

A COMPARATIVE STUDY OF SCLERACTINIAN CORAL DIVERSITY IN MO'OREA, FRENCH POLYNESIA, AND THE GREAT BARRIER REEF, AUSTRALIA

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Abstract. Studies on island biogeography in the Pacific have shown a biodiversity gradient that decreases from west to east, a pattern followed by numerous land and marine organisms. Based on this gradient, it has been hypothesized that Scleractinian coral biodiversity should follow the same gradient and be considerably lower in Mo'orea, French Polynesia, than in the Great Barrier Reef (GBR). Rapid ecological assessments on six barrier reef sites surrounding Mo'orea, as well as transects following the line intercept method at one site, provided data on Scleractinian coral species richness and composition. A phylogenetic study of character evolution was also performed to examine the evolutionary history of four characters related to coral reproduction and dispersal. Results revealed site-to-site heterogeneity between the six Mo'orea sites and a mean site species richness of 30 species. Alpha diversity of the Mo'orea barrier reefs and the GBR were not found to be statistically different, but total diversity was found to be considerably higher in the GBR than in Mo'orea, suggesting that beta diversity is what accounts for most of the difference in species richness. Phylogenetic character analysis revealed that the broadcast spawning character was highly conserved throughout evolutionary history, and that patterns in the other three characters, brooding, fragmentation, and rafting ability were not quite as clear. Increased knowledge on coral diversity patterns and dispersal can help focus conservation efforts to preserve maximum biodiversity and protect coral reefs from adverse human impact.

Key words: Scleractinian corals; biodiversity; alpha and beta diversity; phylogenetics; character evolution; Mo'orea, French Polynesia; Great Barrier Reef

INTRODUCTION

Biogeography, the examination of the distribution of organisms on our planet, can provide many insights into their evolutionary and dispersal history. Numerous studies have been conducted on island biogeography in the Pacific and have suggested a decreasing biodiversity gradient from the species-rich Indo-Pacific region eastward to the remote Eastern Pacific islands (Carlquist 1972). This biodiversity gradient applies to many groups of organisms, plant and animal, marine and terrestrial (see for example Kohn 1967; Duke *et al.* 1998; Briggs 1998; Mueller-Dombois 1999; Karlson *et al.* 2004). The gradient pattern can be explained by the theory of island biogeography, developed by MacArthur and

Wilson in the 1960s, which states that smaller island size and greater island isolation will result in lower species richness, as limited habitat increases extinction rate and the distance from the species-rich mainland reduces immigration by providing a filter on the dispersal of organisms (Gilbert 1980). Mo'orea, French Polynesia, a small volcanic island situated in the South Pacific, is very remote: located around 5700 km from mainland Australia, Moorea is thus near the low end of this biodiversity gradient.

Throughout the world, many studies have focused on the biodiversity of coral reefs, highly diverse ecosystems composed of the accumulation of the calcium carbonate skeletons of corals, mostly of the Scleractinian order, and the living organisms dependent on

them (Thurman 1993; Veron 1995; Connolly *et al.* 2003). The Great Barrier Reef (GBR), bordering Australia, is at the high end of the Pacific biodiversity gradient and is highly diverse, with an estimated 300 to 500 species of Scleractinian coral. This is in contrast to Mo'orea, which only has an estimated 50 to 100 coral species (Veron 1995). This gradient is the result of limits on coral dispersal, which occurs through larval transport by ocean currents, fragmentation, and rafting (Highsmith 1982; Jokiel 1984; Veron 2000).

This study has several goals. The first goal is to describe the Scleractinian coral diversity of Mo'orea and compare it to data from the literature on the GBR. I hypothesize that species richness of Mo'orea will be considerably lower than that of the GBR, following the gradients of biodiversity across the Pacific. The second goal is to examine and analyze any potential taxonomic disharmony between the corals of Mo'orea and the GBR. I expect that there will be disproportionate representation of corals that are good dispersers, as well as strong competitors and successful settlers. The third and final goal is to perform a phylogenetic character analysis on the Scleractinian coral genera of Mo'orea using four reproductive and dispersal characters to observe patterns and draw conclusions regarding their evolutionary history. I hypothesize that these traits will not be randomly dispersed on the phylogeny, but will rather reflect the evolutionary history of the coral genera in a logical manner.

METHODS

Study area

All field work was conducted on the island of Mo'orea (17°30'S, 149°50'W), French Polynesia, in October and November, 2009. Mo'orea is a high volcanic island located in the Society Island archipelago in the South Pacific. The island is small, with a surface area of 134 km², and is surrounded by fringing and barrier reefs, which combined, never exceed 2 km wide (Stievenart 2007). There have been various disturbances over the years, including cyclones, bleaching events, and *Acanthaster*

planci outbreaks throughout the last three decades (Adjeroud 1997, Salvat *et al.* 2008), although in general, the coral reefs of Mo'orea are considered to be in good health (Salvat *et al.* 2008). Recent evidence has suggested that *Acanthaster planci* numbers have been increasing in Mo'orea since 2005, and that the beginning stages of an outbreak are currently occurring in certain regions of the island, especially in the north (Lison de Loma *et al.*, 2006; Stievenart 2007).

Field Observations

Field observations were in two parts. In the first part of the study, six barrier reef sites on all sides of the island were surveyed to obtain a representative view of Mo'orea's Scleractinian biodiversity (Figure 1, Table 1). The barrier reefs at 'Afareaitu, Ma'atea, Nu'urua, and Vaipahu were reached by kayak, while those on the north side of Motu Tiahura and at Temae public beach were reached by swimming. At each of these sites, a rapid ecological assessment, modeled on that conducted by DeVantier *et al.* (2006), was performed on the back reef (0.5-3m depth) at each site. In this procedure, an estimated rectangular area of about 100 m by 20 m was surveyed by snorkeling (mask, fins, and snorkel) over a period of one hour. A prepared checklist of Scleractinian corals was used to mark off which corals were seen, and these corals were then placed into the following categories: dominant, abundant, common, uncommon, rare, and absent. Percent coral cover was also estimated according to one of six categories: 0%, 1-10%, 11-30%, 31-50%, 51-75%, and 76-100%. Corals were identified in the field to species level if possible, or down to genus and general morphology if too difficult, as was the case for the massive Porites. Photos of each coral species were taken (**Appendix A**), and unknown corals were later identified using J. E. N. Veron's *Corals of the World* (2000) as well as the CalPhotos database ("CalPhotos" 2008).

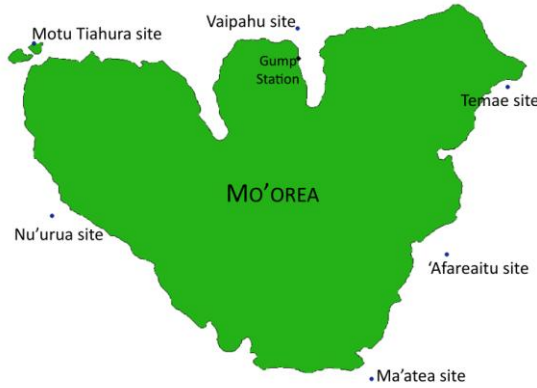


FIG. 1. Map showing the six barrier reef study sites, selected all around Mo'orea to obtain a more representative view of the island's Scleractinian coral biodiversity. Rapid ecological assessments were performed at each of these sites.

In the second part of the study, more in-depth field observations were conducted at the Temae barrier reef. At this site, the line intercept transect method, as used by Pichon and Morrissey (1981), was followed: four 30 m transects were laid out parallel to shore roughly fifteen meters apart, and every coral species intercepting the line was identified to genus and species when possible, as well as measured to the nearest cm. If multiple corals were present at different levels below the transect line, each of these was identified and measured as well.

Data analysis for field observations

For the first part of the project, the rapid ecological assessments of six sites around Mo'orea, species diversity was analyzed through the calculation of species richness at several different levels: alpha diversity was defined as the species richness of each individual site, whereas beta diversity was defined as the difference in species composition between pairs of sites (Legendre *et al.* 2005). Using presence-absence data describing the species composition of each site, beta diversity was calculated via Whittaker's beta diversity index, $\beta_w = S/\alpha - 1$, where S is the total species number of two

TABLE 1. List of study sites and their GPS coordinates

Study sites	GPS Coordinates
'Afareaitu	17° 33' 14.57" S, 149° 46' 38.50" W
Ma'atea	17° 35' 37.65" S, 149° 48' 06.74" W
Nu'urua	17° 32' 31.02" S, 149° 54' 23.80" W
Motu Tiahura	17° 29' 8.77" S, 149° 54' 45.33" W
Vaipahu	17° 28' 51.39" S, 149° 49' 35.45" W
Temae	17° 29' 57.70" S, 149° 45' 27.29" W

sites and α is the average number of species found within the two sites.

For the second part of the project, the more detailed field observations at Temae, relative abundance of each coral species was calculated for each transect by dividing the cover of each species by total coral cover. Layering of corals was accounted for by adding the additional measurements to the total transect length. For each transect, species richness was recorded and the Shannon-Weaver index was calculated by using the

formula $H' = - \sum_{i=1}^S p_i \ln p_i$, where p is the relative abundance of each species (Pichon and Morrissey 1981). A rank abundance curve was constructed to represent species abundances relative to each other.

Comparative analyses

Data from field observations performed in Mo'orea were compared to the results from various studies conducted in the Great Barrier Reef. One geographic region, the North Inner region (NI), was selected from the 2006 DeVantier *et al.* study because its latitudinal range (15° to 18° S) was similar to that of Mo'orea (17° 30' S). Mean site richness, defined as the region's alpha diversity, was compared to the mean site richness calculated for the six sites in Mo'orea, and tested for statistical significance using a t-test (not assuming equal sample sizes nor equal variances) using the program JMP. The same statistical methods were used to compare mean site hard coral cover as well.

Data from a study performed at South Island Reef (14°40'S, 145°28'S), off of Lizard Island in the Great Barrier Reef (Pichon and Morrissey 1981), were compared to the results from the Temae transects. The GBR study covered the entire reef from reef flat to reef slope, so results from stations A-D, covering the inner reef flat, were selected as more comparable to the transects performed at the Temae back reef. Average species richness and Shannon-Weaver values were calculated for each of these stations. These values were then compared to the results from the Temae transects through the use of an ANOVA for Shannon-Weaver values and a Kruskal-Wallis test followed by a Tukey-Kramer HSD for species richness using the program JMP. Results involving genus dominance in both the Great Barrier Reef and Mo'orea were also compared graphically.

Phylogenetic analysis

The third and final part of this project was a phylogenetic analysis of characters. A list of Mo'orea's genera of Scleractinian corals was formed based on field observations and work performed by Adjeroud (1997). These eighteen genera were then selected on a recent Scleractinian supertree (Kerr 2005) and a new supertree with solely these genera was constructed using the program MacClade (Maddison and Maddison 2001). Evolutionary relationships among species from the original tree were maintained.

Four traits (**Appendix B**) related to reproductive strategy and dispersal were then mapped onto the tree. Brooder species are corals that undergo internal fertilization: male gametes are released and then fertilize the egg, and the larva is released at a later time. Broadcast spawners release both male and female gametes, and fertilization occurs externally. In general, broadcast spawning results in more numerous, less developed larvae with a lower rate of successful settling than brooders. Broadcast spawning is also often associated with long-distance dispersal, while brooding is associated with nearby settling. Fragmentation is the ability of certain corals to reproduce asexually through a fragment breaking off and settling elsewhere, and is often involved in nearby dispersal (Highsmith 1982). Finally, rafting is the ability of certain corals to settle onto a floating piece of wood or other medium and be carried by currents to other potentially distant areas (Jokiel 1984). As these reproductive strategies can vary within species depending on geographic location, it should be noted that presence and absence of these characters was determined based on available literature (Highsmith 1982, Fadlallah 1983, Veron 1995, and Riddle 2008), and does not necessarily pertain to Mo'orea's coral genera in particular (Veron 1995). Genera were considered to have the trait if at least some of their species possessed it: *Porites*, *Acropora*, and *Pocillopora*, for example, have some species that are brooders and others that are broadcast spawners, and are thus considered to possess both characters.

TABLE 2. Table showing number of species in common between sites (across), as well as beta diversity values calculated using the Whittaker index (down). Vaipahu and Motu Tiahura are the most similar, and Vaipahu and Nu'urua are the most different.

# of species in common (across)/ Whittaker diversity index (down)	'Afareaitu	Ma'atea	Nu'urua	Temae	Motu Tiahura	Vaipahu
'Afareaitu		17	20	18	19	17
Ma'atea	0.292		21	18	20	19
Nu'urua	0.298	0.263		23	21	18
Temae	0.279	0.379	0.313		24	22
Motu Tiahura	0.321	0.286	0.354	0.273		24
Vaipahu	0.404	0.333	0.455	0.343	0.262	

RESULTS

Scleractinian coral diversity around Mo'orea

The first part of the field observations, rapid ecological assessments at six sites around Mo'orea, revealed a total of 56 species of Scleractinian corals within 17 genera (**Appendix C**). Site species richness, or alpha diversity, ranged from 24 species at 'Afareaitu and Ma'atea to 34 species at Temae, with a mean \pm SD of 30 ± 4.69 species.

Species composition of each site was compared in a pairwise manner (Table 2). Whittaker diversity indices indicated that Vaipahu and Motu Tiahura were the least similar sites, and that Vaipahu and Nu'uru were the most similar based on presence-absence data of coral species.

The second part of field observations, the line intercept transects at Temae, revealed a total of 30 species within 10 genera, with an average \pm SD of 19.5 ± 2.65 species per transect (Table 3). Coral cover was considerably high, reaching 70% on one transect. Shannon-Weaver indices indicate species evenness of the transects.

The corals at Temae were ranked from most abundant to least abundant and represented graphically (**Appendix D**).

TABLE 3. This table reports the results from four 30 m transects at Temae, spaced roughly 15 m apart, parallel to shore. The line intercept transect method was used, in which all coral species intercepting the line and below the line were identified and measured. Percent hard coral cover was defined as the total coral cover, including layering, divided by the transect length (including the additional lengths from the layering of the corals).

Transect	# species	% hard coral cover	Shannon-Weaver index
1	16	49.33	1.756
2	19	70.22	2.341
3	22	53.11	2.217
4	21	51.06	2.28
average	19.5	55.93	2.1485

The most abundant taxon was the "massive *Porites*" group, which made up 45% of total hard coral cover, followed by the branching *Acropora formosa** with 15% and the purple encrusting *Montipora calcarea** with 13% of the total coral cover. *Porites irregularis*, an endemic stubby *Porites* species, was the least abundant, making up only 0.1% of total coral cover.

*As mentioned in the appendix, these species names are best estimates but not entirely certain due to difficulties involved in identifying certain coral genera to species.

Comparative analyses

Results relating to the North Inner (NI) region of the Great Barrier Reef (GBR) were obtained from DeVantier *et al.* (2006) (Table 4).

Mean site species richness of the NI region of the GBR was not significantly different from mean site species richness in Mo'orea (Figure 2). However, total species richness of the North Inner region was approximately five times that of Mo'orea.

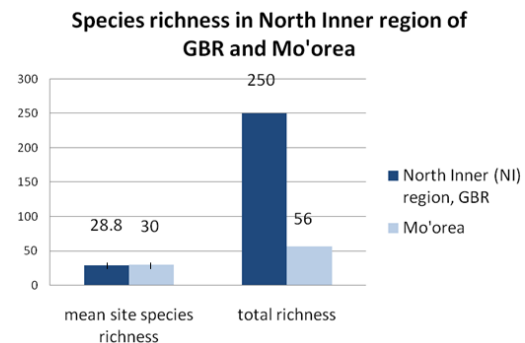


FIG. 2. This figure compares the mean site species richness of the North Inner region of the GBR (DeVantier *et al.* 2006), of similar latitude to Mo'orea. Standard error bars are shown for mean species richness (1.245 for NI, 1.915 for Mo'orea). A two-tailed t-test, not assuming equal variances nor equal sample size, showed that mean site species richness of NI and Mo'orea are not statistically significant ($t(10.0658)=0.526$, $p=0.610354$). Total richness in NI is almost five fold that of Mo'orea.

TABLE 4. Results from DeVantier *et al.* (2006) study in the Great Barrier Reef and this study. Mean coral cover is based on a categorical scale ranging from 0 to 5: 1 (0%), 2 (1-10%), 3 (11-30%), 4 (31-50%), 5 (51-75%), and 6 (76-100%).

Site	Mean species richness	standard deviation (richness)	number of sites	total richness	mean coral cover	Standard deviation (coral cover)
NI	28.8	15.7	159	250	2.11	1.23
Mo'orea	30	4.69	6	56	3.5	1.0488

Mean site hard coral cover was significantly greater in Mo'orea than in the NI region of the GBR. Average coral cover in Mo'orea was in the 11-30% cover category, while that of the NI region was in the 1-10% cover category (Figure 3).

Data collected on the Temae transects were compared to the results from Pichon and Morrissey (1981), a study performed at South Island Reef, GBR. Site species richness was found to be significantly greater at Temae than at stations A, B, and C, but not significantly different from station D (Figure 4).

A similar analysis was performed to compare Shannon-Weaver indices between the four GBR stations and Temae (Figure 5). The average Shannon-Weaver index for all four transects was not significantly different at Temae than at any of the other four GBR sites.

Percent hard coral cover was considerably higher at Temae than at any of the GBR sites, with an average \pm SD over the four transects of $55.93 \pm 9.65\%$. Average coral cover for each of the GBR stations varied between 6.13% and 10.78%, with an overall mean \pm SD of $8.49 \pm 4.21\%$.

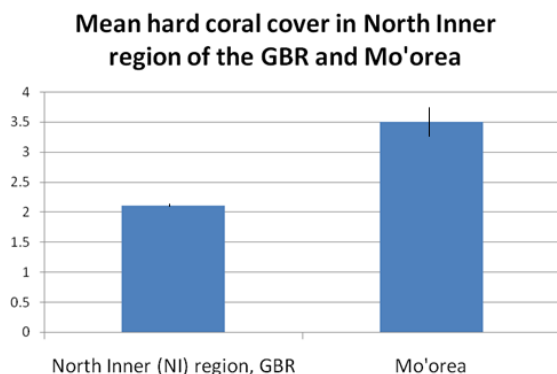


FIG. 3. Mean site hard coral cover in the North Inner region of the GBR and Mo'orea. Standard error is shown (0.097 for NI, 0.428 for Mo'orea). A two-sided t-test, not assuming equal sample size nor equal variances, showed that hard coral cover of Mo'orea is significantly higher than that of the NI region ($t(5.53)=3.165$, $p=0.0194$).

A grand total of 119 species of Scleractinian corals were found at South Island Reef, GBR, by Pichon and Morrissey (1981). This value, however, includes all parts of the reef, from reef flat to reef slope, as opposed to the total number of 30 species found on the back reef at Temae. Four genera in the GBR, *Acropora*, *Montipora*, *Porites*, and *Favia*, were ranked in order of proportion of species (Figure 6).

The same process was repeated for Temae data, and the order was found to be the same, although *Montipora* and *Porites* dominated more in numbers of species than they had at the GBR (for this calculation, the category "massive *Porites*" was broken down into four species, *Porites australiensis*, *P. lobata*, *P. lutea*, and *P. solida*, which were best estimates of their identification).

Comparison of species richness data at four GBR stations and Temae

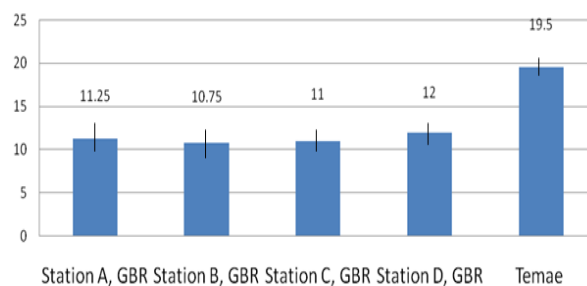


FIG. 4. Stations A-D are located at South Island Reef, GBR (Pichon and Morrissey 1981). Species richness values were averaged over the four transects at each site and values are reported in the graph. Standard error is indicated (1.93 for stations A and B, 1.78 for stations C and D, and 1.325 for Temae). Temae has significantly higher species richness than stations A, B, and C, but is not significantly different from station D (Kruskal Wallis, $H=9.56$, 4 d.f., $p=0.0488$). Bars sharing the same letter are not significantly different from each other at the $p=0.05$ level using a Tukey-Kramer HSD test.

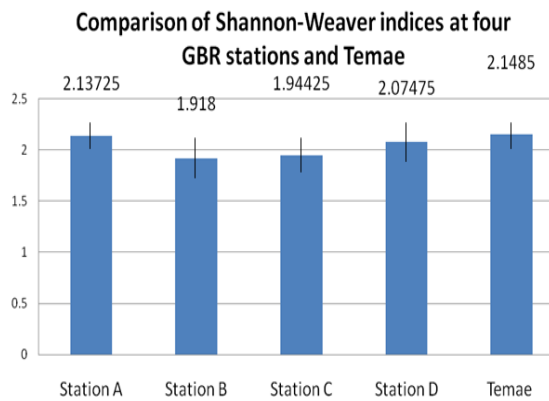


FIG. 5. Stations A-D are located at South Island Reef, GBR. Standard error is indicated on the graph (0.131 for Station A, 0.154 for B, 0.158 for C, 0.201 for D, and 0.124 for Temae). Statistical analysis using an ANOVA test revealed that average Shannon-Weaver indices at Temae and all four GBR sites are not significantly different ($F=0.469$, $p=0.758$).

Phylogenetic analysis

Mapping of the broadcast spawning character (Figure 7a) revealed that the ancestral character was also broadcast spawning. This character was highly conserved throughout evolutionary history: it was lost in only two genera, *Stylophora* and *Leptoseris*, and is possessed by 16 out of the 18 extant coral genera found in Mo'orea. For the remaining three characters, patterns were not as clear, as there were several equivocal, or ambiguous, constructions of the phylogenies that were equally parsimonious. In the case of the brooder trait, four transitions occurred over time, with the ancestor either having the trait or not. The brooder trait was concentrated in one of the four major clades (Figure 7b). The rafting trait underwent transitions five times; again, the ancestral trait was ambiguous. This time the rafting characteristic was focused in three out of the four major clades (Figure 7c). The fragmentation trait also had an ambiguous ancestral state, underwent four transitions, and was present in two of the major clades (Figure 7d). In each of these evolutionary histories, it appears that the character evolved in a parallel manner among several taxa.

DISCUSSION

Scleractinian biodiversity around Mo'orea

Results showed considerable variation in Scleractinian coral richness and species composition among sampled sites in Mo'orea. Abiotic factors that may lead to such variability include depth, wave action, sand coverage, and nutrient availability (Adjeroud 1997). Studies in Hawaii revealed that more exposed sites, i.e. those subject to chronic wave action, tend to have higher species richness than less exposed sites (Huston 1985). According to meteorological data from French Polynesia, Motu Tiahura and Vaipahu are chronically exposed to northern swells, and Nu'urua is exposed to powerful south-western swells (Adjeroud *et al.* 2007). It is thus possible that this has caused these sites to have higher site species richness than the less exposed sites of 'Afareaitu and Ma'atea. Biotic interactions may have also have an effect on coral species diversity: algae, if in high enough abundance, can smother coral and prevent its growth. Sea urchins such as *Diadema* species graze on algae and can thus help reduce algal coverage, allowing smaller corals more prone to algal smothering to survive, and thus potentially increasing local species richness (Huston 1985).

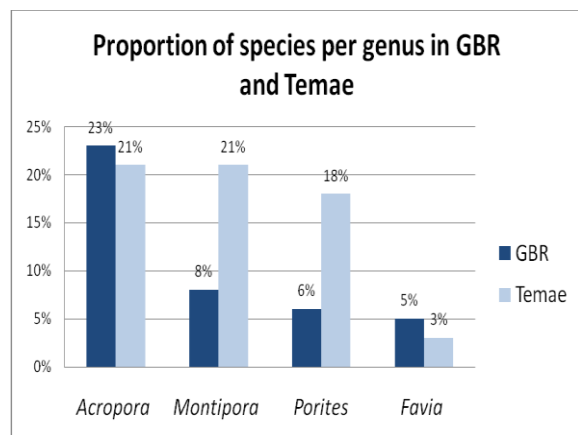


FIG. 6. Proportion of species per genus for a few of the more common genera in the GBR (Pichon and Morrissey 1981) and at Temae. *Montipora* and *Porites* are both more represented in numbers of species at Temae than at the Great Barrier Reef.

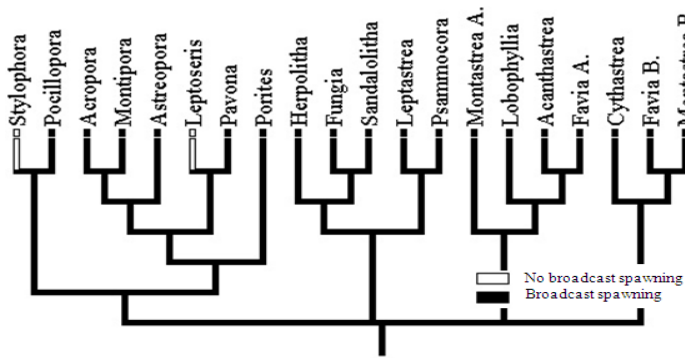


FIG. 7a

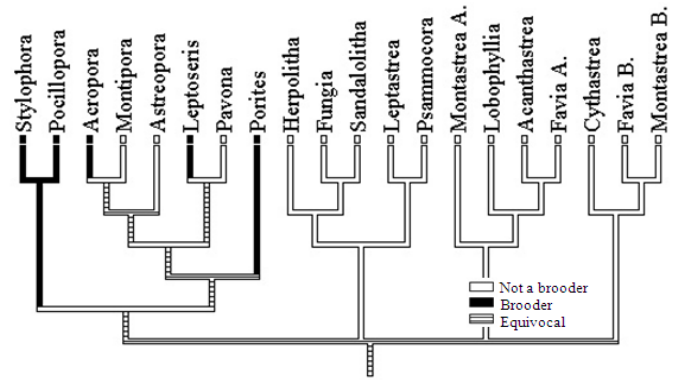


FIG. 7b

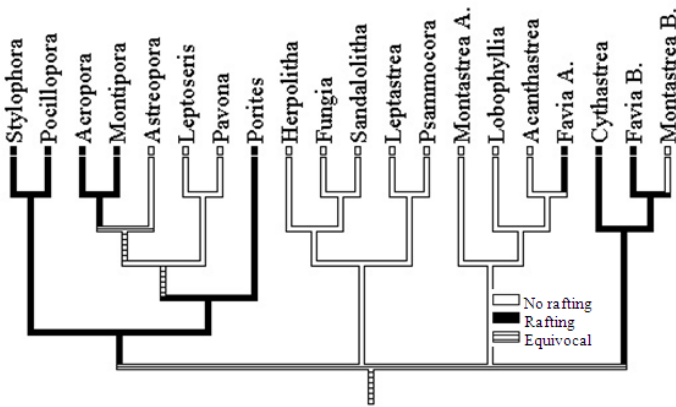


FIG. 7c

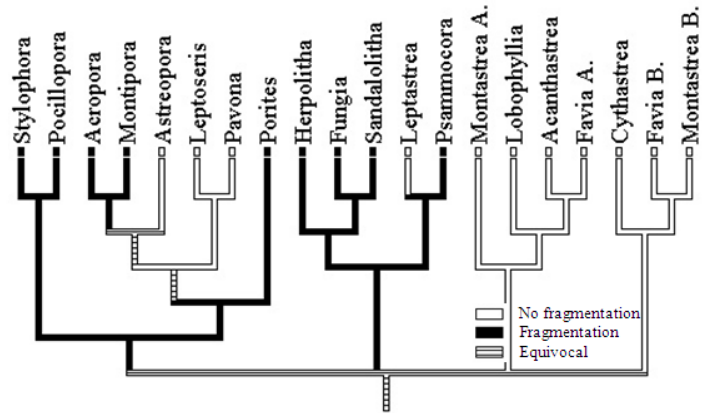


FIG. 7d

FIG. 7a-d. Supertrees showing evolutionary relatedness of genera of Scleractinian corals found in Mo'orea. These trees were constructed based on work performed by Kerr (2005), and characters were mapped on using the program MacClade (Maddison and Maddison 2001). White branches signify absence of character, black branches signify presence of character, and hatched branches signify equivocal character (ambiguity).

- a. Broadcast spawning
- b. Brooder
- c. Rafting ability
- d. Fragmentation ability

As there are large populations of *Diadema* and *Echinometra* urchin species at Temae (pers. obs.), there is a possibility that these have contributed to its higher species richness.

Geographic proximity does not appear to be a factor in species composition. Based on beta diversity values, Vaipahu and Nu'uruua were found to be the most similar in species composition, although Vaipahu is on the north side of the island and Nu'uruua is on the west. For comparison, Vaipahu and Motu Tiahura were the least similar in species composition, but both are located on the north side of the island, and considerably closer together than Vaipahu and Nu'uruua. There must thus be other factors involved in controlling species composition. One possible cause for such differences is extreme disturbance. From 1980 to 1981, there was a devastating *Acanthaster planci* outbreak at Tiahura Reef that led to a decrease in coral cover by 61% (Berumen and Pratchett 2006). This targeted *Acropora*, the preferred prey, in particular, evidence of which still remained in 2003. According to Faurea (1989), there was no *A. planci* infestation at the part of Vaihapu surveyed in this study, so it is possible that may have contributed to the variation in species composition between the two sites despite their location on the same side of the island.

It should be noted that the line intercept transect method at Temae revealed 30 species of coral, as opposed to the rapid ecological assessment that resulted in a species richness of 34 species for Temae. The two methods only had an overlap of 24 species: rapid ecological assessments revealed 10 species that were not found via the transects, including not only small species such as *Montastrea curta*, but also large, distinct species such as *Gardineroseris planulata*. Likewise, the transects revealed 7 unique species, including the encrusting *Stylocoeniella armata* and various *Acropora* species. This discrepancy may be due to incongruent identifications, especially in the *Acropora* genus, but it may also be a factor of spatial heterogeneity within the Temae site itself, as the rapid ecological assessment and transects were performed weeks apart and not at the exact same location.

Rank abundance data from Temae shows that the massive *Porites* taxon, which likely encompasses three species (*Porites australiensis*, *P. lobata*, and *P. lutea*) or more, dominates the Scleractinian coral community at Temae. This taxon is followed by the branching *Acropora formosa** and the purple, encrusting *Monitpora calcarea**. All three of these taxa are widespread across the Indo-Pacific, probably as a result of traits that promote dispersal and success, including broadcast spawning, an ability to reproduce asexually via fragmentation, and an ability to raft (Veron 1995, Riddle 2008). The *Porites* genus is composed of resistant species that are not very sensitive to temperature and are less susceptible to bleaching than many other coral genera (Magsoudlou 2008). The *Acropora* genus is not temperature-sensitive either and has been successful due to its rapid and determinate growth as well as its highly branched morphology that promotes fragmentation (Veron 1995). It is important to note that *Acanthaster planci*, which prey preferentially on *Acropora* (De'ath and Moran 1998), are present only in very low abundance at Temae (Lison de Loma 2006, Stievenart 2007), which may also explain why *Acropora* are able to dominate at this site.

*As mentioned in the appendix, these species names are best estimates but not entirely certain due to difficulties involved in identifying certain coral genera to species.

Comparative analysis

The results from the comparison with literature from the GBR suggest that at a small spatial scale, species richness is actually not much different in the GBR than it is in Mo'orea: site species richness was only statistically different in one case, and it was Mo'orea, not the GBR, that had the higher richness (Figure 4). Although this may seem contrary to the theory of island biogeography, which suggests that Mo'orea's small size and isolation should cause it to be species poor (Gilbert 1980), total species richness was still considerably higher in the GBR, suggesting that it is the beta diversity, or variation in

richness between sites (Legendre *et al.* 2005), that is responsible for this difference.

Alpha diversity is defined as species richness within a community, in this case within each study site. It is controlled by biotic and abiotic factors, in particular by niche relations, the interactions between species and with their habitats (Shmida and Wilson 1985). It seems possible that even in a region with a large species pool, site species richness could be limited by niche availability; this is dependent on the community being saturated, an assumption made by Veron with regards to the central GBR (Karlson and Cornell 1998). However, some studies on coral species richness have shown that coral communities in the Indo-Pacific are not saturated, and that regional species pool size and diversity at the local level are positively correlated (Cornell and Karlson 1996, Karlson and Cornell 1998). If this is true, then there must be other factors besides niche limitations that explain why alpha diversity in the GBR is so similar to that of Mo'orea despite higher regional species richness. Anthropogenic effects may play a dominant role: the NI region studied by DeVantier *et al.* (2006) was affected by polluted river input as well as *Acanthaster planci* infestations, both of which probably lowered site species richness (DeVantier *et al.* 2006). Coral reefs in French Polynesia, however, are considered to be in good health (Salvat *et al.* 2008) and all sites studied were PGEM or protected marine areas (Lison de Loma *et al.* 2008), suggesting that anthropogenic effects may not be as influential in reducing coral species richness as in the GBR. Coral cover might affect species richness as well, as studies have revealed positive correlations between coral cover and species richness (Guzman *et al.* 2004, DeVantier *et al.* 2006). As coral cover was significantly lower in both the NI region of the GBR and at South Island Reef than in Mo'orea, this may have had the effect of lowering GBR alpha diversity values.

Despite the similarity in alpha diversity values in the Great Barrier Reef and in Mo'orea, the GBR still had greater total species diversity than Mo'orea, as predicted by the theory of island biogeography. Since total diversity can be thought of as the sum of

alpha and beta diversity (Cornell *et al.* 2007), and alpha diversity was found to be constant between the GBR and Mo'orea, it can be deduced that the difference in total diversity must be based on differences in beta diversity.

While alpha diversity is controlled by niche relations, beta diversity is controlled by the heterogeneity of habitats (Shmida and Wilson 1985). The GBR is at a much greater spatial scale than Mo'orea's barrier reefs: the equivalent of 2 km in Mo'orea is more than 100 km on the GBR (Adjeroud 1997). This huge difference in size creates a greater range of habitats in the GBR, allowing it to support a more diverse group of species (Shmida and Wilson 1985), which increases its site-to-site heterogeneity and thus its beta diversity.

Comparisons with Temae transect data revealed taxonomic disharmony in favor of the *Montipora* and *Porites* genera, as these were overrepresented in numbers of species at Temae compared to the GBR. As mentioned, this is a reflection of the overwhelming success of these genera due to characteristics that promote good dispersal and settlement, as well as the fact that these genera have high numbers of species: *Acropora* has 150 species, and *Montipora* and *Porites* have 80 around the world, as opposed to *Favia*, for example, which has 30, or *Pocillopora*, which has 10 (Veron 1995). As there were 38 genera at South Island Reef (Pichon and Morrissey 1981) and only 10 at Temae, it is not surprising that these successful genera dominate.

Despite variations in species composition between sites in the GBR and in Temae, Shannon-Weaver indices were not statistically different. This is interesting: even though there are many important differences in biotic and abiotic factors between South Island Reef, including scale, coral cover, and geographic location, species evenness is still essentially the same.

It is important to note that coral identifications simply based on morphology have a degree of uncertainty: the term "species" is used out of convenience and simplicity, as coral "species" can hybridize easily and have extreme geographic and genetic variation. A coral species can look completely different in one part of the world than in another, as well as in two different

parts of the same reef, simply based on physical factors such as depth and wave action (Veron 2000). In this study, best attempts were made at identifying corals down to species, more for convenience than for taxonomic purposes; regardless of whether the identification is correct, species richness values should still be relatively accurate. This is especially true for the *Acropora*, *Porites*, *Montipora*, and *Fungia* genera, which all have a wide range of morphologically similar species.

Phylogenetic analysis

Phylogenetic analysis of four characters pertaining to dispersal and reproductive strategy revealed much about their evolutionary patterns. Broadcast spawning appears to have been a highly successful trait, as demonstrated by its high level of conservatism throughout evolutionary history. This reproductive strategy has allowed many corals to become highly successful as it is thought to allow long-distance dispersal and colonization of new habitats, increasing genetic diversity in the process, although there is some evidence that in some cases, the planulae do not travel far (Miller and Mundy 2003). While broadcast spawning is dependent on the release of large numbers of larvae, only a small percentage of which successfully settle and develop into an adult coral, brooder corals release already fertilized planulae that settle nearby and have a higher success rate (Veron 1995). There are advantages to both reproductive strategies, and many coral genera have species that are brooders, broadcast spawners, and sometimes both depending on geographic location (Veron 1995). In trying to understand the evolution of these characters, it is important to understand these trade-offs: the loss of the broadcast spawner trait in some genera, for example, may have allowed more effective localized colonization.

It is interesting to examine the correlation between traits: it appears that broadcast spawning was lost in *Stylophora*, but rafting either evolved in the ancestor or was conserved if it was already the ancestral trait; this suggests that although *Stylophora* was limited in its long-distance dispersal due to a

change in reproductive strategy, it could still potentially colonize far away habitats due to its ability to raft (Veron 1995). Another correlation that can be observed among certain genera is that between the ability to reproduce asexually through fragmentation and broadcast spawners: it is possible that fragmentation evolved as a mechanism for local dispersal among corals utilizing the broadcast spawning reproductive strategy. This inverse correlation is a trend among three out of the four clades on the phylogenetic tree.

CONCLUSION

It was hypothesized at the beginning of this study that following the biodiversity gradients across the Pacific, Scleractinian coral biodiversity of Mo'orea would be considerably lower than that of the Great Barrier Reef. This did not turn out to be correct at every scale - while it was true that at the regional scale, the GBR had far greater species richness, this was not found to be true at the local scale, most likely due to abiotic and biotic factors leading to low alpha diversity at the GBR.

Understanding such patterns of diversity is crucial for its conservation. This study reveals two aspects that pertain to this purpose: 1. Low coral cover in the GBR, probably due in large part to anthropogenic cause, has adversely affected alpha diversity; and 2. Total coral cover is highly dependent on beta diversity. Conservation efforts must protect both alpha and beta diversity, through the reduction of negative anthropogenic effects and the preservation of as wide a range of habitats as possible. A better understanding of the patterns and mechanisms of coral dispersal is also helpful in conservation efforts as it allows more directed efforts in promoting coral recruitment and dispersal, as well as mitigating human impact.

These conservation concepts can be applied to many other organisms besides corals, as similar patterns emerged among other groups as well. A study performed on coral-dwelling fish, for example, also concluded that smaller scale, or alpha, diversity was less influenced by increasing

regional diversity than was larger scale, or beta, diversity (Belmaker *et al.* 2008).

Future studies should focus on gaining a better understanding of the factors involved in site-to-site heterogeneity in Mo'orea and their effects on coral biodiversity. A better understanding of species composition patterns could be applied to predicting the potential effects of the beginning *Acanthaster planci* outbreak on coral biodiversity, for example, and thus devising a plan to mitigate these effects.

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APPENDIX A

APPENDIX A. Photos of Scleractinian coral species observed at six sites around Mo'orea, French Polynesia (all photos by the author). Some coral genera, including *Acropora*, *Montipora*, and *Porites*, are particularly difficult to identify down to species level based on morphology alone. Coral species with an asterisk (*) have been identified to species for convenience; species names are best estimates and not completely confident. Species richness numbers should not be heavily affected by false identifications.



*Acropora abrotanoides**



*Acropora anthoceris**



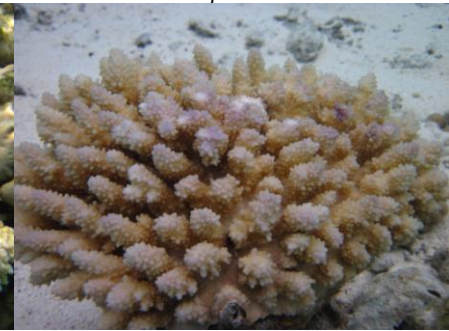
*Acropora austera**



*Acropora formosa**



*Acropora gemmifera**



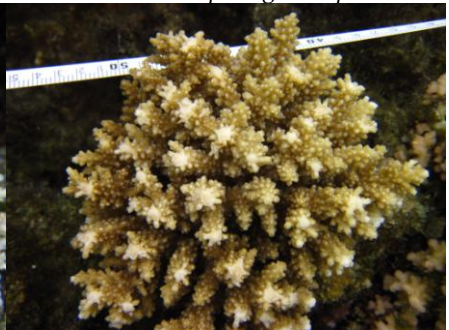
*Acropora globiceps**



*Acropora hyacinthus**



*Acropora latistella**



*Acropora listeri**



*Acropora nasuta**



*Acropora palmerae**



*Acropora pulchra**



*Acropora retusa**



*Acropora samoensis**



*Acropora tenuis**



*Acropora tortuosa**



*Acropora valida**



Astreopora myriophthalma



Cythastrea serailia



Favia stelligera



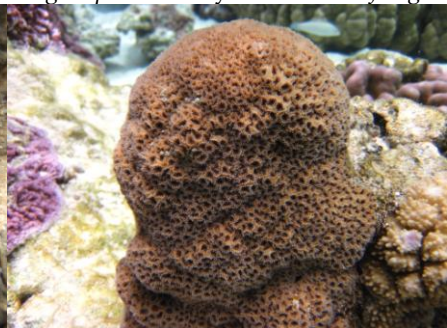
Fungia sp. (Possibly *concinna* or *fungites*)*



Gardineroseris planulata



Herpolitha limax



Leptastrea pruinosa



Leptastrea transversa



Lobophyllia heprichii



Montastrea curta



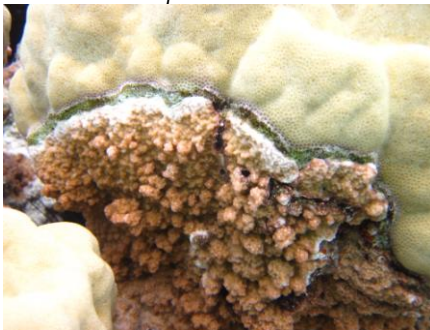
*Montipora calcarea**



*Montipora caliculata**



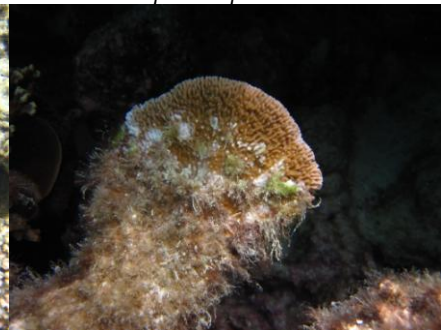
*Montipora capicornis**



*Montipora efflorescens**



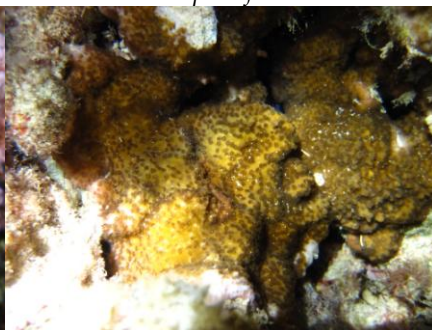
*Montipora floweri**



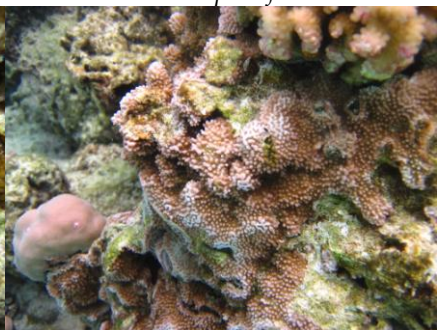
*Montipora foliosa**



*Montipora nodosa**



*Montipora spumosa**



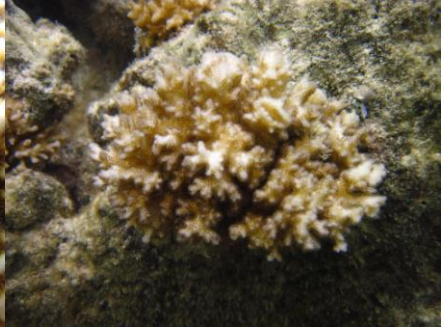
*Montipora verrucosa**



Pavona cactus



Pavona varians



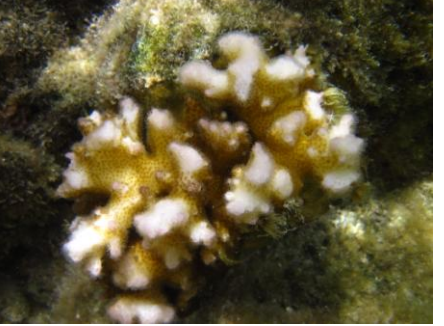
Pocillopora damicornis



Pocillopora elegans



Pocillopora eydouxi



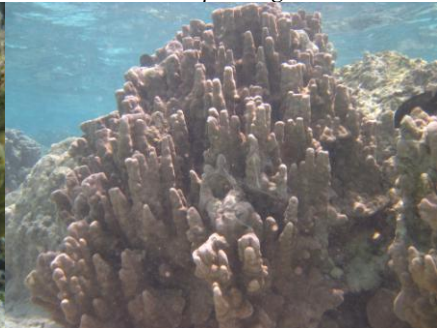
Pocillopora ligulata



Pocillopora meandrina



Pocillopora verrucosa



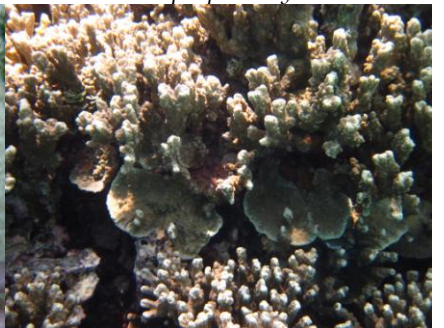
massive Porites sp. (possibly P. australiensis)



Massive Porites sp. (possibly P. lobata)



Porites irregularis



Porites rus



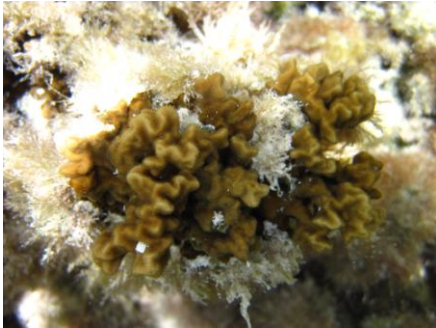
*Porites solida**



*Porites stephensoni**



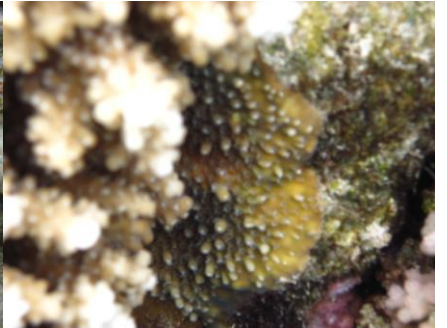
Psammocora haimeana



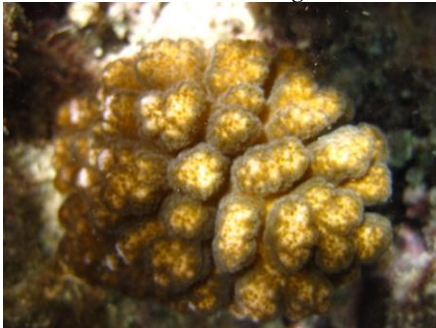
Psammocora obtangulosa



Psammocora profundacella



Stylocoeniella armata



Stylophora pistillata



Coral community at Temae

APPENDIX B

APPENDIX B. Presence-absence data for four characters among Scleractinian coral genera found in Mo'orea (0=absence, 1=presence), obtained from various studies on coral reproductive strategies (Highsmith 1982, Fadlallah 1983, Veron 1995, and Riddle 2008). Character was listed as "present" if at least some of the species within the genus were documented as possessing that character (. *Acropora*, *Pocillopora*, and *Porites* have some species that are brooders and others that are broadcast spawners, and were thus placed in both categories.

Genus	brooders	broadcast spawner	fragmentation	rafting ability
<i>Acanthastrea</i>	0	1	0	0
<i>Acropora</i>	1	1	1	1
<i>Astreopora</i>	0	1	0	0
<i>Cythastrea</i>	0	1	0	1
<i>Favia</i>	0	1	0	1
<i>Fungia</i>	0	1	1	0
<i>Gardineroseris</i>	1	0	0	0
<i>Herpolitha</i>	0	1	1	0
<i>Leptastrea</i>	0	1	0	0
<i>Leptoseris</i>	1	0	0	0
<i>Lobophyllia</i>	0	1	0	0
<i>Montastrea</i>	0	1	0	0
<i>Montipora</i>	0	1	1	1
<i>Pavona</i>	0	1	0	0
<i>Pocillopora</i>	1	1	1	1
<i>Porites</i>	1	1	1	1
<i>Psammocora</i>	0	1	1	0
<i>Sandalolitha</i>	0	1	1	0
<i>Stylophora</i>	1	0	1	1

APPENDIX C

APPENDIX C. Table showing coral species observed at each of six sites in Mo'orea and their abundance category, as well as estimated total live coral cover per site and species richness (total number of species at that site). Massive *Porites* were put into one category due to the impossibility of distinguishing species in the field. Taxa with an asterisk (*) were identified to species level for convenience; these identifications are a bit uncertain due to difficulties identifying coral species within these genera based solely on morphology, as well as their extreme regional variability.

Coral species	'Afareaitu	Ma'atea	Nu'urua	Motu Tiahura	Vaipahu	Temae
Family Pocilloporidae						
<i>Pocillopora damicornis</i>	rare	absent	rare	uncommon	uncommon	rare
<i>Pocillopora elegans</i>	dominant	common	dominant	abundant	absent	abundant
<i>Pocillopora eydouxi</i>	rare	uncommon	rare	common	abundant	abundant
<i>Pocillopora ligulata</i>	absent	absent	absent	rare	absent	absent
<i>Pocillopora meandrina</i>	dominant	dominant	common	abundant	abundant	abundant
<i>Pocillopora verrucosa</i>	dominant	dominant	dominant	abundant	abundant	abundant
<i>Stylophora pistillata</i>	absent	absent	absent	absent	rare	absent
Family Astrocoenidae						
<i>Stylocoeniella armata</i>	absent	absent	absent	absent	common	absent
Family Acroporidae						
<i>Acropora abrotanoides</i> *	absent	absent	uncommon	absent	absent	common
<i>Acropora anthoceris</i> *	uncommon	absent	absent	absent	absent	uncommon
<i>Acropora austera</i> *	absent	absent	uncommon	absent	absent	uncommon
<i>Acropora digitifera</i> *	absent	absent	absent	absent	absent	uncommon
<i>Acropora Formosa</i> *	absent	absent	uncommon	common	absent	abundant
<i>Acropora gemmifera</i> *	uncommon	absent	uncommon	absent	absent	absent
<i>Acropora globiceps</i> *	absent	common	common	common	common	absent
<i>Acropora hyacinthus</i> *	common	rare	common	abundant	common	abundant
<i>Acropora latistella</i> *	absent	absent	uncommon	absent	absent	uncommon
<i>Acropora listeri</i> *	absent	absent	absent	absent	common	common
<i>Acropora nasuta</i> *	abundant	common	common	absent	common	absent
<i>Acropora palmerae</i> *	uncommon	absent	rare	uncommon	absent	absent
<i>Acropora pulchra</i> *	absent	common	common	absent	absent	absent
<i>Acropora retusa</i> *	absent	absent	absent	common	common	absent
<i>Acropora samoensis</i> *	uncommon	absent	absent	absent	absent	absent
<i>Acropora tenuis</i> *	absent	absent	absent	common	absent	common
<i>Acropora tortuosa</i> *	absent	absent	absent	common	uncommon	absent
<i>Acropora valida</i> *	common	common	common	common	absent	absent
<i>Acropora verweyi</i> *	absent	absent	uncommon	absent	absent	absent
<i>Astreopora myriophthalma</i>	absent	absent	rare	absent	absent	absent
<i>Montipora calcarea</i> *	dominant	abundant	dominant	common	common	dominant

<i>Montipora caliculata</i> *	absent	Absent	absent	uncommon	common	absent
<i>Montipora efflorescens</i> *	absent	Absent	absent	absent	common	common
<i>Montipora floweri</i> *	dominant	Abundant	absent	common	common	abundant
<i>Montipora foliosa</i> *	absent	Absent	absent	absent	absent	common
<i>Montipora nodosa</i> *	absent	Abundant	absent	abundant	absent	abundant
<i>Montipora spumosa</i> *	absent	Absent	absent	absent	common	absent
<i>Montipora verrucosa</i> *	abundant	Dominant	dominant	common	common	dominant
Family Poritidae						
Massive <i>Porites</i>	abundant	Dominant	dominant	dominant	dominant	dominant
<i>Porites irregularis</i>	abundant	Absent	abundant	dominant	dominant	uncommon
<i>Porites rus</i>	common	uncommon	abundant	dominant	dominant	dominant
<i>Porites stephensoni</i> *	uncommon	Absent	absent	absent	absent	absent
Family Siderastreidae						
<i>Psammocora haimeana</i>	uncommon	Common	uncommon	common	abundant	common
<i>Psammocora obtangulosa</i>	absent	Absent	absent	uncommon	absent	absent
<i>Psammocora profundacella</i>	absent	Common	absent	absent	uncommon	absent
Family Agariciidae						
<i>Gardineroseris planulata</i>	uncommon	Common	abundant	uncommon	uncommon	uncommon
<i>Pavona cactus</i>	absent	Absent	absent	rare	uncommon	common
<i>Pavona varians</i>	abundant	Common	abundant	dominant	abundant	dominant
Family Fungidae						
<i>Fungia concinna</i> *	abundant	Common	uncommon	rare	abundant	common
<i>Herpolitha limax</i>	absent	uncommon	uncommon	rare	abundant	uncommon
Family Mussidae						
<i>Lobophyllia hemprichii</i>	absent	Absent	rare	absent	absent	absent
Family Faviidae						
<i>Cythastrea serailia</i>	absent	Rare	rare	absent	absent	absent
<i>Favia stelligera</i>	absent	Absent	common	absent	absent	uncommon
<i>Leptastrea pruinosa</i>	absent	Absent	absent	absent	absent	uncommon
<i>Leptastrea purpurea</i>	absent	Absent	absent	abundant	common	rare
<i>Leptastrea transversa</i>	absent	uncommon	abundant	common	uncommon	dominant
<i>Montastrea curta</i>	abundant	Common	abundant	uncommon	common	uncommon
Species richness	24	24	33	32	33	34
Total live coral cover	11-30%	51-75%	31-50%	31-50%	51-75%	76-100%

APPENDIX D

APPENDIX D. Rank abundance plot showing Scleractinian coral species at Temae as a proportion of total hard coral cover, ranked from most abundant to least abundant.

