequencing of a mtDNA fragment using the polymerase chain reaction

(PCR) as outlined in references from Table 1. In general, a segment of approximately 600–800 base pairs of the mtDNA cytochrome *b* (Cytb) was amplified from most of the fishes, and cytochrome oxidase subunit I (COI) was amplified from the majority of invertebrate species, but some used other mitochondrial or nuclear sequence regions or microsatellite markers (see Table 1 for details). PCR recipes and cycling conditions for individual species are provided in the publications cited in Table 1 and upon request from the authors. PCR products to be sequenced were treated with 1.5 units of Exonuclease I and 1.0 units of Fast Alkaline Phosphatase (ExoFAP, Fermentas) per 15 μL PCR products at 37°C for 60 minutes, followed by deactivation at 80°C for 10 minutes. DNA sequencing was performed with fluorescently–labeled dideoxy terminators on an ABI 3130XL Genetic Analyzer (Applied Biosystems) at the Hawai‘i Institute of Marine Biology EPSCoR Sequencing Facility. All specimens were initially sequenced in one direction and unique genotypes were confirmed by sequencing in the opposite direction. For analysis of microsatellite loci, amplification products were visualized on an ABI 3130XL Genetic Analyzer using GS500LZ size standards, and analyzed using GENEMAPPER 4.0 (Applied Biosystems).

2.2. Genetic Analyses. For each species, details of the analyses are provided in the studies cited in Table 1, or upon request from the authors. In brief, overall genetic variation was partitioned among sites as pairwise Φ_{ST} using the best fit model of sequence evolution, as determined by MODELTEST 3.7 [62], that could be implemented by ARLEQUIN 3.11 [63]. For most of the studies, F_{ST} was standardized for within population levels of heterozygosity [64, 65], and calculations of D_{est} [66] were done manually using formula macros in MICROSOFT EXCEL ([67] in review). The number and location of shared genetic breaks among species across the Archipelago are unchanged whether corrected or uncorrected F- statistics or D_{est} was used because the relative differences between these values are all highly correlated with our data set (data not shown). Because any set level of divergence selected is ultimately arbitrary, we use a significant pairwise F_{ST} among populations sampled on either side of the channel of interest as our metric of divergence. Significance of pairwise values was determined by permutation testing in Arlequin, with False Discovery Rate (FDR) correction for multiple tests [68] unless otherwise specified in the original publication (Table 1). Significant pairwise differences among adjacent islands, were overlaid visually on a map of the Hawaiian Archipelago (Figure 1) species-by-species. The number of significant pairwise differences among locations was summed across all 27 species and those that exceed random expectations (see below) are depicted in Figure 2.

2.3. Statistical Testing of Shared Genetic Barriers. Because not all species are collected in all locations, we looked only at the channels between adjacent islands where samples of that species were available on both sides so that a test for pairwise population differentiation was possible at that site. We initially excluded any sites for which there were fewer than 20 individuals from each location on adjacent sides of the channel being tested, but found that the presence and location of barriers was unaffected in these analyses with any sample size greater than 5 individuals per site (data not shown). Thus, in the interest of including as much data as possible in this comparison, we include all sites for which the sample size was 5 or more (Table 2). We observed a total of 73 significant pairwise differences among the 178 possible pairwise tests for these species (Tables 1 and 2). The distribution of these pairwise differences was tested using a χ^2 test with 13 degrees of freedom (14 between island channels); we calculate the expected number of the 73 pairwise differences that would occur, weighted by sample size between each island, at random within each channel. The validity of a shared genetic break at any given location was also tested using a χ^2 to determine if the number of observed significant pairwise differences across the species sampled at that location differed significantly from the null expectation that all detected breaks were distributed equally among the 14 interisland channels.

3. Results

Although each species differs in the particular pattern of population structure and the inferred magnitude of larval exchange among sites, some consistent genetic breaks are apparent among these divergent species (Figure 2). In particular, the data indicate four strong barriers to gene flow in the channels between: (1) the Big Island of Hawai‘i and Maui, (2) the islands of O‘ahu and Kaua‘i, (3) the MHI and NWHI, and (4) the far NW end and the rest of the NWHI chain around Pearl and Hermes Reef (Figure 2). The presence or absence and the strength of a given barrier vary among species (see references in Table 1). Likewise, there are some significant barriers that appear for only one or a few species, but do not appear in the majority of study organisms (e.g., Laysan Island for the sea cucumber, *Holothuria atra*, see Skillings et al. [56], or Gardner Pinnacles for the endemic grouper *Epinephelus (=Hyporthodus) quernus*, see Rivera et al. [51]).

Despite the vast differences in natural history among taxa, more than 50% of the species surveyed to date share the same four concordant barriers to gene flow across the Hawaiian Archipelago (Figure 2). Notably 8 of 19 species also show a break between O‘ahu and Maui Nui, but this partition is not significantly different from random expectations ($\chi^2 = 0.17$, df = 1, $p > 0.05$). Essentially, roughly 50% of the sampled species must share a genetic discontinuity in order to deviate from the random expectation of 5.2 significant differences in each channel ($\chi^2 = 4.4$, df = 1, $p < 0.05$). Other than the four significant breaks depicted in Figure 2, and the nonsignificant split between O‘ahu and Maui Nui, no other inter-island channel constitutes a barrier for more than 4 of the sampled species. Thus, with the caveat that additional sampling may yet demonstrate a fifth significant barrier between O‘ahu and Maui Nui, there are currently four significant shared barriers to gene flow that divide the Hawaiian Archipelago into a minimum of five distinct ecoregions with limited exchange. In stark contrast to those locations, other inter-island channels have

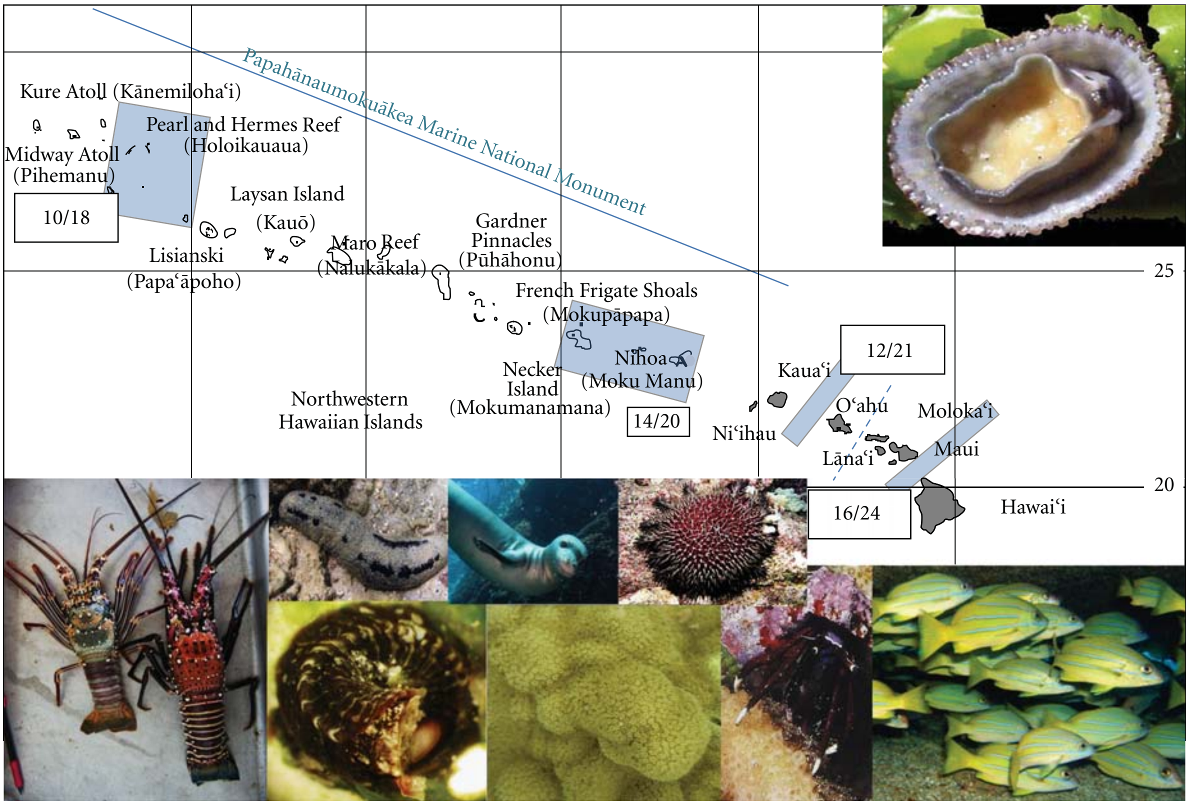

Figure 2: Map of the Hawaiian Archipelago with significant consensus genetic breaks among the 27 taxa listed in Table 1 overlaid as blue bars between islands. In each bar, the number of species that show evidence for restricted gene flow across the barrier is listed in the numerator, and the total number of species for which we have data across that geographic area is listed in the denominator. The total number of sites included for each species is variable because not all species have been collected or analyzed at each site. The dotted line between Maui Nui and Oʻahu highlights the location of the barrier that is shared by 8 of the surveyed species but is not significantly different than random expectations. The images include some of the species included in these analyses (left to right): *Panulirus penicillatus, Panulirus marginatus, Holothuria atra, Dendropoma rhyssoconcha, Monachus schauinslandi, Porites lobata, Acanthaster planci, Calcinus hazletti, Lutjanus kasmira, and Cellana sandwicensis* (photo credits to Derek Smith, Joe O'Malley, and the authors).

significantly fewer barriers than expected by chance (e.g., the region between French Frigate Shoals and Pearl & Hermes Atoll in the NWHI, $\chi^2 = 3.85$, df = 1, $p = 0.05$). This overall pattern of high connectivity among some locations and shared genetic barriers in others across the archipelago is significantly nonrandom ($\chi^2 = 56.18$, df = 13, $p < 0.0001$).

Distance alone is a poor predictor of the locations of these barriers to dispersal. The distance between areas that are isolated can be quite small (such as the ʻAlenuihāhā Channel between Hawaiʻi and Maui, ~45 km) whereas much larger distances between atolls in the NWHI generally show no consistent barriers to dispersal (for example Gardner Pinnacles is ~180 km northwest of French Frigate Shoals). Likewise, more of the significant barriers to dispersal are found in the geographically smaller (600 km) MHI with the significant absence of barriers occurring in the geographically larger (2000 km) NWHI. Because adjacent sites can be highly differentiated whereas more distant sites are not, relatively few species (7/27) show a significant signal of isolation-by-distance across the Hawaiian archipelago (see Table 2 for highlighted exceptions).

4. Discussion

These data are striking in that more than half of the species surveyed show significant concordant barriers to gene flow concentrated in the four highlighted regions of the Archipelago (Figure 2). Given the broad differences in taxonomy, life history, and ecology of the species surveyed, including limpets, sea cucumbers, vermetid tube snails, reef fishes, monk seals, and spinner dolphins (Table 1), there is no *a priori* reason to expect that patterns of connectivity would be shared among the majority of the species. However, the four shared barriers to dispersal highlighted here indicate that these species are responding to common factors that limit dispersal and delineate independent units in terms of connectivity over management-relevant time scales. We hypothesize that the dominant factors are likely abiotic as opposed to biotic, given the diversity of species with radically divergent life histories that share the pattern of isolation.

4.1. Discordance between Genetic and Oceanographic Predictions. The most obvious candidates for such physical

Table 1: Species of marine organisms, total sample size, total number of sites, genetic marker(s) used, and study citation for each of the organisms surveyed for population genetic structure across the Hawaiian Archipelago to date. Not all samples were included in subsequent analysis, therefore, the actual sample sizes by site for each species in this analysis are provided in Table 2. Abbreviations for genetic markers used are: SSR = microsatellites; NIS = nuclear intron sequence data; Cytb = cytochrome *b*; COI = cytochrome oxidase subunit I; COII = cytochrome oxidase subunit II; CR = control region.

Species name	Sample size	Number of sites	Marker	Reference
Fishes:				
(1) *Epinephelus* (=*Hyporthodus*) *quernus*	301	10	SSR, CR	Rivera et al. (see [50, 51])
(2) *Stegastes fasciolatus*	219	7	CR	Ramon et al. [44].
(3) *Dascylus albisella*	102	7	CR	Ramon et al. [44].
(4) *Ctenochaetus strigosus*	499	15	Cyt*b*	Eble et al. [52].
(5) *Zebrasoma flavescens*	528	15	Cyt*b*	Eble et al. [52, 53].
(6) *Acanthurus nigrofuscus*	305	11	Cyt*b*	Eble et al. [52].
(7) *Lutjanus kasmira*	385	9	Cyt*b*, NIS	Gaither et al. [54].
(8) *Squalus mitsukurii*	112	6	CR	Daly-Engel et al. [55].
Gastropods:				
(9) *Cellana exarata*	150	7	COI	Bird et al. [28].
(10) *Cellana sandwicensis*	109	6	COI	Bird et al. [28].
(11) *Cellana talcosa*	105	5	COI	Bird et al. [28].
(12) *Dendropoma gregaria*	176	15	COI	Faucci et al. (unpubl. data)
(13) *Dendropoma platypus*	143	15	COI	Faucci et al. (unpubl. data)
(14) *Dendropoma rhyssoconcha*	94	11	COI	Faucci et al. (unpubl. data)
(15) *Serpulorbis variabilis*	73	13	COI	Faucci et al. (unpubl. data)
Crustaceans:				
(16) *Calcinus haigae*	146	5	COI	Baums et al. (unpubl. data)
(17) *Calcinus hazletti*	179	12	COI	Baums et al. (unpubl. data)
(18) *Calcinus seurati*	161	4	COI	Baums et al. (unpubl. data)
(19) *Panulirus marginatus*	449	14	COII	Iacchei et al. (unpubl. data)
(20) *Panulirus penicillatus*	227	9	COI	Iacchei et al. (unpubl. data)
Echinoderms:				
(21) *Holothuria atra*	399	15	COI	Skillings et al. [56]
(22) *Holothuria whitmaei*	427	10	COI	Skillings et al. (unpubl. data)
(23) *Acanthaster planci*	338	11	CR	Timmers et al. [57]
Scleractinian:				
(24) *Montipora capitata*	551	13	SSR	Concepcion et al. (unpubl. data)
(25) *Porites lobata*	443	11	SSR	Polato et al. [58]
Marine Mammals:				
(26) *Monachus schauinslandi*	2409	8	SSR	Schultz et al. [59, 60]
(27) *Stenella longirostris*	386	8	SSR, CR	Andrews et al. [61].

barriers to gene flow are geographic distance and oceanic currents. For most species there are enigmatic restrictions to dispersal that appear to have little to do with geographic distance. Many of the studies listed in Table 1 provide cases of divergence among proximate sites in the face of lower divergence among more distant sites elsewhere in the archipelago. Regardless, the overall dataset indicates that much of the NWHI is well connected despite greater average distances among the sites whereas the MHI show greater structure on average despite geographic proximity. Although some species do show isolation-by-distance, there appears to be a substantial taxonomic effect because three of the seven cases are sister species of *Cellana* limpets, and two of the remaining four are scleractinian corals (Table 2). While we cannot rule out the role of distance in limiting dispersal within the Hawaiian Archipelago, the impact of distance on the probability of dispersal does not appear to be a simple linear effect for the majority of species surveyed to date. This discord is not particularly surprising given the complexity of oceanographic current patterns. Recent analyses of larval dispersal in the Southern California Bight showed that probability of exchange among sites was uncorrelated with

Table 2: Sample size per location (refer to Figure 1 for Hawaiian names of sites) for each of the 27 species included in the combined multispecies analysis of population genetic structure across the Hawaiian Archipelago to date. Locations with fewer than 5 individuals were excluded from all analyses and are not included here (see text). Species with * show a significant isolation-by-distance signature across the archipelago.

Species Name	Hawaiʻi (=Big Island)	Maui Nui	Oʻahu	Kauaʻi	Niʻihau	Nihoa	Necker Island	French Frigate Shoals	Gardner Pinnacles	Maro Reef	Laysan Island	Lisianski	Pearl & Hermes Reef	Midway Atoll	Kure Atoll
Hyporthodus (=Epinephelus) quernus	36	30	9	30		44	30		30	46		29	27		
Stegastes fasciolatus	27		42	49				24					15	20	42
Dascylus albisella	10		8					25					28	7	14
Ctenochaetus strigosus	102	100	40	28		29		37	29	31			33	32	38
**Zebrasoma flavescens*	146	122	35	42		20		40		26			29	33	35
Acanthurus nigrofuscus	33	65	39	26		39		33	28				28	6	9
Lutjanus kasmira	101	39	50	36			49	40		21				40	9
**Cellana exarata*	41	18		21		11	23	36							
**Cellana sandwicensis*	42	21		20			18	8							
**Cellana talcosa*	43	24		38											
Dendropoma gregaria	53	25	39	20			5	5	5	5		5	5		5
Dendropoma platypus	16	20	40	21		5	5	5	5	5	6		5	5	5
Dendropoma rhyssoconcha	29	24	25						6			5			
Serpulorbis variabilis	13	25	15	8											
Calcinus haigae	51	21													
Calcinus hazletti	21	31		12		7		34		33			22		11
Calcinus seurati	9	30	78	44											
Panulirus marginatus		19	48				56		56	53	53	36	47	29	46
Panulirus penicillatus	46	43		47			5	33		5		18	30		
Holothuria atra	30		24	30	5			28			12		37	35	23
Holothuria whitmaei	26			33				26			22		57	24	59
Acanthaster planci	106	81	25	24	30			13					27		
**Montipora capitata*	47	47	51			25		40		47	48	50	44	43	51
**Porites lobata*	23		16			18	21	23	34	33			44	21	22
Squalus mitsukurii	7		91		8										
Monachus schauinslandi	**54**					7		766			656	310	260	134	222
**Stenella longirostris*	79	59	40	32	45			33					47	119	51

geographic distance, but strongly correlated with a derived "oceanographic distance" including realistic annual water movement patterns across many years [26, 69].

In Hawai'i, however, the patterns of genetic differentiation do not generally match predictions for larval dispersal based on water movement information from either a two-dimensional Eulerian advection-diffusion model [70, 71] or a Lagrangian particle-tracking model [72, 73]. One of the primary predictions of both simulation models is that the average distance of larval dispersal is short, roughly on the order of 50–150 km, and that the Main Hawaiian Islands (MHI) ought to be consistently connected and well mixed whereas the NWHI ought to show a number of isolated populations [70, 71]. For a PLD of less than about 45 days, the larval dispersal simulations predict a majority of local recruitment of larvae to their natal island/atoll or the adjacent ones (see [51]). In stark contrast to the primary prediction of the available larval dispersal simulation models (a well-mixed MHI and comparatively patchy NWHI), the consensus finding across 27 taxa to date is the opposite: the MHI show far more population structure than any equivalent geographical scale within the NWHI, and the primary dispersal barrier predicted by Eulerian simulation models is located in the region of the NWHI in which there is a significant paucity of population structure among surveyed species (Figure 2). Possible reasons for oceanographic simulations failing to predict the structure observed in the empirical genetic data are many (reviewed by [22, 74, 75]), but given the number and diversity of taxa across which the pattern holds, the genetic inference of isolation between the four regions highlighted in Figure 2 is robust.

4.2. Multispecies Approaches to Measuring Connectivity. All connectivity studies face practical limitations in terms of the number of specimens, sample sites, and taxonomic scope of study, which is why the vast majority of studies to date have focused on one or a few exemplar species to draw generalizations. Exemplar species are an attractive compromise to guide conservation and management efforts given the imposing logistic and resources challenges of conducting connectivity studies on all species of management relevance. However, the utility of exemplar species depends on whether they represent the community as a whole. Unfortunately, in most cases where this assumption has been tested explicitly, the patterns of dispersal and genetic structure differ significantly and unpredictably even among closely related species with similar life histories (e.g., [28, 52, 54, 76–78]). Despite the perceived potential for long-distance dispersal and broad mixing in the ocean, many taxa show unique archipelagic diversity (e.g., [79]) and even finer scale population structure than expected (e.g., [31, 80]). Regardless of whether we compare within taxonomic groups or between them, some of the species we have surveyed (e.g., *Myripristis berndti*, *Centropyge loricula*, *Lutjanus kasmira*, *Acanthaster planci*, and *Calcinus* spp.) appear to live up to their expected potential for dispersal and show no significant population structure across the Central Pacific (see [54, 57, 81–84]). In contrast, other species that appear capable of extensive dispersal (*Epinephelus quernus*, *Ctenochaetus strigosus*, *Stenella longirostris,* and *Zebrasoma flavescens*) show significant population differentiation within the Hawaiian Archipelago [50, 52, 53, 61, 85] and island-by-island or in some cases even site-by-site differences in population structure (e.g., [28, 44] Faucci et al. unpubl. data). Despite the potential for wide dispersal, Christie et al. [85] use individual parentage analyses to document self-recruitment in the Yellow Tang (*Zebrasoma flavescens*) and illustrate that at least some larvae recruit to the same region of the Kona coastline from which they were originally spawned.

Such variability among species greatly complicates efforts to generalize management implications from single-species studies and severely restricts the utility of exemplar species for decision making in conservation and management. While there is a consistent push to move beyond single-species management plans and implement EBM at a national and international level (e.g., [86, 87]), the exact geographic scale at which EBM should be applied is seldom obvious, and the accumulating data indicate that studies of marine connectivity cannot be generalized easily for this purpose. It is clearly impractical to study every species individually, and even if we could, how would the connectivity matrix from all those species be combined into a single coherent data set to guide EBM? For example, the multispecies conservation plan for U.S. federal lands states: "conservation objectives will not be achieved with a single reserve or a single population. Rather, local populations widely scattered across the landscape, but connected by movement, will be necessary. Few of these populations will be large enough to avoid problems faced by small populations, such as extirpation due to stochastic factors and inbreeding depression. Connectivity maintenance is therefore one of the most critical aspects of multispecies conservation. Connectivity, however, is notoriously difficult to directly measure" [88, p.64]. A variety of landscape genetic approaches to identifying cryptic barriers to connectivity have been proposed (e.g., [69, 89, 90]), but with few exceptions (e.g., [26]) such work has also been conducted on single-species. The push to implement EBM highlights an explicit need for multi-species comparisons of connectivity across all trophic levels to define the boundaries for management and resolve shared avenues of exchange among ecosystems.

Due to resource constraints as well as the logistical difficulties in completing such multispecies comparisons, only a few such studies exist. The few explicit multispecies connectivity studies that have been conducted to date (e.g., [29–31]) all face the limitation that there is no generally accepted method by which to analyze the aggregate connectivity data. Thus, like the study presented here, the primary method of analyzing shared genetic breaks is by counting the number or proportion of species that share a genetic discontinuity among locations. For example, a survey of 50 coastal marine species along the west coast of North America concluded that a greater proportion of species show significant genetic differentiation between the central (40% of species between Monterey, CA and Cape Blanco, OR) and northern sites (33% of species between Cape Blanco and Sitka, AK) than between the southern sites

(15% of species between Monterey and Santa Barbara, CA; [30]). Likewise, a survey of 9 species of fish and 10 species of invertebrates in Indonesia defines partitions where more than two or three species share a phylogenetic break [31]. We have employed a similar approach with counting up shared genetic discontinuities in the data set, but elected to test whether these shared breaks deviate significantly from random. In our study, a surprisingly high number of species need to share a break to deviate significantly from random: even where 8 of the 19 species show differentiation between O'ahu and Maui Nui, that result was non-significant. The overall pattern of genetic divergence among sites within the Hawaiian Archipelago is highly non-random, with the central region of the NWHI having significantly fewer genetic breaks, and four individual channels emerge as having significantly more species sharing a break than expected at random (Figure 2).

There are substantial caveats to comparing F_{ST} and Φ_{ST} values directly among studies and marker classes (reviewed by [91–93]). Further, several recent publications have pointed out that the maximum attainable F_{ST} is inversely proportional to the mean within-population heterozygosity [64, 65], and therefore does not accurately measure population differentiation [66]. Thus, for highly polymorphic genetic markers, such as microsatellite loci, the maximum attainable F_{ST} is reduced far below one [64]. Contrary to the intuition that more polymorphic loci will reveal finer population structure, F_{ST} values are actually constrained to be lower as allelic diversity gets higher [67]. This limitation has led some to advocate the use of "true genetic differentiation" (D_{est}) as the primary or only means of comparison (e.g., [66]). While an attractive alternative in theory, there is as yet no means of significance testing for D_{est}, and researchers have to pick an arbitrary value at which to determine a genetic break before comparisons can be made; however, in the absence of statistics any cutoff value selected can be arbitrary and problematic [94]. For example, Kelly and Palumbi [30] chose $\Phi_{ST} = 0.10$ as the delineation between strong ($\Phi_{ST} = 0.11 - 0.60$) and moderate ($\Phi_{ST} = 0.02 - 0.10$) population structure. While there is nothing wrong with this delineation, one could have also chosen $\Phi_{ST} = 0.05$ or $\Phi_{ST} = 0.15$ with equal justification, and there is no consistent and defensible level of population structure that determines the cut-off at which management decisions ought to be made [60]. Most published estimates of population structure remain uncorrected for marker variation and heterozygosity; thus, a value of 0.10 in one species may be on a completely different scale than in the next species if they have different levels of mean within population heterozygosity [64, 66, 67]. For this reason we use statistical significance as our cut-off and draw no inferences regarding the magnitude of the barriers beyond the number of species that share them. A method by which the boundaries of an ecosystem can be defined with multi-species data sets, and linkages between ecosystems can be quantified, is a logical prerequisite for successful implementation of EBM in the sea.

4.3. Connectivity in the Hawaiian Archipelago: Not 1 But at Least 5 Distinct Regions. The primary finding of this work is that the Hawaiian Archipelago is not a single, well-mixed community, but rather there are at least four significant multi-species barriers to dispersal along the length of the island chain. Additional sampling or more sophisticated statistical analyses may reveal additional barriers, but we report four strong concordant breaks here. As outlined above, some species cross these barriers, others do not, and the patterns of connectivity can, and do, vary dramatically among individual species (see refs. in Table 1). Regardless, a strong and consistent pattern emerges from the multispecies comparison in which the majority of 27 taxonomically diverse species share four significant concordant genetic breaks across the archipelago. It is noteworthy that the variability among individual species studies of connectivity published to date certainly does not lend itself to an expectation of such strong concordant patterns. Despite the suite of taxonomic, ecological, and biological differences that might lead us to expect highly divergent patterns among these diverse taxa, some unknown barriers appear to consistently limit dispersal in a majority of the 27 species surveyed to date. These results illustrate that while a single species is rarely representative of the average connectivity, concordant patterns can emerge when many species are examined simultaneously. Insofar as this is a general result, it would mandate that a broad suite of reef species across multiple taxonomic groups and ecological niches ought to be surveyed to resolve general trends and to provide connectivity information pertinent to management of any large marine management area such as the PMNM.

The two primary caveats to this finding are that: (1) the basis for these shared genetic restrictions is poorly understood and discovering the location of these barriers is only the first step, and (2) it is an overly simplistic statistical model to show significant deviations from random pairwise differences across species as a measure of the strength of dispersal barriers. Nonetheless, such summing is the primary means of comparison available at this time, and this is the only multispecies study that employs even this simplistic statistical approach. In terms of the first caveat, it will be valuable to determine the ecological and oceanographic factors driving regional, island, or site specific genetic structure; this will likely be important for ecosystem-based management of both the Main and Northwestern Hawaiian Islands, and may provide general characteristics to predict ecosystem-level partitions among coral reefs elsewhere. Discovering the existence and location of these barriers leads to questions about the underlying cause for so many species sharing these concordant patterns, and what maintains those barriers to dispersal among taxa as diverse as limpets and dolphins. In terms of the second caveat, as outlined above, we need to develop a quantitative method for multispecies studies of connectivity among many locations. Ultimately, it would be ideal to bring the multispecies data sets together in a single analysis to determine both the relative strength and statistical confidence in each of the detected barriers, but no such method exists currently.

4.4. Conclusions and Management Implications. This multi-species approach to understanding population connectivity across the Hawaiian Archipelago reveals four previously unrecognized barriers to dispersal that delineate five relatively isolated regions of the Hawaiian Archipelago. In contrast to predictions based on either geographic distance between islands (isolation by distance) or on larval dispersal model predictions using pelagic larval duration, there are more barriers to dispersal within the Main Hawaiian Islands (MHI, ~600 km) than the Northwestern Hawaiian Islands (NWHI, ~2000 km). The underlying mechanism of this isolation remains unknown, but the concordance across 52% to 70% (depending on the barrier) of the 27 taxonomically and ecologically divergent species sampled here demonstrates that the pattern is robust and likely to derive from physical rather than biologically intrinsic factors.

These data provide information pertinent to current management issues facing the broader Pacific and efforts to implement ecosystem-based management (EBM) in Hawaiʻi. In particular, these data directly address the controversy about whether the NWHI is a series of isolated (and therefore relatively fragile) island ecosystems, and whether the Papaphānaumokuākea Marine National Monument provides spillover benefits to the highly exploited waters of the MHI [35]. We find that the NWHI are far more connected on average (and therefore comparatively robust) than the MHI, but that connectivity between the MHI and NWHI is limited. The results highlight that the Main Hawaiian Islands are isolated in terms of resource management and will not receive substantial subsidy from the Papahānaumokuākea Marine National Monument; the MHI must stand alone in management of marine resources. Furthermore, even the comparatively small MHI are not a single panmictic unit, and future management plans should incorporate knowledge of the substantial isolation among multiple regions within the MHI. For example, Bird et al. [28] argue that each island should be considered a separate management unit for the culturally important Hawaiian limpets (ʻopihi, genus *Cellana*). Likewise, the impact of invasive species is felt globally and with 343 alien marine species documented in Hawaiʻi thus far [95], there is considerable concern regarding the vulnerability of Hawaiian reefs to invasion and the likely spread of aliens that are already introduced. Our findings predict barriers through which invasive species should have difficulty advancing, and indeed recent studies of several species of invasive fishes and invertebrates appear to corroborate those predictions (e.g., [96, 97].

This study is one of the few multispecies surveys of marine connectivity to date and confirms that this approach can illuminate general patterns pertinent to management that do not emerge from single-species exemplar studies. The manner in which policy makers delineate the boundaries for ecosystem-based management remains a subject of considerable debate, but we argue this multispecies approach offers a possible solution. Here, we resolve concordant patterns of connectivity in an objective and quantitative manner to define a minimum of five marine spatial management units in the Hawaiian Archipelago.

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