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# RESEARCH

# BULLETIN

## NORTHWESTERN HAWAIIAN ISLANDS
### Third Scientific Symposium
### November 2 - 4, 2004

**Gerard DiNardo and Frank Parrish**
**Co-Chairs**

**ATOLL RESEARCH BULLETIN**

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Northwestern Hawaiian Islands
Third Scientific Symposium
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# ACKNOWLEDGMENT

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## Logistics

The Symposium sponsors and steering committee wish to thank all of the agencies and individuals that participated in and contributed to the very successful public outreach event and want to recognize Lee Ann Choy and Jon Ordenstein of Pacific Rim Concepts who coordinated all of the logistics for the symposium and the public outreach event.

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**Map of the Hawaiian Archipelago, including the Northwestern and Main Hawaiian Islands.**

# PREFACE

The Northwestern Hawaiian Islands (NWHI) ecosystem is home to a variety of spatially structured communities connected by both explicit and implicit pathways. Research to assess NWHI resources was initiated in the late 1970s as part of a Tripartite Cooperative Agreement between the National Marine Fisheries Service (NMFS), the U.S. Fish and Wildlife Service (FWS), and the Hawaii Division of Aquatic Resources. This agreement was concluded in the early 1980s, but not before two symposiums convened to exchange research results and ideas (Grigg and Pfund, 1980[1]; Grigg and Tanoue, 1984[2]). Since the last symposium, significant changes in NWHI resources have occurred, prompting sweeping management changes and the development and implementation of discrete research initiatives. Many of these initiatives target single species (i.e., monk seals) or functional groups (i.e., lobsters). More recently, multidisciplinary research programs have been implemented. Despite the breadth of the research, there is presently no mechanism by which the various research elements can be openly discussed, research findings presented, and ideas exchanged. This is problematic because many of the research programs observe the same species but at different life stages, and integration among the programs is needed to understand the ecological requirements of a particular species.

The Northwestern Hawaiian Islands Third Scientific Symposium was conceived to provide a forum for the review and synthesis of recent research, as well as a mechanism for identifying knowledge gaps and delineating future research needs. While the symposium focuses on recent scientific developments in ecological, biological, oceanographic, and resource assessment research in the NWHI, linking recent data with historical data was a high priority and is reflected in the presentations. The Third Symposium builds on the success of the previous symposia, and demonstrates the need for a formal symposium series.

Gerard DiNardo and Frank Parrish
Chairs, NWHI Third Scientific Symposium

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[1]Grigg, R.W., and R.T. Pfund
   1980. Proceedings of the Symposium on Status of Resource Investigations in the
      Northwestern Hawaiian Islands, Honolulu, Hawaii. UNIHI-SEAGRANT-MR-
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[2]Grigg, R.W., and K.Y. Tanoue.
   1984. Proceedings of the Second Symposium on Resource Investigations in the
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      84-01.

# HISTORY OF RESEARCH AND MANAGEMENT

# THE HISTORY OF MARINE RESEARCH IN THE NORTHWESTERN HAWAIIAN ISLANDS: LESSONS FROM THE PAST AND HOPES FOR THE FUTURE

BY

RICHARD W. GRIGG[1]

It is a well-known fact of history that the European discovery of the Hawaiian Islands was by Captain James Cook in 1778, and it is perhaps fair to say that this date marks the beginning of formal scientific discovery in the Hawaiian Archipelago. Of course, it is equally well known that over 1,000 years of natural history had already been accumulated by the Hawaiians.

It is perhaps therefore appropriate that my first lessons in coral-reef ecology were from a very experienced Hawaiian fisherman. His name was Buffalo Keaulana. Buffalo taught me how to spear fish with a three-prong spear, and he taught me that the best fishing grounds were in high relief areas, or fish houses called koas. He also taught me that huge waves were the major force that sculpted Hawaiian coral reefs. Some 15 years later, Dr. Steve Dollar and I documented this in the scientific literature in a series of papers between 1974 and 1982 (Grigg and Maragos, 1974; Dollar, 1982). In the last five years, this fact has been rediscovered by both the Coral Reef Assessment and Monitoring Program (CRAMP) in the Main Hawaiian Islands (MHI) and the Northwestern Hawaiian Islands Reef Assessment and Monitoring Program (NOWRAMP) in the Northwestern Hawaiian Islands (NWHI). The high correlation between high-relief areas and fish abundance also has also been documented in the scientific literature by Alan Friedlander and co-workers in recent years (Friedlander et al., 2003). These are but a few examples that demonstrate that our present knowledge has been built on multiple layers of history that go back generations.

In fact, it was 165 years ago that James Dana first recognized during the U.S. Exploring Expedition in 1840 that the Hawaiian Islands appear to be progressively older moving from the Big Island of Hawaii to Kauai. Dana assumed that all of the islands originated simultaneously, and so he surmised that they must have become progressively extinct first Kauai, then Oahu, Molokai, Maui and finally Hawaii, which, of course, is still volcanically active. Interesting, the Hawaiians had developed the exact same theory 100s of years earlier. They viewed Kauai as being the first home to the Goddess Pele, who then moved southeastward, jumping island by island, as they became extinct, until reaching Hawaii where her home is now Kilauea Volcano.

Of course, neither Dana nor the Hawaiians knew about plate tectonics, or about the hotspot under Hawaii, or that plate motion to the northwest is what spawned the island archipelago. They had no way of knowing that the crust of the earth upon which

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the islands were resting was steadily moving to the northwest.  Thanks to the scientific achievements of great men like Harry Hess and Robert Dietz who discovered sea floor spreading in the early 1960s (Dietz, 1961), we now know that the floor of the Pacific is moving to the northwest at a relatively constant speed of 8-10 mm/yr., and that it has been doing so for over 70 million years.  Nor did Dana or the Hawaiians know about the hotspot discovered by Jason Morgan in 1970 (Morgan, 1972).  The hotspot is a relatively stable plume of lava anchored in the mantle of the earth that has been issuing forth a new Hawaiian island about once every million years producing all-toll all told about 107 volcanoes, all moving from southeast to northwest, as silent passengers on a great undersea conveyor belt. Over millions of years, this process has built the longest and oldest island archipelago on the face of the earth.

It was on the shoulders of these men, Hess, Dietz, and Morgan, that I conceived and tested the Darwin Point Hypothesis in the 1970s and 1980s (Grigg, 1982).  By then, it was generally known that the long trail of islands in the Archipelago underwent gradual subsidence and erosion until they sank below sea -level at about 30 degrees North latitude.  My idea was to measure the net upward growth of corals on every island from Hawaii at the beginning of the chain, to Kure Atoll at the very northwestern end, a span of distance of almost 1,500 miles (2,400 kilometers) and a displacement to the north of about 10 degrees latitude.  What I discovered was that the corals steadily declined in growth rate reaching a net value of nearly zero at Kure Atoll, thus explaining why the chain ends where it does.  The islands simply drown at that latitude because coral growth cannot keep up with subsidence and erosion, and I named it the Darwin Point after Charles Darwin who first described the mechanism by which atolls form.

This is yet another lesson from the past; that ideas are often the integration of many past theories, of many past researchers.

But let us return to the era of the great explorer/naturalists.  James Dana on the U.S. Exploring Expedition, charted many of the Hawaiian Islands for the first time in the 1840s.  The British Challenger Expedition passed through Hawaiian waters from 1872-1876 and produced 50 volumes of scientific results (Brook, 1889).  Compare this to what we commonly produce today from our expeditions!  Then there was the Albatross Expedition of 1902 that mostly dredged the deep waters around the Hawaiian Islands.  Skipping over some smaller ventures, the next great expedition in the history of marine science in Hawaii was the Tanager Expedition of 1923-24.  And like those that it followed, the Tanager Expedition was primarily designed to collect data and specimens. It was a second phase of exploration (after the Hawaiians) but perhaps the first one driven entirely by scientific inquiry.

 The science conducted by the Challenger Expedition, the Albatross Expedition, and the Tanager Expedition was mainly biological surveys.  Of course, one of the first steps in science is to simply describe what is there.

But the Tanager Expedition also documented something else at Laysan Island. And that, of course, was the many changes in vegetation and birdlife that had taken place by 1923 compared to the turn of the century, when mining for guano and the harvest of seals and birds for their eggs and feathers took an enormous toll on the island ecosystem. Out of 27 species of plants that existed there before these activities, only four remained

in 1923.  Among the plants that were lost was sandalwood.  The introduction of rabbits to establish a rabbit-canning business (if you can imagine), wrought further havoc to the island.  Today, nearly 100 years later, the terrestrial ecosystem there is nearly recovered except for those species driven to extinction.  Interestingly, we could find no remnant damage or any clue of previous disturbance to the coral reef at Laysan during our quadripartite studies there in the early 1980s (see below).  This, along with many similar findings in the Main Hawaiian Islands (MHI), suggests that terrestrial ecosystems in Hawaii are far more fragile and more vulnerable than their marine counterparts.  One exception to this pattern was the near extinction of the pearl oyster at Pearl and Hermes Atoll near the beginning of the last century.  Even today, it has still not fully recovered (James Maragos, personal communication).

During this great period of exploration and collection of data and specimens, there were other major events that punctuated history and should be mentioned, simply for the sake of completeness.  Although not scientific, we should pause to point out the annexation of the Hawaiian Islands by the United States in 1898.  Also, in 1909 Teddy Roosevelt established a National Wildlife Bird Reservation including all of the NWHI, except Midway Atoll.  In 1940, the whole area was re-designated "The Hawaiian Islands National Wildlife Refuge."  And then, of course, there was World War II between 1941 and 1945.  Few people know that on that fateful day of December 7, 1941, when the Japanese attacked Pearl Harbor, they also bombed Midway Island.  The battle of Midway in June of the following year in 1942 is famous and sometimes claimed as one of the turning points of the war in the Pacific.

But now let us turn to the next phase of scientific research in the NWHI that took place in the mid 1970s and early 1980s.  It was a phase exemplified by cooperation and integrated research.  Of course, what I am talking about is the well-known Cooperative Tripartite Program that in fact quickly evolved into the Cooperative Quadripartite Program.  Its scientific name was "The NWHI Fishery Investigations" (NWHI-FI) (Fig. 1).  The three major agencies involved were the National Marine Fisheries Service (NMFS), the U.S. Fish and Wildlife Service (USFWS), and the Hawaii Division of Fish and Game (now Division of Aquatic Resources).  These agencies were quickly joined by the University of Hawaii (UH) Sea Grant Program.  The lead agency was the NMFS, and the major force in terms of leadership was Richard Shomura, the Director of the NMFS Honolulu Laboratory at that time.

The whole idea of a massive cooperative study of the NWHI was not only an idea whose time had come but it was facilitated by a huge governmental mandate, the extension of U.S. jurisdiction to 200 miles off all U.S. States, Territories, Commonwealths, and other U.S. Possessions.  This bill was passed by the U.S. Congress in 1976.  The act created a Fishery Conservation Zone (FCZ) between 3 and 200 miles in which the federal government had regulatory power over all fisheries in these waters.  Extended Jurisdiction (EJ) money, as it was known back then, amounted to about $30 million annually in the late 1970s, and it provided a huge source of funding for the Quadripartite Study.  With the addition of the University of Hawaii Sea Grant Program, enlarging the Tripartite to a Quadripartite Program, additional monies from National Oceanic and Atmospheric Administration (NOAA) and the State of Hawaii were available to fund the research.

The NWHI-FI was a huge success.  Actually, the studies encompassed all marine resources on the land, in the air, and of course the sea.  In terms of agency responsibility, the nearshore research was done by the State and the UH Sea Grant Program, the NMFS studied offshore, bank and seamount resources, and the USFWS dealt with onshore and seabird resources.
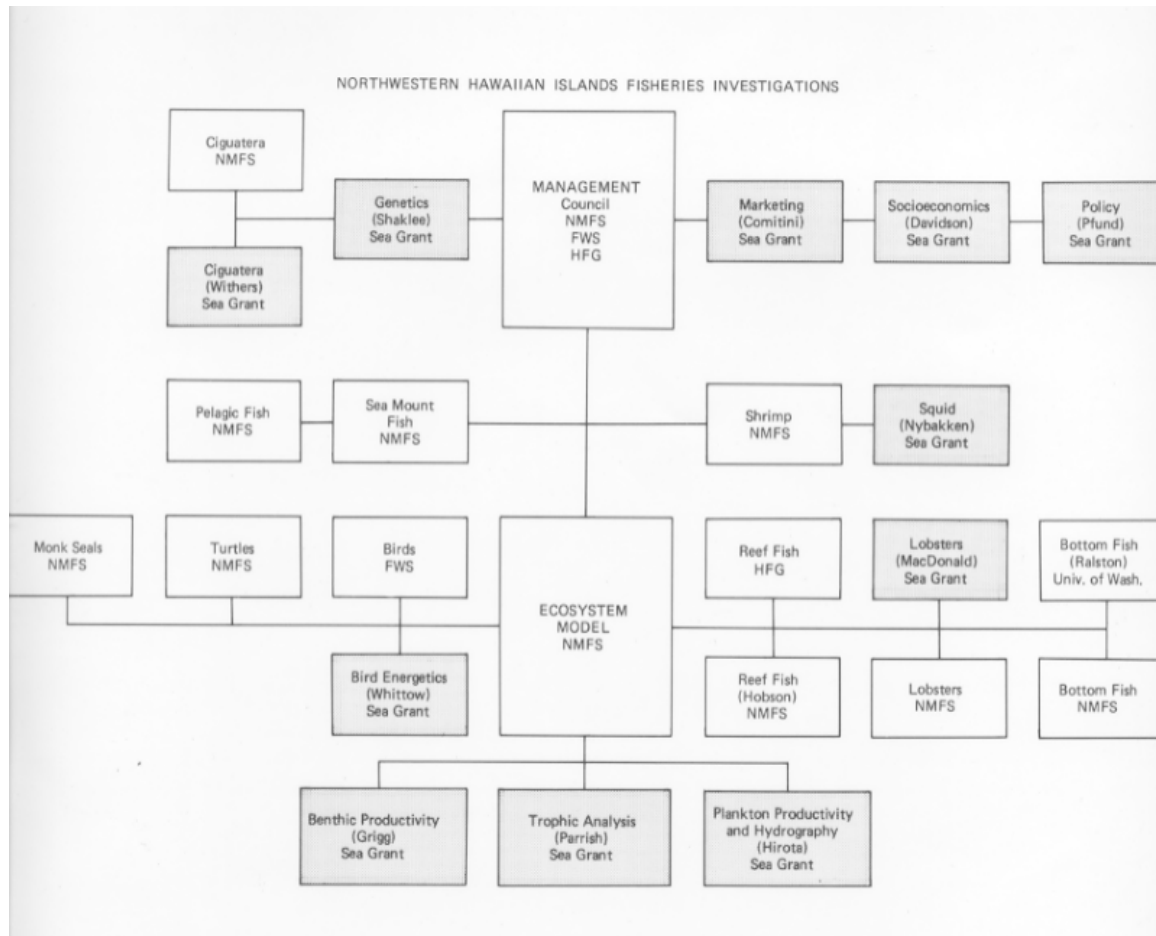


**Figure 1.**  The organizational structure of the NWHI-Fishery Investigations in 1980.

At the beginning of the study, a Council for Coordinating Research (CCR) was established with representation from each agency.  The Council met regularly once a month and did everything from establishing research priorities to coordinating day-to-day logistics.  Overall, about 200 scientists participated in the study which eventually lasted about 8-10 years.  Over this time period, approximately $10 million were invested in the Program.  Two symposia were held to present the results of the study, the first on April 24-25, 1980 and the second on May 25-27, 1983.  A total of 115 papers or abstracts were presented and now constitute three volumes of proceedings (Grigg and Pfund, 1980; Grigg and Tanoue, 1984).

Before briefly describing some of the results of the Program, I would like to comment on the underlying design of the research. Stock assessment of the major fishery resources and the data needed for their management were the over-riding themes that drove the research. Another was question-driven-science: testing of hypotheses and measuring ecological and oceanographic processes on large scales in space and time. We were intimately aware of the pitfalls of snapshot ecology and therefore tried to plan long-term programs. We recognized that ecological change is the norm, in both directions positive and negative, not just a downward shifting baseline as people often assume today.

Therefore, we hoped that some of the elements of the program would continue, in some cases indefinitely, notwithstanding limitations in funding and personnel. This is where the cooperation between supporting agencies was very important. Again, we did not assume a negative shifting baseline, but rather, hoped to enumerate and evaluate seasonal as well as decadal change. One project focused on the paleoecology of the entire Archipelago, stretching back in time 70 million years, to the origin of the first island. We presume that island to have been Meiji, which, of course, now marks the end of the chain of volcanoes and is in the process of subduction back to the mantle from whence it came.

Compared to the first phase of research dominated by the explorer/naturalists, whose research design was to collect any and all data possible and to collect specimens, the Quadripartite Study was driven by questions and hypotheses designed to evaluate long-term processes in space and time. We were hopeful that many sites would be revisited over and over again well into the future.

Now let us review some of the results. First it must be said that much of the research was centered on species of commercial importance: bottomfish, crustaceans, precious corals, and pelagics. Out of all of this research, four fishery management plans (FMPs) were developed, one for each of the fisheries. The NWHI-FI provided the initial baselines from which these fisheries continue to be managed. Also, in terms of management, two recovery plans were created, one for the endangered Hawaiian monk seal and the other for the threatened Hawaiian green sea turtle. Since that time, the monk seal population has remained fairly stable between 1,200 and 1,450 animals although not uniformly throughout the Archipelago. The Hawaiian green turtle however, has increased in abundance dramatically. Finally, the USFWS wrote a master plan for the entire Leeward Islands.

At the time of the last symposium in 1983, the thinking about fishery development was much more proactive than it is today. A major question that faced the second symposium was whether or not to establish a mothership or barge to process, freeze, store, and ship the catch from a number of smaller catcher vessels fishing for bottomfish, tuna, alfonsins, shrimp, lobster, and precious coral at either Midway Island or Tern Island, French Frigate Shoals. In looking back, it is interesting to ask why neither of these potential developments took place. The answer has to do with the economics of the fisheries and a gradual and continuing shift in societal thinking toward environmental protection and the precautionary principle. For Tern Island, Skip Naftel, one of the high-liner fishermen of the era, put it this way. "To turn Tern Island into a fishing camp for support gear, fuel, R&R, or whatever is ludicrous. I'll tell you it's a no-win proposition

to take on the environmental concerns there. We're going to lose." And, of course, it never happened.

As for Midway, economics, distance, and competing interests with the military and the USFWS, acting together, although not intentionally, prevented this idea from materializing there.

Mention should also be made of the results of more basic scientific studies during the Quadripartite Program. I have already described the Darwin Point study and its hypothesis concerning the birth and death of all the emergent Hawaiian Islands. Another very important product of the NWHI-FI was the creation of the ECOPATH Model by Jeff Polovina (Polovina, 1984). What Polovina did was to integrate the results of several dozen studies at French Frigate Shoals at all levels of the ecosystem, from measurements of benthic primary productivity on the coral reef, to trophic studies of herbivores, to primary, secondary and tertiary carnivores, all the way up the food chain to tiger sharks. He built the model from the bottom up, and he then tested it from the top down. Now he has refined and extended the predictive capabilities of the model which he has relabeled ECOSIM. ECOSIM can be and should be used by resource managers to predict outcomes of many different management scenarios and strategies.

During the NWHI-FI, we also discovered three new species of *Acropora* coral, as well as their probable route of colonization to Hawaii by way of Wake Island and Johnston Island within the Subtropical Counter Current. This southwesterly route has probably been the route of colonization for all 57 or so Hawaiian corals since all are Indo-West-Pacific in origin and all are temperature-sensitive. Another cooler route of origin was discovered by Ted Hobson for some Hawaiian fishes with Japanese affinity that probably arrived in Hawaii by way of the North Pacific Drift (Hobson, 19843). Fishes such as the sling-jaw wrasse probably arrived by way of this oceanic pathway.

I could continue describing more of the results but time of course limits the discussion. One final point to mention, is that all of these basic findings have been published in the scientific literature and like many of the lessons we have learned from the Hawaiians and the early explorer/naturalists, they add to that huge knowledge base upon which present day research should be based.

Let us now turn to the present day and what I call for in my title "hopes for the future." Some of what I have to say may sound a bit critical but my remarks are intended to be taken positively in terms of how we can improve research in the future.

I must also limit my critique to just coral-reef studies in the NWHI because of time constraints. And for this I must digress for a few brief moments in order to explain a little history.

In 1993, a symposium entitled "Global Aspects of Coral Reefs; Health, Hazards and History" was held in Miami, Florida and was attended by 125 coral reef scientists. In brief, this exercise was the beginning of what was to become "The Year of the Reef" in 1997. This event in turn led to the creation of a U.S. Coral Reef Task Force several years later. The Coral Reef Task Force was made up primarily of government personnel and environmental organizations. Very few scientists have had the time to participate in what was to become a series of very lengthy and bureaucratic meetings.

The main worry then and the main worry now, is that coral reefs were and

continue to be in ecological crisis.  It is commonplace to hear today, mostly in the media, that 20% of all coral reefs in the world are now irreparably degraded and that another 30-50% will follow suit in the next decade or two.  I will not argue here the validity of these numbers except to point out that nothing ecological under the sun is irreparable, except, of course, extinction. There is not one species of the 700 plus species of coral that exist in the world today that has recently become extinct. .

   Now the upshot of all this has been another huge mandate, and like EJ money back in 1976, the U.S. Congress has generated about $30 million annually for coral reef research, filtering down this time mostly through NOAA.  It should also be understood that several areas of research have been heavily earmarked for study as a result of political advice from the Task Force.  The buzz words are monitoring, mapping, and assessment.  For Hawaii, this means all three activities in the NWHI, the U.S. Territories of Samoa and Guam, the Commonwealth of the Northern Marianas, and the U.S. Pacific Island possessions of Johnston, Jarvis, Baker, Wake, Howland, Palmyra Islands, and Kingman Reef.

   The NWHI received particular emphasis because several studies showed erroneously that the NWHI constituted about 70% of all reefs under U.S. Jurisdiction (Hunter, 1995; Miller and Crosby, 1998).  This number has been recently revised downward recently by NOAA to about 5%!  The magnitude of this error was caused basically by omitting the reef habitat on the west Florida shelf which constitutes about 84% of the total (Rohmann et al., 2005).

   Now if you combine this sudden influx of government funding with the mandate to survey a gigantic chunk of the Pacific and combine that with all the new high-tech instrumentation that is now available to science, ranging from remote sensing satellite imagery, to multibeam acoustic bottom profilers, to Doppler current meters, to satellite tracked drifter buoys, to anchored wave/weather buoys, to CTDs (spell out), to temperature loggers, to seal cams, etc., what we have upon us today is another age of discovery.

   The research design is once again one of massive data collection and discovery, not unlike the explorer/naturalist phase of scientific research in the Hawaiian Islands over 100 years ago.  One must also add the deep-sea and the high-tech submersibles now available for study.  This is truly a new phase of discovery, and I do not infer that this is bad.

   For the past 5 years an enormous amount of new information has been gathered. By necessity, the approach has been somewhat "shotgun" in nature.  One could even describe it as fragmentary, and like the early expeditions of discovery, the idea was to collect as much data about as many subjects as possible.  Some correlations will undoubtedly result from the data analysis, and this is happening as I speak.

   And now comes the exciting part, for I think we are entering once again into a new phase of research which may be one of synthesis.  With understanding there can be focus.  Hypotheses can be erected and tested.  A wealth of new information is coming to light, as we will hear in this symposium.  All of this these new data need to be synthesized and integrated within the existing literature.  A new paradigm can be built by combining new information with the old.  This is exactly what happened in 1970

when Jason Morgan discovered the hotspot and combined it with the knowledge of plate tectonics. Suddenly, the Hawaiian Islands were moving in the opposite direction; instead of eroding sequentially to the southeast, they were drifting on the Pacific Plate to the northwest!

But before any of this can take pace we need to take stock of where we are. We need to develop a 5- or 10- year plan. This means cooperation and coordination among agencies and scientists. Priorities for research need to be identified and agreed upon. A cohesive program needs to be built and it should be put together by scientists, not politicians. Resource managers need to identify their information needs but the actual plan should be put together by scientists who have first-hand experience in the NWHI. The model provided by the Western Pacific Regional Fishery Management Council (WPRFMC) is a very good one. Decision-making by the Council is based on the work of the Scientific and Statistical Committee (SSC), and of advisory panels, and plan teams.

In 2000 and 2001, President William Clinton issued Executive Orders (EO 13178 and 13196) that created the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve from 3-50 nm around the NWHI, which in turn will likely be redesignated as a National Marine Sanctuary in the near future. If the new Coral Reef Reserve is to become a National Marine Sanctuary, an organizational structure similar to the WPRFMC will become all the more important to establish. Scientists, fishermen, and other people with first-hand knowledge should be the basic decision-makers for generating a long-term operational research plan. Most importantly the science should be driven by scientific problems, not politics.

In my view, the focus should be on specific issues and the problems. A partial list is given below following management priorities that existed during the Quadripartite Study in the 1980s but are still extremely relevant.

- Abundance levels (varying baselines) of commercial species, such as bottomfish, lobsters, precious corals, and pelagics need to be known.
- The same information is needed for seabirds, monk seals, and green sea turtles, and other major species in the ecosystem.
- We need to understand the natural variability of the systems: the reef, primary production of the surrounding ocean, the current systems, annual temperature patterns, etc.
- All of these new and basic data should be updated and reanalyzed in the ECOSIM Model.
- Is coral bleaching in the NWHI a first-time event? Will the corals recover? Corals have been there for at least 35 million years. Future studies must be retrospective in design, not just surveys and snapshots.
- Marine Protected Areas (MPAs) need to be identified by location and size.
- Marine debris must be understood as a process not just removed. Rates of recruitment, decay and actual impacts vis-à-vis natural disturbance (storms) need to be quantified.
- Impacts from vessel groundings need to be objectively assessed. An acre of blue green algae around a grounded vessel may add to the biodiversity of the bottom and may not actually damage the reef.

- Impacts from introduced species need to be studied and understood.
- We need to know what the present-day managers plan to do, and what their information needs are.
- We need to know what the present day managers plan to do, and what their information needs are.

Five years of data collection is now maturing to a point where it represents a time series; patterns are emerging, and various pieces of the ecosystem puzzle are beginning to fall into place. It is time to reanalyze this new database. It is time to identify priorities and develop a plan. This, in fact, is a major objective of this symposium.

In summary, what have we learned from past lessons? First, a vast inventory of integrated knowledge has been accumulated by many generations of scientists and also by the Hawaiians, who in some instances have been our teachers. Secondly, and very interestingly, terrestrial ecosystems appear to be more fragile than their marine counterparts. This may be due to the "openness" of marine ecosystems to constant colonization (recruitment). In other words, marine ecosystems appear to be much less isolated than terrestrial ecosystems. Third, we have learned that team research produces not only cooperation but also a synergy of understanding. Fragmented data can only lead to fragmented ideas. Finally, the science should not be driven by politics. Rather, it should be a response to ecological problems in need of solution.

Looking back, we have seen four historical phases of formal research; first, the era of the discover/naturalists and massive data collection; second, a phase of synthesis; third, a new phase of discovery and data collection brought on by new instrumentation and high technology; and finally, a phase that we are now entering, which again may be a phase of synthesis. I can think of no better way to end my paper than to quote William Shakespeare in *Julius Caesar* in which he said, "There is a tide in the affairs of men, when taken at their flood leads on to fortune." Indeed, it does appear that "it is on such a full sea that we now stand, and we must take the current as it serves, or lose our ventures."

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# HISTORY OF MANAGEMENT IN THE NORTHWESTERN HAWAIIAN ISLANDS

BY

ROBERT J. SHALLENBERGER[1]

I appreciate the opportunity to speak here today. I'm encouraged by the inclusion of a management paper at a conference focused on research. The distinction between research and management in the Northwestern Hawaiian Islands (NWHI) is necessarily blurred.

I'll start by letting you know what I will not be doing today. I will not speak as an official representative of The Nature Conservancy or the U.S. Fish and Wildlife Service. I will not provide a detailed, chronological review of NWHI management. Also, I will not talk much about fishery management, as there are those who are far more knowledgeable on that subject. I will, however, address what I believe to be the most significant management challenges faced by those responsible for stewardship of NWHI resources.

One of the perks that come with the Refuge Chief job is the opportunity to consult with people in high places. When I asked President Teddy Roosevelt for guidance, he told me "The Nation behaves well if it treats the natural resources as assets which it must turn over to the next generation increased, and not impaired in value." I think it is worthwhile to look back now and then and consider how we have done when measured against this standard. Only then can we make the right decisions about our future course.

## PROTECTION

Commercial exploitation was the earliest management challenge in the NWHI, and the pressure to increase harvest of fishery resources makes it a significant challenge today as well. Commercial harvest of whales, seals, turtles, sharks, and sea cucumbers dates back to the 18th century, from the earliest European explorers. Sealing expeditions in the 19th century drove the monk seal to the brink of extinction. In excess of a million albatross and other NWHI seabirds were taken for their feathers and eggs, both by Japanese poachers and by others under permit from the Hawaiian Kingdom. Nearly a half million tons of guano were taken from Laysan Island alone (Rauzon, 2001). These activities would prove to have significant and lasting biological and political impacts on the NWHI.

Legal protection, as a management tool, comes in many forms. A critical first step occurred when each of the NWHI was claimed on behalf of the Kingdom, the Territory or, in the case of Midway, the United States Government. This solidified the jurisdiction

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issue and avoided the balkanization of management that would have occurred had other nations successfully claimed some of these islands and atolls.

Lasting official protection for fish and wildlife of the NWHI came over time in the form of presidential and congressional action. But it did not come easy. The commercialization of wildlife in the late 19th century was a tragic chapter in the history of resource management. Hundreds of thousands of birds were being sold for their feathers at weekly auctions in America and Europe. An upwelling of concern about the staggering loss of colonial birds resulted in action to ensure permanent protection for important nesting sites and to prevent the marketing of bird products. In 1900, the Lacey Act was passed. This critically important statute provided federal authority over wild birds and gave the Secretary of Agriculture authority to adopt measures necessary to protect game birds "and other wild birds" (Reffalt, 1993).

Achieving protection specific to the NWHI took even longer. At the turn of the century, prominent members of the American Ornithologists Union were focusing their attention on a five-acre island in east-central Florida, called Pelican Island. After several years of unsuccessful efforts to acquire and protect the Island, they discovered an 1890 Deputy Attorney General's legal opinion that the President could reserve public lands by proclamation or executive order under the "implied powers" of the presidency (Reffalt, 2003). This opinion, bolstered by the Lacey Act, was all it took to convince President Theodore Roosevelt to sign the executive order in March 1903 that would establish the first federal bird reservation. It is likely that no one had any idea that the Pelican Island Reservation would mark the inauspicious beginning of the National Wildlife Refuge System, a network of lands and water that a century later would have grown to nearly 550 refuges and nearly 95 million acres.

The floodgates of bird protection did not open immediately. It took more than a year to establish the next bird reservation, at Breton Island in Louisiana. Four more were added in 1905. The deluge came in Roosevelt's last year in office. In all, Roosevelt created 51 bird reservations and 2 big game reservations. The Hawaiian Islands Reservation, created by Executive Order 1019 in February 1909, was number 27 on Roosevelt's list.

The inclusion of the NWHI in the list of new executive orders appears to have been a case of fortuitous timing. Word of poaching in the NWHI had filtered back to Washington, particularly as a result of events taking place at Midway. The confrontation between Commercial Pacific Cable Company employees and Japanese poachers at Midway had resulted in Executive Order 199-A, signed by Roosevelt in 1903. This Executive Order put Midway under Navy control and was followed by a decision to send a detachment of Marines to the Atoll in 1904, to protect both the birdlife and the Cable Company employees.

Regrettably, there were shortcomings in the 1909 Executive Order that proved to be an impediment to effective management that remains unresolved. The Executive Order language describing the Reservation refers to "islets and reefs" of the NWHI. It lists and illustrates all the emergent islands (except Midway, under Navy control) and major reefs, including some with no emergent land. But it did not define the limits of "reefs." The map which accompanied the Executive Order includes an elliptical dotted line around the

Archipelago, but no legend to indicate whether this line was meant to be illustrative or to actually portray a more expansive reservation. So, in the face of an ambiguous Executive Order, the debate over the actual "legal" boundary of the Reservation (later Refuge) has persisted.

Although it did not happen overnight, Roosevelt's 1909 Executive Order provided the direction and authority necessary to stop both the poaching and the previously permitted harvest of seabirds and guano in the NWHI. More importantly, this Executive Order led to the inclusion of the NWHI in the National Wildlife Refuge System, making it subject to, and the beneficiary of, several laws, regulations, and policies put in place to protect lands and waters within this System.

This Executive Order was followed by several federal laws that would further enhance the protective status of sensitive habitats and wildlife of the NWHI. Among the most important statutes were the Migratory Bird Treaty Act, the National Wildlife Refuge System Administration Act, the Endangered Species Act, the Marine Mammal Protection Act, the Magnuson-Stevens Fishery Conservation and Management Act, and the National Marine Sanctuaries Act. More recently, the executive orders establishing the NWHI Coral Reef Ecosystem Reserve have set in motion the process to establish a marine sanctuary in the NWHI.

Enforcing these new protections turned out to be a significant challenge as well. Frequent trips by the Revenue Cutter *Thetis* provided a modest, but critical level of enforcement against poaching in the NWHI until 1916. Yet, it was more than 50 years after the Executive Order before a refuge manager was stationed in Hawaii. In the interim, Pearl Harbor and Midway were attacked, Tern Island was converted for military use, other NWHI were used as bombing targets, and LORAN stations were established at French Frigate Shoals and Kure.

It's easy to understand, in retrospect, how the Pacific war would lead to military use of refuge lands, even without concurrence of the federal agency charged with management of the refuge. It is more difficult to grasp how commercial exploitation of refuge resources would be allowed to occur long after the 1909 Executive Order. In 1927, a large population of black-lipped pearl oysters was discovered at Pearl and Hermes Reef. Owners of the Hawaiian Sea Products Company removed more than 150,000 oysters during a three-year period. Biologists surveying this site in 1930 found the oyster population seriously depleted, and it has not recovered to this date (Rauzon, 2001). The second, more recent commercial project began in 1946, when a private company was issued a Territorial permit to fly fish and green sea turtles to Honolulu, using the Tern Island airstrip.


## VESSEL TRAFFIC


Vessel traffic in the NWHI has proven to be a difficult management challenge of international scope. NWHI reefs are littered with the remains of sailing ships that ran aground in the 18th and 19th centuries. It should not be surprising that these vessels would fall victim to these treacherous reefs. What is more difficult to explain, given the

widespread availability of sophisticated navigational equipment, are the more recent groundings of fishing vessels and freighters. Examples include a Japanese fishing boat on Laysan in 1969 and one each on Kure and Laysan in 1976. The *Anangel Liberty* grounded at French Frigate Shoals in 1980, the *Paradise Queen II* at Kure in 1999, and the *Swordman 1* at Pearl and Hermes in 2000. The burning and sinking of the *Hawaiian Patriot* north of French Frigate in 1977 was a particularly troubling wake-up call, because it demonstrated that grounding was not the only navigation hazard. More than five million gallons of fuel oil entered the ocean but, fortuitously, it was far enough away from the Atoll to avoid serious contamination of this critically important seal and turtle habitat. We'll never know how many birds were oiled at sea.

The good news is that the direct impacts of these recent groundings appear to have been relatively minor, but that was largely a matter of luck. The *Anangel Liberty* dumped 2,200 tons of kaolin clay over the side to lighten the ship enough to pull it off the reef. Fortuitously, currents on that day carried most of the clay out to sea, rather than into the Atoll. Both of the Japanese fishing boats that grounded on Laysan had evidence of rats on board, but they did not take up residence on the Island. Most of the fuel was removed from the *Paradise Queen II* before it broke apart, but the debris from that shipwreck continues to pollute the reef and shoreline at Kure. *Swordman 1* was successfully pulled off the reef, although at considerable cost.

While we have largely dodged the bullet in these recent events, it is almost certainly only a matter of time before a vessel grounding or an at-sea vessel fire becomes a catastrophic event with very serious wildlife and habitat impacts. Considerable spill-response training has taken place in Honolulu and Midway. But the truth is that we are not well prepared to mitigate wildlife impacts at a large spill event, particularly if it occurs at any one of the uninhabited islands and atolls.

Marine debris is another very significant management challenge, made even more difficult by the international scope of the problem. The entanglement of wildlife has prompted an aggressive and collaborative effort among diverse agencies to locate and remove accumulated debris. The significant increase in debris collected in the last two years suggests it may actually be possible to stay ahead of the accumulation of new material. Yet, the long-term solution to this and the related plastic pollution challenge must be found in global efforts to address the source.

## RARE SPECIES

Many of us involved in both research and management in the NWHI have spent the lion's share of our time in the recovery of rare species**.** Indeed, the line between research and management of rare species is particularly blurred. Many of the actions taken to promote recovery have been grand experiments in themselves.

By the time Executive Order 1019 was signed, some NWHI species were already in serious jeopardy. Both the Hawaiian monk seal and Laysan duck were nearly extinct. The Laysan honeycreeper and Laysan millerbird were gone by 1923 after introduced rabbits denuded their habitat. A translocated population of Laysan rails persisted on

Midway, but succumbed in 1941 when rats were inadvertently introduced. Sadly, that loss could have been avoided. A request to ship 20 rails from Midway to Laysan in 1940 was denied by the Territorial government (Rauzon, 2001).

By mid 20th century, the monk seal population had rebounded. Regrettably, and despite a very aggressive management effort, the seal population has since declined by more than half. The commercial harvest of seals was replaced by beach disturbance, entanglement, and depletion of prey as factors contributing to the decline of this species. Laysan ducks have fared much better, but are not out of the woods. A very recent translocation of birds to Midway will serve as an important hedge against a catastrophic event at Laysan.

As we consider our management priorities in the 21st century, I think it is useful to put the recovery program in the NWHI into perspective. This is the only refuge where the entire range of a listed animal species is confined to the limits of the refuge and, in this case, there are at least five that qualify. Most alarming, it is the only refuge on which an animal is known to have gone extinct, and this refuge lost at least three.

## ALIEN SPECIES

Alien species represent an almost intractable management challenge in the NWHI. Of more than 300 plant species recorded in the NWHI, only 37 are indigenous, and 12 are endemic (Rauzon, 2001). The growing list of alien insects is even more disturbing, because the prospect of wholesale conversion of terrestrial ecosystems is very real. Regrettably, we researchers and managers have almost certainly contributed to the problem through the inadvertent transport of alien species.

The good news is that there has been an aggressive effort to address the most serious problem species and to stem the invasive tide. The elimination of rabbits on Laysan and Lisianski, early in the 20th century, reversed the path of destruction created by this thoughtless act of introduction. The much more recent "Cenchrus War" on Laysan was successful in preventing sandbur from converting this relatively simple ecosystem. Strict protocol to prevent further introductions is being aggressively enforced. On Midway, the successful elimination of rats has now resulted in an almost immediate response in the Bonin petrel colony. Rats have also been eradicated at Kure.

The bad news is that for every successful control effort there is another problem species waiting in the wings. Now we are challenged by big-headed ants on Kure and Midway and grasshoppers at Nihoa. In the latter case, the prospect of a total conversion of habitat and potential extinction of the Nihoa millerbird is a real possibility (E. Flint, pers. comm.). We've also seen a rapid spread of weedy plants, such as golden crownbeard and mustard, to Southeast Island at Pearl and Hermes Reef, presumably the result of inadvertent transport from Midway (E. Kridler, pers. comm.). Finally, researchers have documented the presence of alien marine species at several locations and, in particular, at Midway. This underscores the risk that movement of vessels through the NWHI in the future could inadvertently expand the scope of that problem.

## MILITARY ACTIVITIES

Military and Coast Guard presence in the NWHI has left a permanent mark, dating back to the mid-19th century when dredging of a channel at Midway was first begun. The 1903 Executive Order that put Midway under Navy control set in motion the eventual transformation of this atoll for military use. Leading up to the Pacific War, French Frigate Shoals were used for ship and aircraft maneuvers. Creation of the Tern Island runway began in 1942 (Amerson, 1971). Some of the NWHI were used as bombing targets during the war. The Navy pulled out of Tern Island in 1946, while remaining at Midway until base closure in 1997. The Coast Guard operated a LORAN station at French Frigate Shoals until 1979 and at Kure until 1992.

It is impossible to fully assess the impacts of military and Coast Guard activity on fish and wildlife resources of the NWHI, but we do know some things for certain. Military construction and dredging did convert substantial marine habitat. Human activity on beaches at Kure, Midway, and Tern did inhibit use of this habitat by seals and turtles. Nearshore waters were contaminated by fuel and other chemicals, and the use of lead paint at Midway does present a wildlife hazard that was not resolved at base closure. On balance, the military played a critical role in the early control of poaching and enforcement of refuge regulations. The military has also provided indispensable logistical support in transporting managers and researchers throughout the Archipelago. Finally, the military has expended in excess of $100 million to clean up the contamination at Midway and Tern islands, resulting from decades of activity.

## CHANGES AT MIDWAY

I think that the Midway Project deserves some discussion of its own, because it highlights the difficulty in managing costly infrastructure and the challenge of providing legitimate opportunity for public access. The U.S. Fish and Wildlife Service (FWS) had been interested in the wildlife resources of Midway for decades prior to the 1993 announcement of base closure. The FWS signed a co-management agreement with the Navy in 1982 that led to creation of an "overlay" national wildlife refuge in 1988. It, then, should have been no surprise that the FWS was eager to manage this site when the Navy announced it was leaving. However, the disturbing prospect of operating and maintaining this complex facility led the FWS to consider other options. Also, knowing that this heavily modified site could accommodate public use with minimal impact, the FWS explored ways to make public visitation a management objective.

The selected approach was to enter into a cooperative agreement with a private entity with the manpower and experience necessary to operate the facility and to develop a viable public-use program. The premise was that income derived from the public-use program would pay for the cost of the operation. Two companies submitted proposals, and Midway Phoenix Corporation was selected. The cooperative agreement was signed, and the first visitors arrived in 1996.

The project succeeded in achieving its principal objectives in the first three years

of operation. Regulations in place to minimize disturbance to monk seals seemed to have worked, as monk seal use of Sand Island beaches gradually increased. Several thousand visitors enjoyed Midway's natural and historic resources. Unfortunately, the relationship with the Midway Phoenix Corporation deteriorated, eventually resulting in termination of the partnership.

The termination of the relationship has forced the FWS to put most of the public-use program on hold and consider alternative strategies for future operation of the facility. It remains to be seen whether a solution will be found that ensures adequate funding for facility operation and enables rebuilding of a visitor program. Regardless, there are some lessons to be learned. Midway does, in my opinion, represent the single most viable opportunity for providing the public with a "window" on the refuge. The trick is to do so without adversely impacting the site or the fish and wildlife resources that inhabit the area.

## INTERAGENCY COLLABORATION

The last, but certainly not least serious management challenge I will mention is interagency collaboration. The critical need for collaboration has its origin in the various executive orders and acts of Congress that have divided responsibilities among many players (Shallenberger, 1984). The Navy was given jurisdiction over Midway in 1903. Teddy Roosevelt's 1909 Executive Order gave responsibility for the Hawaiian Islands Reservation to the Department of Agriculture. The Hawaii Organic Act and Hawaii Admission Act gave the Territory responsibility for nearshore waters of the NWHI, except Midway. In 1936, Franklin Delano Roosevelt gave jurisdiction at Kure Atoll to the Navy. President Truman mistakenly "restored" jurisdiction over Kure Atoll to the Territory in 1952, despite the fact it had been included in the Hawaiian Islands Reservation by EO 1019 in 1909. More recent legislation split management responsibility for seals and turtles among FWS, NMFS, and the State. National Ocean Service joined the game in December 2000 when Executive Order 13178 created the NWHI Coral Reef Ecosystem Reserve.

Let me qualify this discussion by noting that there have been numerous examples of very effective interagency collaboration in the NWHI, in spite of the jurisdictional quagmire. Just a few notable examples include the State/FWS agreement in the 1950s for joint surveys in the NWHI, the Tripartite studies in the early 1980s, the NOWRAMP expeditions, the Sanctuary Advisory Council, the net debris retrieval project, the Head Start seal recovery project and, more recently, the "Navigating Change" Hokulea project.

Let me also point out that the division of jurisdiction and authorities in the NWHI does not have to be an impediment to successful resource management. In fact, it can be a huge asset. Truly effective collaboration enables the agencies to pool their authorities, their money, and their staff expertise to achieve common objectives. For some reason, this level of collaboration seems easier to achieve among researchers than among managers. The recently published summary of information needs in the NWHI demonstrates that fact. I think we managers spend too much time strutting our stuff and

arguing about who is in charge. That sounds more like "egosystem" management to me.

In order to promote effective management collaboration, we will have to step back and view the resource issues on an ecosystem level first. Then, and only then, can we begin to explore how our individual authorities, resources, and expertise can be strategically applied and complement one another.

The management agencies involved have taken an important step forward by developing a draft memorandum of agreement to promote coordinated management in the NWHI. Although this document has stalled for the moment in the bowels of one or more agencies, it does hold promise for the future. To be truly collaborative, agencies must explore how their differing authorities and regulations can complement one another and provide the depth of protection needed. It remains to be seen whether or not the sanctuary proposal can provide the framework necessary for this level of collaboration. I suspect it will only happen if the agencies decide that collaboration to achieve ecosystem-based goals is a whole lot more productive than turf.

## CONCLUSIONS

I'll end where I started, with reference to Teddy Roosevelt's management standard. As we close the first century of active management in the NWHI, is it fair to say that we are passing on this natural resource increased, and not impaired in value? I think the candid answer is that we have won some and lost some. We face a greater array of threats, but we're armed with a far more substantial body of knowledge and greater layers of protection.

I'd like to wrap this up by passing on some advice for those of you who will carry the torch beyond this point:

1. Resource managers must find ways to collaborate effectively at the ecosystem level.
2. The application of new technologies to resource management and research in the NWHI is already changing the way we look at this place. The best is almost certainly yet to come.
3. Most of the major management challenges in the NWHI are proving to be global in scope. The solutions must be global as well.
4. Strict protocols to minimize the threat posed by alien species must be developed and rigorously enforced. The prospect of radical ecosystem conversion is very real.
5. A very cautionary approach to resource exploitation is warranted, particularly in the absence of adequate information.
6. The tools for effective management lie in the information generated by research.
7. Finally, do not underestimate the critical importance of an enlightened public and support from people in high places. Indeed, nothing of lasting significance will ever be accomplished without both.

Of course, resource management can only work well if supported by the body

of knowledge that derives from research. I am both inspired and awed by the dramatic growth in interest in the NWHI by the research community. I wish you the best success in your endeavors here and beyond.

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# ECONOMIC RESEARCH ON THE NWHI – A HISTORICAL PERSPECTIVE

BY

SAMUEL G. POOLEY[1] AND MINLING PAN[1]

## ABSTRACT

Economic research on the Northwestern Hawaiian Islands (NWHI) living marine resources began as early as the State of Hawaii's fishery development plan in the late 1970s.  Subsequently, there was more detailed economic research on the NWHI lobster and bottomfish fisheries.  More recently, there has been economic analysis concerning the value of the NWHI as a coral-reef ecosystem.  While the economic value of fisheries is fairly straightforward, valuation of ecosystems is much more difficult.  In this paper we review the literature and offer suggestions for future research directions.

## INTRODUCTION

Commercial operations have been conducted in the NWHI since the early birding, sealing, and guano mining operations in the 1800s and early 1900s.  Commercial fisheries have been conducted since at least the immediate post-World War II years, and it is likely there were economics studies conducted on these fisheries and fishing opportunities during those formative periods that we have not uncovered.  We are aware of economic research and analysis of these fisheries since the late 1970s, when the State of Hawaii's *Fishery Development Plan* (1979) was prepared.  We surveyed economic research that has been published (including some papers that were released as technical reports) for both the NWHI fisheries and its ecosystem as a whole.  Given the broad variety of research available, we subdivided this research into four categories based on research objective and topic (Fig. 1).  These categories include production economics (e.g., cost-earning studies, production efficiency, and harvest capacity), marketing, decision support, and ecosystem and natural resource valuation.  We first summarized the economic research in each category, and then assembled a bibliography of all research articles reviewed and referenced.

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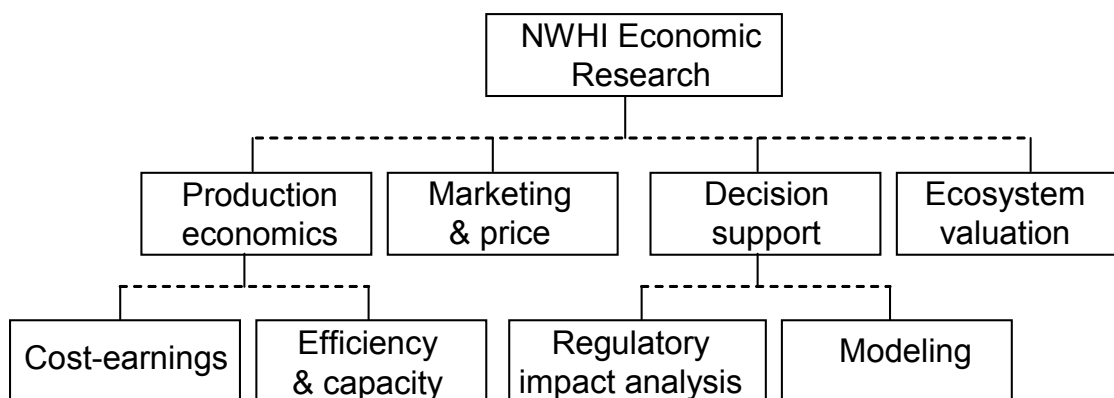
**Figure 1**. Categorization of NWHI economics research..

## PRODUCTION ECONOMICS

Economic research in the late 1970s addressed the potential for expansion of fishery production in Hawaii..  The first *Fishery Development Plan* for the State of Hawaii was prepared by the Department of Land and Natural Resources in 1979 where the economic benefits of potential expansion of Hawaii's fishing industry were estimated in terms of landings, value, and employment.  The central components for the NWHI portion of this plan were lobster and bottomfish, where the estimated present discounted value of direct income derived from the projected increase in catch was $168 million through the year 2000.

Subsequently, a number of discrete studies of the costs and earnings of commercial fishing vessels operating in the NWHI were conducted, primarily by economists at the National Marine Fisheries Service (NMFS) Honolulu Laboratory or others working with these economists.  The lobster fishery for spiny and slipper lobsters was the dominant commercial fishery in the modern era, followed by the bottomfish fishery for snappers, groupers, and jacks.  The first economic feasibility study on the lobster fishery was conducted by the NMFS Honolulu Laboratory as part of the fishery exploration and development effort of the late 1970s (Adams, 1978).  Like much applied research, that study focused on what was then an important management question, the optimal harvest size of lobsters.  Subsequently, studies focused more on the catch rates required for economic feasibility, which were the primary management tools following minimum size regulations.  Clarke and Pooley (1988) conducted an intensive cost-and-earnings survey of all vessel owners (and in some cases, captains) in the NWHI lobster fishery.  Interestingly, and probably not surprisingly, the authors showed that mid-sized, owner-operated vessels had clear economic advantages over larger or smaller vessels (larger vessels had high fixed costs while smaller vessels had trouble generating adequate revenue to cover travel costs), and over the vessels with hired captains (suggesting the classical principal-agent problem could be exhibited simply by looking at relative economic returns).  Because the lobster fishery had some unique characteristics from an economic research perspective, the NWHI lobster fishery also attracted studies of fleet dynamics (Gates and Samples, 1986) and governance (see the following section on Decision Support).

Probably the most significant production economics study was the creation of an original bioeconomic model of the lobster fishery by Clarke et al. (1992). These authors wedded the earlier cost-earnings analysis to several surplus production models of the lobster resource, including a new variation on the Fox model. The economic model utilized an opportunity-cost-of-labor approach at open-access equilibrium to modeling wage rates, instead of proxy wage rates from other (usually shoreside) businesses, as used in most bioeconomic models. The conclusion of this study was that given the cost structure of the fishery (dominated by the travel distance to the fishing grounds), the fishery could be self-regulating, absent some exogenous event, which would spur new entry (e.g., the subsequent moratorium on longline fishing in Hawaii).

There were also two cost-earnings studies of the NWHI bottomfish fishery (Pooley and Kawamoto, 1990; Hamilton, 1993). Both studies were classic cost-earnings survey studies. Because the NWHI bottomfish fishery was more heterogeneous than the lobster fishery (in the sense of vessel characteristics and target species), fewer generalizations could be gleaned from these studies. An issue facing the NWHI bottomfish studies was the modeling of economic vs. financial returns for these vessels, particularly given a period of high economic returns for alternative investments. The average net economic benefit was found to be negative in both studies, but both studies also showed a positive financial return when standard accounting was applied to the cash flow. What was clear upon discussion with the fishermen was that bottomfishing was more of a way of life than lobster fishing, whereas the lobster vessel owners and captains tended to be more business-oriented in a classical microeconomic, opportunity-cost perspective.

Once the basic cost-earnings structure of the commercial vessels operating in these fisheries was determined, it became possible to undertake assessments of the economic efficiency and capacity of the NWHI lobster and bottomfish fleets as a whole. The first such study used a "topographic" approach to individual vessel operations data (termed "data envelopment analysis," or DEA) for the NWHI bottomfish fishery (Pan, 1994). This method was used to evaluate the impact of fishery regulations, ownership patterns, and ex-vessel fish prices on the production efficiency of bottomfish vessels. Results indicated that the large vessels fishing in the Ho'omalu Zone, the more distant limited-entry area, had higher production efficiency and more stabilized fishing behavior than the smaller vessels fishing in the Mau Zone, the open-access area when the research was conducted. The study also found that the owner-operated vessels were more efficient compared to vessels under hired captains (much as found by Clarke and Pooley, 1988, in the lobster fishery). Ex-vessel fish price received by each individual vessel also was a critical factor affecting its production efficiency.

Subsequently, NMFS originated a national approach to estimating the "capacity" of fishing vessels. Pan (2003) used the DEA approach to estimate fleet capacity in both the NWHI lobster and bottomfish fisheries. Preliminary results suggested there was excess capacity in both fisheries, with the very strong caveat that this may have been exacerbated by recent regulatory changes (e.g., the intermittent closures of the NWHI lobster fishery in the late 1990s, followed by its complete closure in 2000, and the effects of an Executive Order on operations of the NWHI lobster and bottomfish fisheries). The

second-stage capacity assessment, through applying a regression analysis, confirmed that over 70% of the excess capacity in NWHI lobster and bottomfish fleets resulted from regulatory changes and declining stocks (Pan and Nguyen, 2004).

## MARKETING AND PRICES

Hawaii's commercial fisheries production is famous for responsiveness to quality, with most seafood being a fresh product. In a conceptual look at Hawaii's seafood markets, Pooley (1986) identified the combination of strong fresh-fish auctions and the ability of commercial fishermen to sell outside the auction systems as particularly important in maintaining a competitive market, ensuring price premiums for high-quality fish and providing some price stability for fishermen. The auctions provided a highly visible spot market where price information was centralized, while the bilateral arrangements between individual fishermen and wholesale dealers (and in some cases restaurants and other retail outlets) helped compensate for fluctuations in price.

This was not the case for most of the history of the NWHI lobster fishery, where a frozen-tail product was preferred. But even in this case, identifying Hawaiian spiny and slipper lobster tails as a high-quality product helped establish a strong market niche for their product form (although, ironically, one of the most successful vessels accomplished its profitability by minimizing costs at the expense of lower per unit revenue). Samples and Gates (1987) examined the market conditions facing the lobster fishery in the middle of its heyday. Subsequently, at the nadir of the lobster fishery, there was an effort to land live lobster for the Asian export market with mixed success largely due to recessions in many Asian economies at the time.

In the bottomfish fishery, in both the Main Hawaiian Islands (MHI) and the NWHI, the market was a critical determinant of success. Pooley (1987) examined price flexibility functions (the relationship of changes in price to changes in quantity supplied) for fresh bottomfish in Hawaii. As with an earlier study of Hawaii's commercial fishery markets (Adams, 1981), he showed strong competitive pressures in the market, as well as a long-term growth in demand. The latter accounted not only for demand growth in terms of Hawaii's resident population and as a tourist destination (particularly the growth of the Japanese tourist market in the 1980s) but also concerted efforts on the part of Hawaii's fishing and seafood industry, assisted by the State of Hawaii, in promoting locally caught fish for "white table cloth" restaurants.

## DECISION SUPPORT

There is a suite of studies focused on regulatory impact analysis which could be used by fishery managers in their decision process. Samples and Sproul (1987) predicted the potential gains in profitability of the NWHI lobster fleet from a hypothetical limited-entry program. In their subsequent study (1988), they assessed five different types of regulations to determine the feasibility and outcome of these management alternatives in the NWHI lobster fishery. This study indicated that all five management measures considered were enforceable, but only licensing could generate higher profits to the

NWHI lobster industry.  After limited entry and catch quotas were implemented in the NWHI lobster fishery, Townsend and Pooley (1995) considered that the management regime might have created unnecessary uncertainty and hardship in the fishery, and they suggested a corporate management approach which invokes the same set of private incentives that a market economy relies on.  Interestingly, evidence of private bargaining to reduce fishing effort (the number of participants) was found in the NWHI lobster fleet in 1998 (Townsend and Pooley, 2003).  The authors suggested more sophisticated understanding of private and public decision-making, which might lead to a better way to manage fisheries.

In 1986, the Western Pacific Regional Fishery Management Council called for an annual report comprised of a series of independent reports (modules) on the aspects of each fishery.  Pooley and Kawamoto (1988) presented the first economic "module" under the bottomfish fishery management plan for the Council.  These modules compile economic data and research findings, and have provided fundamental information to support the decision-making process of fishery management in western Pacific areas.

The project "Economic Contributions of Hawaii's Fisheries (1997-1998)" by Sharma et al. (1999) measured the economic impacts of the various fisheries in Hawaii through an Input-Output (I-O) model by computing output, income, and employment multipliers for Hawaii's fishery sectors.  NWHI fisheries were included as one of the five fishery sectors.  These scientists provided estimates of the linkages of the fisheries sector to the other sectors of the State's economy, its relative importance compared to the other sectors, as well as income contribution effects.  Therefore, this model can be used to help to assess the impact of fishery regulations on various sectors of Hawaii's economy.  This model was updated and modified by SMS research Inc. (2004).  Cai et al. (2005) applied this model to analyze the regulatory impacts of the swordfish closure to the fishing industry and Hawaii's economy.

Another set of research efforts was focused on building a functional model that allowed decision-makers to quantify regulatory impacts, and predicted changes in associated fishing activities.  The first modeling effort associated with NWHI fisheries was a linear programming model of Hawaii's commercial fisheries developed by E.R.G. Pacific, Inc. (1986), subsequently modified and extended by the NMFS  (Kasaoka, 1989 and 1990).  The initial objective of the model was to analyze the potential impact of limited-entry programs on various fisheries and on the economic performance of various fishing fleets.  However, the results of the baseline run of the model did not realistically depict the actual fishery situation in Hawaii, probably due to the omission of the micro-level decision-making by fishermen.

Pan (1998) and Pan et al. (2001) presented a Multilevel and Multiobjective Programming Model (MMPM) in an attempt to incorporate the micro-level decision of the fishermen.  To depict the reality of the fisheries, the decision variables of the model were defined as fishing effort by fleet, target species, area, and season.  The model covered nine fleet categories, ten target species, five areas, and four seasons.  Catch per unit of effort (CPUE) included targeted and incidental catch species as a nonlinear relationship between CPUE and effort.  Detailed formulations and data sources of the model were documented in technical reports by Leung et al. (1999) and Pan et al. (2000).

The NWHI lobster fishery was included in the MMPM as one of the fishing activities of the multipurpose fleets, and the NWHI bottomfish fishery was included as one of the activities of the commercial handline fleet.

However, direct applications of the MMPM in evaluating new area or seasonal closure regimes were limited given restrictions inherent in the model's area classification. Since area closures are a common practice in fishery management, it was necessary to modify the MMPM by incorporating a flexible area classification to meet the unique management needs of Hawaii's pelagic fishery. An on-going study is modifying the allocation model (MMPM) to include more flexible fishing areas and seasons and develop a user-friendly framework (Nemoto, 2004).

## ECOSYSTEM AND NATURAL RESOURCES VALUATION

Traditionally, benefits associated with the consumption of fishery resources have been the main focus in fisheries economics research. However, since purported fishery interactions with protected species and related environmental issues recently threatened the continuation of the NWHI fisheries, there is also value to be gained from research on economic valuation of these non-tradable resources (e.g., protected species, coral reefs).

The first economic valuation of protected species (Hawaiian monk seals) in the NWHI was done by Hollyer (1989). Given that monk seals might have been harmed by fishery development, the study assessed the social costs and benefits of a closure of the <20-fathom range under a variety of discrete circumstances using the contingent-valuation method. Assuming a situation where there would be a 100% loss of the lobster fishery due to closure of the 10-20 fathom range, the study found that households in Hawaii would be willing to pay a lump-sum contribution to save monk seals. This study demonstrated that seals had a positive social value. However, as the author indicated, such conclusions were derived using a method with numerous caveats. In reality, the public's willingness to pay (WTP) might not be as large as the estimated $93.84 per household due to ambiguities in valuation based on inability to separate monk seal "values" from other endangered species values and on budget allocation problems within income categories. There was also a lack of solid evidence linking lobster fishing with the decline in the birth rate and general health of the monk seal population that challenged underlying premises of the WTP approach.

Cesar et al. (2002) conducted an economic valuation of Hawaii's coral reefs. This study estimated the total economic value based on the goods and services provided by the ecosystem. The total economic value of coral-reef ecosystems was derived from use (including direct use and non-direct use) and non-use values. Since the total economic value was estimated mainly by goods and services provided by the coral-reef ecosystem, the study concluded that the economic importance of the MHI outweighs that of the NWHI where non-market use was limited. Thus, the value of Hawaii's coral-reef ecosystem focused solely on the MHI. Based on the estimation by Cesar et al., the average annual value of Hawaii's coral-reef ecosystem amounts to $364 million; of that, 70% was recreational value.

**FUTURE DIRECTIONS**

This broad variety of economic research on the NWHI fisheries has provided information useful to fishery management. As fishery management moves toward an ecosystem approach, economic research on Hawaii's fisheries will face new and challenge issues including 1) non-market valuation of ecosystems, protected species, and fishing as a way of living, 2) impacts of fishing restrictions on local supply to restaurants (tourists) and residents, 3) fishermen's (commercial and non-commercial) behavior and how they respond to ecosystem-based regulatory changes, and 4) user-friendly decision support models for fishery managers. While the economic value of fisheries is fairly straightforward, particularly where most value is commercial and not non-market, putting a market value on an ecosystem such as coral reefs or protected species presents a major challenge. That begins with the design and establishment of a data-collection system that views the fishery as one element in terms of the benefits fishery resources provide in an ecosystem setting.

**BIBLIOGRAPHY**

**Adams, M. F. 1978. The economic feasibility of lobster fishing in the Northwestern Hawaiian Islands. Southwest Fisheries Center Administrative Report H-78-23.**

The author evaluates the economic efficiency of a vessel's lobster-harvesting operations given projections of investment cost, operating cost, and revenues. The economic feasibility of the investment was based on a discounted cash-flow analysis for different combinations of discount rate, sustainable catch rate, average lobster weight, and ex-vessel price. The study concluded that for a likely range of discount rates (0.05 to 0.15), the minimum feasible catch rate was between 1.00 and 2.50 for all the average lobster sizes considered.

**Adams, M. F. 1981. Competition and market structure in the Hawaii fish industry. Southwest Fisheries Center Administrative Report H-81-5.**

The objective of the paper was to determine if market structure conditions exist in Hawaii's fishing industry which would permit sellers or buyers to exercise market power and create market distortions. This paper was prompted by previous studies which concluded that sellers or buyers of fish in Hawaii collude. This paper concluded that the market structure conditions do not exist in Hawaii's fishing industry which would permit sellers or buyers to exercise market power and create market distortions. This conclusion was based on the presence of a large number of sellers and buyers who operate in the industry, the share of the market for the largest sellers and buyers, entry conditions, and how the largest firms maintain their market shares over time.

**Cai, J., P. S. Leung, M. Pan, and S. G. Pooley. 2005. Economic linkage impacts of Hawaii longline fishing regulations. Fisheries Research 74:232-242.**

The authors updated the previous Hawaii Fisheries Input-Output (I/O) Model with the most current data and modified model structure so the current version of the model can be used to assess the regulatory impacts of the swordfish closure to the fishing industry and Hawaii's economy. Based on the updated model estimation, if swordfish fishing were shut down (the first scenario), the industry sector's $23 million of output, $11 million in value-added, $5.6 million in income, 218 jobs, and $0.67 million in state tax revenue would be lost.

**Cesar, H., P. V. Beukering, S. Pintz, and J. Dierking. 2002. Economic valuation of the coral reefs of Hawaii. Cesar Environmental Economics Consulting, the Netherlands.**

The objectives of the study were 1) to assess the economic value of selected case study areas and of Hawaii as whole, 2) to determine the economic costs of reef degradation; and 3) to compare the costs and benefits of various management options. The authors estimated the total economic value based on the goods and services provided by the various reef ecosystem functions. Each of these goods and services has an associated economic benefit. The total economic value of coral reef ecosystems was subdivided into use and non-use values. Use values are benefits that arise from the actual use of the ecosystem, both directly and indirectly, such as fisheries, tourism, and beach-front property value. Non-use values include an existence value, which reflects that value of an ecosystem to humans, irrespective of whether it was used or not. Since the total economic value was estimated by goods and services, the study concluded that the economic importance of Main Hawaiian Island coral reef ecosystems outweighs that of the Northwestern Hawaiian Islands, and it focused solely on the Main Hawaiian Islands. Based on the estimation, the average annual value of the coral reef ecosystem amounts to $364 million. This leads to a net present value at a discount rate of 3% (within 50 years) of nearly $10 billion.

**Clarke, R. P., and S. G. Pooley. 1988. An economic analysis of Northwestern Hawaiian Islands lobster fishing vessel performance, NOAA Technical Memorandum, NOAA-TM-NMFS-SWFC-106.**

The economic and operational performance of three classes of lobster fishing vessels in the NWHI was examined. Operational information, from logbook catch and effort data, and economic information, with emphasis on cost-earnings data, was supplied by 12 vessels active during the 1985 and 1986 seasons. Only the Class II, midsized owner-operator vessels were clearly profitable, whereas the larger Class I vessels faced a variety of cost constraints, and the Class III hired-captain vessels faced a number of operational problems. Return on investment was estimated to be 4.0, 36.0, and –8.5% on Classes I, II, and III, respectively. Lobster prices were determined outside Hawaii's

fishery and most often reflected worldwide conditions.  The authors indicated that one particular problem had been the rapid turnover of vessels participating in the NWHI lobster fishery.

**Clarke, R. P., S. S. Yoshimoto, and S. G. Pooley.  1992.  A bioeconomic analysis of the Northwestern Hawaiian Islands lobster fishery.  Marine Resource Economics 7:115-140.**

The authors applied several surplus production-based bioeconomic models to the NWHI commercial lobster fishery.  They found the model which best explains the biological dynamics of the fishery was a modification of the Fox model developed by the authors.  Economic costs were applied within a number of conceptual frameworks to develop the first integrated bioeconomic model of the fishery.  In another development, the opportunity cost of labor based on crew share at the open-access equilibrium level of fishing effort was used instead of proxy way levels.  Given the costs incurred, the fishery appeared to be self-regulating in terms of long-term fishing effort for maximum sustainable yield.  However, exogenous events existed, which could bring a large influx of new vessels into the NWHI lobster fishery.  Therefore, interest in limited entry returned.

**Department of Land and Natural Resources.  1979.  Hawaii Fisheries Development Plan.  State of Hawaii, Honolulu, Hawaii.**

The goal of the "Fisheries Development Plan" was to increase the productivity of Hawaii's fishing industry in terms of landings, value, and employment.  This plan indicated there was resource potential for marine fishery development in the Hawaii region.  While most of the potential exists in the open-ocean tunas, whose boundaries have been defined arbitrarily as 1,500 miles from Honolulu, the potential for development of most other fisheries, essentially all of the bottomfish, lobster, shrimp, *akule*, and *opelu* potential, exists within the NWHI.  The authors indicated a highly positive return from fishery expansion.  However, a variety of constraints and alternatives may affect the development of the fishery.

**E.R.G. Pacific Inc.  1986.  Project Summary: Linear programming model of Hawaii commercial fisheries. Technical in-house report for National Marine Fisheries Service, Honolulu, Hawaii, March 1986.**

The initial intent of the model was to analyze the potential impact of limited-entry programs on various Hawaii fisheries and on the economic performance of various fishing fleets.  In the original Hawaii fishery model, several different fleet types could target various fish and crustacean species.  Seven submodels were created from this generic model of fixed-cost accounting.

**Gates, P. D. and K. C. Samples. 1986. Dynamics of fleet composition and vessel fishing patterns in the Northwestern Hawaiian Islands commercial lobster fishery: 1983-86. Southwest Fisheries Center Administrative Report H-86-17C.**

The authors examined the dynamics of fleet composition and operations of the NWHI lobster fleets during 1983-1986, the period of the expansion of the fishery. The number of permits issued had increased markedly over time. Eleven permits were issued for the 1983 permit season compared with the 51 that were valid during the 1986 permit season. Active vessels increased to 19 in 1986, compared to 1983 when there were only 3 active vessels. Trip effort increased also, and fishing trips had become longer in 1986. The fleet had exerted substantial fishing effort throughout the NWHI. Even though more areas had been fished each year, approximately two-thirds of the total fishing effort was concentrated around three areas.

**Hamilton, M. 1993. Vessel activities, costs, and economic returns. Southwest Fisheries Center Administrative Report H-94-1C.**

This report examined the activity patterns, economic returns, and number of economically sustainable vessels for both the entire NWHI and its components, the limited-entry Ho'omalu Zone and open-access-permit Mau Zone. On average, vessels in the Ho'omalu Zone in 1993 were making a profit on an annual basis, while vessels in the Mau Zone were not making a profit on an annual basis.

**Higuchi, W. K. and S. G. Pooley. 1985. Hawaii's retail seafood volume. Southwest Fisheries Center Administrative Report H-85-6.**

This report presented new and revised tables on Hawaii's 1981 retail seafood volume based on a stratified survey of retail seafood establishments. It provided estimates of retail seafood purchases by source and product state (fresh, frozen, or processed), retail seafood sales by destination, and retail seafood volume by country and species.

**Hollyer, J. R. 1989. Economic allocation of the 10-20 fathom range of the Northwestern Hawaiian Islands: lobster fishery or Hawaiian monk seal critical habitat? Thesis for the degree of Master of Science, University of Hawaii at Manoa.**

In 1986, NMFS signed legislation designating a critical habitat within 10 fathoms for the monk seal. However, the Monk Seal Recovery Team recommended that the best way to reduce risk to the monk seals was to create a critical habitat encompassing the 20-fathom range. This study assessed the social costs and benefits of a closure of the 20-fathom range under a variety of discrete circumstances, using the contingent valuation method. Given that monk seals may be harmed by fishery development, the study suggested that if society chooses to manage the NWHI, a disputed area should be closed to lobster fishing. Such a conclusion was supported by the analysis where: 1)

there will be a 100% loss of the lobster fishery due to closure of the 10-20 fathom range; and 2) households of Hawaii indicated they would willing to pay a lump-sum average contribution of $93.84, or an annual sum of $8.83, to save the monk seals. This study indicated in reality that willingness to pay (WTP) might not be as large as $8.83, but it was important to note that seals had a positive social value that was comparable to the value of lobster fishing. However, the author also indicated several caveats in the study. The most glaring omission was the lack of solid evidence concerning the correlation between lobster-fishing activities and a decline in the birth rate and general health of the monk seal population.

**Laurel D. K. 1990. A linear programming model for the Northwestern Hawaiian Islands multi-fishery. Southwest Fisheries Center Administrative Report H-90-04C.**

The purpose of the project was to modify and expand the linear programming (LP) model for Hawaii's commercial fisheries that was developed initially by Dr. Dennis M. King of E.R.G. Pacific, Inc. This project combined two submodels to form one multifishery model as a new baseline. Many features from the NWHI bottomfish fishery LP model, developed in 1988, were incorporated into this new version. The version of the model enabled the user to simulate different fishery scenarios that may reflect potential industry trends. The model allocated the limited fishing time of each vessel type among fishing areas and target species for each fishing season so as to maximize fleet-wide profits. However, the results of a baseline run of the model did not realistically depict the actual fishery situation in Hawaii. In particular, this baseline solution falsely showed that aku (skipjack tuna) never were caught in any season from any area.

**Leung, P. S., M. Pan, F. Ji, S. T. Nakamoto, and S. G. Pooley. 1999. A bilevel and bicriterion programming model of Hawaii's multifishery. *In*: U. Chakravorty and J. Sibert (eds.), Ocean-scale management of pelagic fisheries: economic and regulatory issues, P. 41-63. Proceedings of an international workshop organized by the Pelagic Fisheries Research Program, JIMAR, University of Hawaii at Manoa, Honolulu, Hawaii, 1997, SOEST 99-01, JIMARContribution 99-321.**

This technical report described the fisheries considered and the procedures and justifications to build a bilevel and bicriterion programming model of Hawaii's multifishery (multiple-species, multi-gear fisheries). The NWHI lobster fishery was included in the model as one fishing activity (target) of the multipurpose fleet, and the NWHI bottomfish fishery was included as one fishing activity (target) of the commercial handline fleet. To illustrate how the model can be used for decision support, the economic tradeoff between the recreational and commercial fisheries was estimated by the model, and results were presented in the report.

**Nemoto, K. 2004. Project progress report: Regulatory impact analysis framework for Hawaii pelagic fishery, Pelagic Fisheries Research Program, JIMAR, University of Hawaii. (http://www.soest.hawaii.edu/PFRP/economics/economics.html)**

The objective of this project was to enhance the multilevel, multiobjective programming model for Hawaii's fisheries that was developed under a previous Pelagic Fisheries Research Program project. This would involve making the basic model structure more tractable for regulatory analysis. It should allow more flexible time-area specification and facilitate updating the underlying data. The update focuses on the Hawaii-based longline fishery. The final technical report is under preparation.

**Pan, M. 1994. Vessel operating efficiency of commercial bottomfish fishery in NWHI. Master of Science thesis in Agricultural and Resource Economics, University of Hawaii.**

This study evaluated the production efficiency of individual bottomfish vessels operating in the NWHI. Through the data envelopment analysis (DEA) method, the study evaluated the impact of fishery regulation, ownership of operation, and fish prices on production efficiency of bottomfish vessels. Vessels fishing in the Ho'omalu Zone, the limited-entry area, had higher production efficiency and more stabilized fishing behavior than vessels fishing in the Mau Zone, the open-access area. In the two areas combined, the owner-operated vessels were more efficient in using owner-paid operating costs than the vessels under hired captains. Ex-vessel fish prices received by each individual vessel also were a critical factor affecting its production efficiency.

**Pan, M. 1998. Multilevel and multiobjective programming model for the Hawaii fishery management. Doctoral Dissertation, University of Hawaii.**

This study developed a multilevel and multiobjective programming model to assist decision-making in Hawaii's fishery. Under various objectives or policy options, the model developed in this study provides optimum solutions by fleet mix, spatial and temporal distribution of the fleet, and harvest level of fish resources.

**Pan, M., P. S. Leung, F. Ji, S. T. Nakamoto, and S. G. Pooley. 2000. A multilevel and multiobjective programming model for the Hawaii fishery: model documentation and application results. SOEST 99-04, JIMAR Contribution 99-324, University of Hawaii at Manoa.**

The authors document the justifications of the formulations of a multilevel and multiobjective programming model and the data that were used to operate the model. To depict the reality of the fisheries, the decision variables of the model were defined as effort by fleet, target species, area, and season. The model covers nine fleet categories, 10 target species, five areas, and four seasons. Catch per unit of effort (CPUE) includes targeted and bycatch species. A nonlinear relationship between CPUE and effort was incorporated into the model. In addition, the current model also improves upon the previous model in the following aspects: 1) the model allows for the inclusion of other fishery management objectives in addition to maximizing fleet-wide profits, 2) several micro-level entry conditions at the fisher's level were incorporated in the current model,

3) unlike the previous model, where fixed cost was charged by season, the current model charges annual fixed cost as long as the vessel was active at least in a season. A baseline model was run, and the model results were compared to the actual fishery activities and performance.

**Pan, M., P. S. Leung, and S. G. Pooley. 2001. A decision support model for fisheries management in Hawaii – a multilevel and multiobjective programming approach. North American Journal of Fisheries Management 21:293-309.**

The authors developed and applied a multilevel and multiobjective programming model to assist decision-making in Hawaii's fisheries. The multilevel aspect of the model incorporated objectives of both policy-makers and fishermen. The use of a multiobjective model was considered essential in fishery management, because the typical fishery policy problem was characterized by more than one objective or goal that decision-makers want to optimize. The current model was applied to evaluate several management issues facing Hawaii's fisheries.

**Pan, M. 2003. Report on quantitative measurement of fishing capacity in Western Pacific Region. National Report to Congress on National Capacity Assessments, National Marine Fisheries Services, NOAA.**

The author presents quantitative analysis of fishing capacity using Data Envelopment Analysis (DEA). The excess capacity defined in the study simply means that a fleet was able to harvest more than it presently does, without being compared with any desired catch level such as maximum sustainable yield. This study covers capacity analysis for four major fisheries under the management of the Western Pacific Regional Fishery Management Council. They were 1) NWHI lobster, 2) NWHI bottomfish, 3) Hawaii longline, and 4) American Samoa longline. Excess capacity may exist in NWHI lobster and bottomfish fisheries. However, additional analyses were needed to determine if the excess capacity resulted from too many boats or from changes in regulations, reduced stock abundances, or fluctuation of the oceanic environment.

**Pan, M. 2004. Quantitative measurement of excess capacity and the implication to fishery management. Proceedings of NMFS Social and Economics Workshop, New Orleans.**

The author discussed the definitions and measurement methods of excess capacity. The study suggested that additional analysis was needed to evaluate excess capacity measurement and to identify possible causes of excess capacity measured by the quantitative methods recommended by NMFS National Capacity Task Force. Through an empirical approach , the study presented analytical tools to examine the causes of excess capacity and to assess whether excess capacity could be a result of changes in regulations, reduced stock abundances, or fluctuation of the oceanic environment. Over 70% of excess capacity of NWHI bottomfish and lobster fisheries may result from regulatory changes and stock reduction.

**Pooley, S. G. 1986. Competitive markets and bilateral exchange: the wholesale seafood market in Hawaii. Southwest Fisheries Center Administrative Report H-86-8.**

This paper explores a seafood market with mixed product forms and types of markets. The Honolulu auction represents a dramatic difference from seafood markets in most places in the U.S. As an auction, it serves to pool information on price, quantity, and quality, creating a quasi-public good in market information and to provide a baseline for nonauction transactions. On the other hand, long-term bilateral arrangements between commercial harvesters and wholesalers serve to overcome transactional problems associated with uncertainty and limited information. As a result, Hawaii's seafood market combines aspects of bilateral exchange with the advantages of a spot market. This study suggested that a combination of competitive auctions and bilateral exchange was a solution to improving the transactional quality of the market.

**Pooley, S. G. 1987. Demand considerations in fisheries management – Hawaii's market for bottomfish. *In:* J. J. Polovina and Ralston, S. (eds.), Tropical Snappers and Groupers: Biology and Fisheries Management, (p. 605-638). Boulder, CO: Westview Press.**

This paper described the market for fresh snappers and groupers in the U.S. as a whole, but emphasized Hawaii in particular. Then the demand for fresh bottomfish in Hawaii was estimated through price-flexibility functions. Finally, some management implications that derive from market demand estimation were explored. Examination of Hawaii's market for bottomfish showed some price volatility in the short run, and long-term demand had been significantly positive, most closely associated with increasing population, tourist arrivals, and exports. Therefore, the author suggested fishery management decisions must take into account the impact of changing supply conditions on the availability and price of fresh bottomfish in the market, since changes in supply may have significant impacts on processors, wholesalers, and the final consumer.

**Pooley, S. G. and K. E. Kawamoto. 1988. Economic report on Hawaii's commercial bottomfish fishery, 1986. Southwest Fisheries Center Administrative Report H-88-1.**

This report described the recent history of Hawaii's bottomfish fishery, provided a preliminary estimate of revenue in Hawaii's bottomfish market for 1986, analyzed fleet dynamics, provided estimates of revenue per vessel for 1986, and proposed a number of research items for Hawaii's fishery.

**Pooley, S. G. and K. E. Kawamoto. 1990. Economic analysis of bottomfish fishing vessels operating in the Northwestern Hawaiian Islands, 1984-88. Southwest Fisheries Center Administrative Report H-90-13.**

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Council's Bottomfish Fishery Management Plan required an estimation of the economic profitability of bottomfish fishing vessels operating in the NWHI. This report provides cost-earnings analysis based on a sample of seven bottomfish vessels, which represented one-quarter of the active vessels in the NWHI bottomfish fishery in 1987. The estimated net revenue on a fleet-wide basis was negative during the period of 1986-1988.

**Pooley, S. G. 1993. Economic analysis of the economic cost of alternative bottomfish regulations. Southwest Fisheries Center, Honolulu Laboratory manuscript 001-93H-MRF.**

Two biological regulations were proposed for Hawaii's bottomfish fishery in the early 1990s. This study estimated the economic cost of those regulations using present-value analysis. The study estimated the annualized present value of the difference in the yield from the fishery over a 14-year period by comparing the baseline (no biological regulations) with three alternatives: a 3-pound size limit, a 3-pound size limit with different assumptions about fishing mortality, and a 3-month seasonal closure. It concluded that revenue in the fishery would decline in the first years of the regulation as yield dropped with a rebuilding schedule then being developed. The yield from the fishery under regulation exceeded the baseline after 6 years of the regulation. However, the cumulative present value of the fishery after implementation of the regulation did not meet the cumulative present value without the regulations. Therefore, this study considered whether the biological benefits from these regulations (especially in terms of reduced risk of catastrophic overfishing) were worth this economic cost.

**Pooley, S. G. 1996. Limited entry in Hawaii's major commercial fisheries. The Economic Status of U.S. Fisheries: 1996. NOAA Technical Memorandum NMFS-F/SPO-22.**

This article discussed the evaluation of limited-entry fishing in Hawaii with an emphasis on the economic impacts. Limited entry had not been a panacea for any of the federally regulated commercial fisheries in Hawaii. Neither of the two NWHI fisheries had prospered in terms of maintaining total revenue from the fisheries. In neither fishery were the population dynamics well understood. Moreover, the potential value of the permits made rebuilding the NWHI fisheries economically viable, with a number of participants in the NWHI lobster fishery agreeing on multiyear closures if required.

**Pooley, S. G. 1996. Economic determination of the optimal number of Northwestern Hawaiian Islands bottomfish vessels. Southwest Fisheries Center Administrative Report H-96-07.**

The author indicated the optimal number of Northwestern Hawaiian Islands bottomfish vessels, through an economic analysis. The procedure of the analysis included: 1) estimating the annual bottomfish pounds taken per NWHI fishing vessel at various levels of economic operation, based on cost-earnings simulators, 2) determining the MSY level of bottomfish in the NWHI and its two regulatory zones, and 3) dividing

the MSY by the annual bottomfish pounds per vessel under various levels or scenarios of economic operations to estimate the optimal number of vessels for the NWHI bottomfish fishery.  It was suggested that the optimal number of vessels was 18.

**Samples, K. C. and P. D. Gates.  1987.  Market situation and outlook for Northwestern Hawaiian Islands spiny and slipper lobsters.  Southwest Fisheries Center Administrative Report H-84-4C.**

The purpose of the report was to portray the past and current marketing situation for NWHI lobsters, and to project market conditions for the next several years.  All indications suggested a positive market outlook for NWHI lobsters.  Demand for NWHI lobster products was projected to grow over the next 2 to 3 years following the general growth in U.S. consumer demand for lobster products, which would tend to generate modest increases in the real price of spiny and slipper lobster tails, somewhere in the range of 3 to 7 percent, annually.  This study concluded that given firm market conditions, NWHI lobster fishermen would have little difficulty marketing their catch.

**Samples, K. C. and J. T. Sproul.  1987.  Potential gains in fleet profitability from limiting entry into the Northwestern Hawaiian Island commercial lobster trap fishery.  Southwest Fisheries Center Administrative Report H-87-17C.**

The Western Pacific Regional Fishery Management Council proposed a limited-entry program for the fishery in the mid-1980s.  Two general forms of entry management were analyzed: control over the types of vessels permitted to fish, and control of the total number of traps permitted.  This purpose of this research was to predict the potential economic gains that could be realized through a hypothetical limited-entry program.  This analysis indicated that, at best, a fully effective limited-entry program, with control over aggregate effort and classes of vessels allowed to fish, would potentially increase annual fleet economic profit from nearly zero to $2.3 million.  However, this report also indicated that there were numerous reasons why gains from an actual limited-entry program may not reach this upper limit.  Actual gains would depend on the composition of the fleet fishing under the limited-entry regime.

**Samples, K. C. and J. T. Sproul.  1988.  An economic appraisal of effort management alternatives for the Northwestern Hawaiian Islands commercial lobster fishery.  Southwest Fisheries Center Administrative Report H-88-12C.**

A variety of analytical tools were used in this report to conduct an *ex ante* evaluation of the feasibility and outcome of effort management alternatives.  This report assessed five different types of regulations in terms of their legal and enforcement feasibility, potential for effort reduction, effects on industry profits, and creation of economic hardship.  The long-run effects of effort management regulation on industry profits were mixed.  Only licensing can generate higher profits due to physical limits placed on effort expansion by licensed operators, or by the potential entrance of new enterprises into the fishery.

**Sharma, K. R., A. Peterson, S.G. Pooley, S. T. Nakamoto, and P. S. Leung.  1999.  Economic contribution of Hawaii's fisheries.  SOEST 99-08, JIMAR 99-327, University of Hawaii.**

The purpose of this research was to estimate the direct and indirect linkages of various fishery sectors, including the NWHI lobster and bottomfish fisheries, to Hawaii's economy.  The study modified the Hawaii Input-Output model and incorporated the recent cost-earnings information of Hawaii's various fisheries into the model.  Therefore, this model could be used to assess the economic significance of each fishery sector to the state economy, in terms of output and income employment.  This model can be used to estimate economic impact of new fishery regulations on fishery sectors themselves as well as the other economy sectors.

**Townsend, R., and S. G. Pooley.  1995.  Distributed governance in fisheries.  *In:* S. Hanna and M. Munasinghe (eds.), Property rights and the environment,.  World Bank.**

Dissatisfaction with traditional fishery regulation led to great interest in distributed governance of fisheries.  In examining the alternative models of distributed governance, the authors found that  rights-based management distributes a very well defined, but narrow, set of responsibilities to individual fishers.  This study suggested that corporate governance, that implements contractual management of fisheries, was an important and powerful alternative for distributed governance in fisheries.  The model of distributed governance, that combines the external structure of contractual management with the internal governance structure of corporate organization, could find applications in the management of other common-pool resources.

**Townsend, R., and S. G. Pooley.  1995.  Distributed governance in the Northwestern Hawaiian Islands lobster fishery.  *In:* S. Hanna and M. Munasinghe (eds.), Property rights and the environment,.  World Bank.**

Alternative management approaches for the governance of the NWHI lobster fishery were evaluated.  Because of the relatively simple nature of the fishery, a wide array of governance structures could be applied to this fishery.  If management options were limited to the traditional rights-based approaches, either individual transferable quota management or transferable trap regulation could be expected to increase the economic rents that the industry would earn.  The administration of either type of rights-based management would be relatively straightforward in this fishery.  On the other hand, the fishery presents a unique opportunity to move beyond government-centered, rights-based management to a contractual model of management between the government and a local cooperative or corporation.

**Townsend, R. and S. G. Pooley. 1995. Corporate management of the Northwestern Hawaiian Islands lobster fishery. Ocean & Coastal Management 28:63-83.**

Limited entry and catch quotas were implemented in the lobster fishery of the NWHI in 1991, during a period of declining stock abundance. However, ancillary rules, such as the use-it-or-lose-it requirement and within-season quota adjustments, had combined to create unnecessary uncertainty and hardship in the fishery. This paper introduces a dramatically different management regime that would create ownership rights in a private management corporation for the current limited-entry permit holders. The corporate management approach invokes the same set of private incentives that a capitalist market economy relies upon for management of most of its natural resources.

**Townsend, R. and S. Pooley. 2003. Evidence on producer bargaining in the Northwestern Hawaiian Islands lobster fishery. Maine Resource Economics 18:195-203.**

The authors documented an example of private bargaining to reduce fishing effort in the NWHI lobster fishery. By 1997, the industry was confronted with a classic derby fishery. In that year, nine boats decided to fish. In the fishing year 1998, holders of 14 NWHI permits agreed that only 4 of the 14 vessels holding permits would fish. Holders of the other 10 permits received compensation not to fish from those who fished. This agreement was frequently referred as the "Hui," which is the Hawaiian word for "group." While ancillary issues frequently deflect regulations, the Hui illustrates low transaction costs of private bargaining as compared to public decision-making. The holders of 14 permits were able to bargain a simple set of rules in a remarkably short period of time, and expensive enforcement mechanisms were avoided entirely. The authors suggested that a more sophisticated understanding of private and public decision-making might lead us to combine their strengths, instead of relying entirely on a government-dominated model of fishery decision-making.

# NORTHWESTERN HAWAIIAN ISLANDS SPATIAL BIBLIOGRAPHY:
## A SCIENCE-PLANNING TOOL

BY

CHRISTINE TAYLOR[1] AND DAVID MOE NELSON[1]

## ABSTRACT

The Northwestern Hawaiian Islands Spatial Bibliography (NWHI-SB) is a science-planning tool that will help the National Oceanic and Atmospheric Administration (NOAA) and partners to plan for future research and project investments in the Northwestern Hawaiian Islands. The main purpose of this tool is to provide text reference and/or spatial metadata on NWHI research using either spatial-area or keyword searches so that scientists may reduce duplicative research, prioritize their efforts, and identify obvious research partnerships in the NWHI region. The NWHI-SB includes a suitable base map of the Northwestern Hawaiian Islands and spatial locations of key characterization information (e.g., published studies and geographic metadata). Using ESRI ArcMap, a user can now pick any combination of polygons from a 100-square-nautical-mile grid layer, and search for bibliographic data that is linked to those squares. One may also search using a combination of query criteria and grid location selections. Conversely, users may also select bibliographic entries and query the system to locate the related 100-square-nautical mile-squares. Standard nautical charts for the area are included as background information. In addition, other geographic data layers may be added into ArcMap for comparison and used as grid selection criteria. This tool is currently available by request.

## INTRODUCTION

In 2002, an unprecedented 351,000 square km were set aside as the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve (NWHI-CRER) by Executive Orders 13178 and 13196. The NWHI-CRER is currently under the management of NOAA's National Marine Sanctuary Program. The National Marine Sanctuary Program (NMSP) is now responsible for future science plans, reserve boundary creation, conservation controls, project planning, joint agency/organizational collaborations, and creation of educational and public relations materials for the NWHI-CRER. Due to the lack of publicly available transportation to the remote Northwestern Hawaiian Islands (NWHI) and the cost of setting up a shipboard expedition, conducting research within the NWHI is very expensive and time consuming. With this in mind, it follows that knowledge of past research, data, and contact information for principal investigators who have

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studied or conducted research in the NWHI is crucial to setting up a new research plan or information-gathering activity for any part of the region. It is for this reason that the NWHI Spatial Bibliography was created.

The Northwestern Hawaiian Islands Spatial Bibliography is a publicly available spatial search engine for bibliographic references, geographic data, and gray literature for the NWHI region. This tool is intended to help guide researchers and scientists toward all available information prior to mission planning, thesis work, or any other research planned for the region. It was conceived from a need to gather the available information, and inspired by the work by David Coleman and Eric Hill (Coleman et al., 2002) at Leeward Community College (LCC) of Hawaii and the *Literature review and cultural, geological, and biological history for the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve* (Eldredge, 2002) put together by Lu Eldredge and his colleagues at the Bernice P. Bishop Museum.

One of the many benefits of this system is its potential for reducing duplication of research in specific areas within the NWHI. In addition, it provides a "who's who" of the experts in the region and will hopefully allow for the formation of new partnerships and cost savings for future research efforts. It also allows the users to visualize where research and information has taken place, which is easier to decipher than a list of references alone. It is essential that any information about the natural and economic resources within the NWHI and the study of them be known to the NWHI-CRER staff, partner programs, and any other organizations or individuals planning to do research about or in the NWHI-CRER.

## METHODS

Existing spatial database projects were investigated in order to determine if a similar tool already existed in which we might be able to incorporate the NWHI bibliographic data rather than starting a project from scratch. LCC's database (Coleman et al., 2002) is similar in concept to the NWHI-SB, but focuses primarily on the main eight Hawaiian Islands, with only a few hundred references for the Northwestern Hawaiian Islands. The majority of LCC's references were for land-based studies in NWHI, and LCC was not in the position to add all the new reference and GIS data. Another geographic data search engine was designed by the Hawaii Natural Heritage Program at the University of Hawaii, but it also focuses on the main eight Hawaiian Islands and could not incorporate data from outside that region. In addition, the University of Hawaii project focuses on linking actual data sets rather than bibliographic references and links to data locations. Clearly, a new spatial database project specific to the NWHI was needed.

ESRI's ArcGIS, the most commonly used GIS product in the world, was chosen as the base program in which to build the spatial bibliography. ESRI's ArcMap 8.1 had just incorporated a feature called a geo-database (Booth et al., 2002). A geo-database enables the user to link a feature-based GIS layer (e.g., points, polygons, lines, grids) to a database using a set of relational tables. Microsoft Access (MS Access) is the default

database format for ArcMap. For this reason, and because of its low cost and popularity, MS Access was chosen to house the bibliographic data and the relational database tables. A user is not required to have both ArcMap and MS Access to use the database; however users must have ArcMap to view and interactively select grids with the geographic component of the system.

A feature data set was created that can represent the differing spatial scales of the represented studies while protecting the potentially sensitive locations of some of the data/information related to the reference information provided (e.g., cultural heritage or natural heritage sites.) Data management is facilitated through a grid-based polygon feature layer representing evenly divided portions of the entire NWHI-CRER. The resulting layer contains 1,364, 100-square-nautical-mile grid squares (Fig. 1). In some cases, a single 100-square-nautical-mile grid square will cover an entire atoll or bank (Fig. 2). It would be extremely difficult for someone to locate specific locations of environmentally or culturally sensitive resources at this scale. Each grid polygon is represented by an alphanumeric code. Every bibliographic or data entry is represented by a project number. The only way to link the two unique identifiers was to create a "many-to-many" relationship table. The "many-to-many" table (Fig. 3) houses every incidence of unique combinations of reference between the grid layer and the bibliographic layer.

Through discussions with LCC's Eric Hill and NOAA's NMFS Honolulu Lab, over 1,500 bibliographic references were obtained. LCC provided the authors with the NWHI portion of its MS Access database, which contained over 300 relevant references. NMFS Honolulu Lab contributed bibliographical references of all the papers for the Pacific region from 1980 to 2003, and The Bishop Museum sent digital text copies of references from the *Literature review and cultural, geological, and biological history for the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve* (Eldredge, 2002). These references, in addition to information that was collected from the NOAA library and Internet resources, form the majority of the references found in the spatial bibliography at this time.

Unfortunately, none of the information came in a format that was easily imported into the database. Every reference needed parsing, and most needed some cleanup. Once the majority of the references were added to the system, all duplicate references were removed, and repetitive or typical typing errors that could be found by querying the database directly were corrected. New references may be typed directly into the system using a data entry and editing form (Fig. 4) created in MS Access specifically for the NWHI-SB or by loading a new table using MS Access' "Append-Query" feature.

Once all of the available data were entered into the database, it became clear that only those references with obvious location names (e.g., Birds of Laysan, Green turtle nesting success in French Frigate Shoals) in the titles or in the descriptions could be geographically linked to the feature layer. In a few cases a name of a type of plant or animal that is endemic to a specific portion of the NWHI was used to determine location. Queries for location names were conducted in MS Access to extract information from the references about location, but this still left many entries without geo-locations. Papers from the Atoll Research Bulletin (ARB) were spatially connected through the ARB Content List and Indexes Report (McCutcheon, 1991) which lists its articles by individual

islands. Spatial locations for each tripartite study (Grigg and Pfund, 1980; Grigg and Tanoue, 1984, vol. 1&2) reference were determined by reading through each study.

Colleagues at the NOAA/NMFS Honolulu Lab suggested that it might be easier to contact the authors to find out where their research had occurred or for what area it represented. However, because many of the references were co-authored, and more than 250 authors were listed in the database, it was difficult to know whom to contact. In order to simplify the task of contacting the authors, the database was queried to sort out the 50 authors that showed up in the database most frequently. MS Access reports linking all of the references to these authors were generated, and each author was sent an Adobe Acrobat file including their references, a map of the grid, and directions on how to fill in the information. Unfortunately, after 2 months, only six authors responded.

## RESULTS

The Spatial Bibliography presently contains over 30 subject categories and can be sorted by over 20 bibliographic or location categories. For the 1,995 references currently available in the database, 930 have some level of geographic location information. These 930 spatially linked references can be sorted within the database and queried by geographic location using ArcMap. The remaining 1,065 references can be found using MS Access' database query functions.

Using ArcMap, a user can now pick any combination of polygons from the polygon grid layer and search for bibliographic data that is linked to those areas (Fig. 5). One may also search the database using a combination of user-defined query criteria and area location selections (Fig. 6). Conversely, users may also find locations of data by selecting bibliographic entries and asking the system to locate the related grids (Fig. 7). A user may also select an individual record and display it in a new window by clicking to the left of any record in a table (Fig. 8). Standard nautical charts for the area are included as background information. In addition, other geographic data layers may be added, by the user, into ArcMap for comparison and use as grid selection criteria.

## DISCUSSION

The NWHI Spatial Bibliography has the potential to be a powerful research tool once it contains all the necessary references for the NWHI, and the spatial connections for all the relevant references are made. The NWHI-CRER office has access to a GIS Specialist at its Honolulu office who will handle the project. The spatial bibliography should enjoy a much faster evolution at the NWHI-CRER office in Honolulu because those researchers, educators, and others knowledgeable in the topics and data referenced in the Spatial Bibliography are much better equipped to maintain it, update it, and ensure the information is correctly geographically linked. They are also much better located to contact authors and data providers for needed information.

The NWHI Spatial Database needs to be made available to the public. The

National Marine Sanctuary Program is looking into porting the tool over to an Arc-IMS (ArcGIS Internet Mapping System), which will allow users to access it online without having a copy on a CD and ArcMap on their desktop. In addition, the system still needs additional references, links to GIS data, and any gray literature relating to the NWHI. Researchers, authors, and data providers should contact Susan Vogt at the NMSP Pacific Region office to obtain a copy of the database or to provide additional information. She can be contacted by email at (`susan.vogt@noaa.gov`).



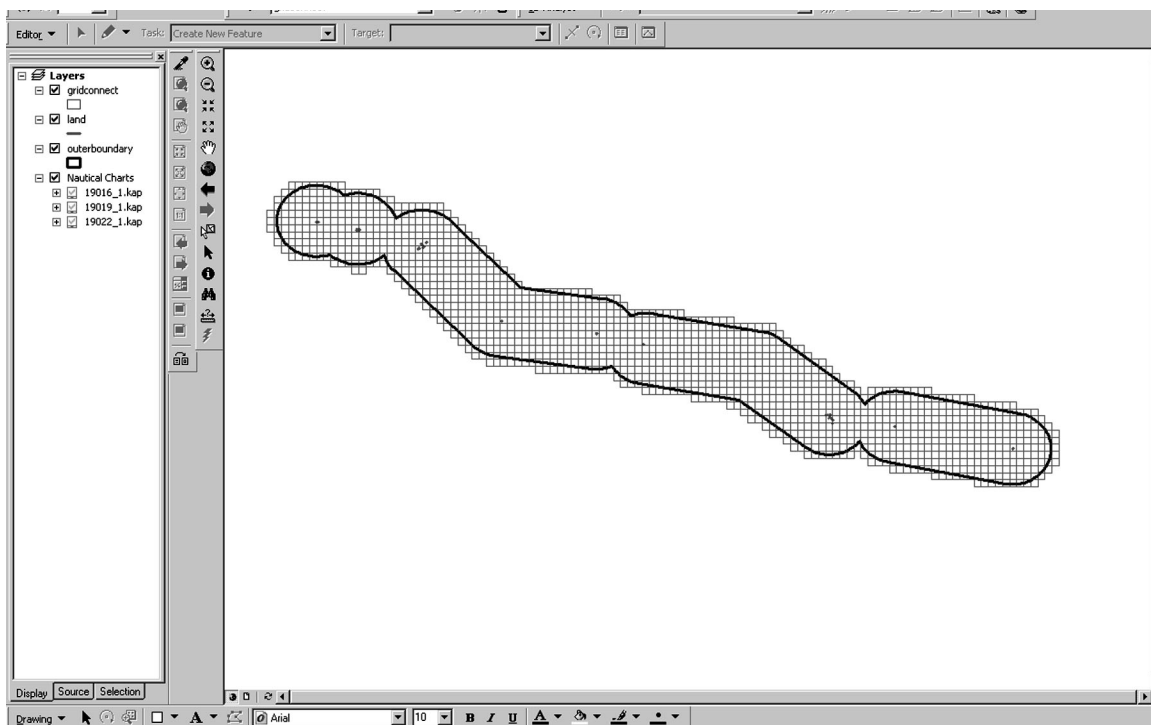**Figure 1**. Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve boundary with 100-sq.-nm grid in ArcMap 9.0
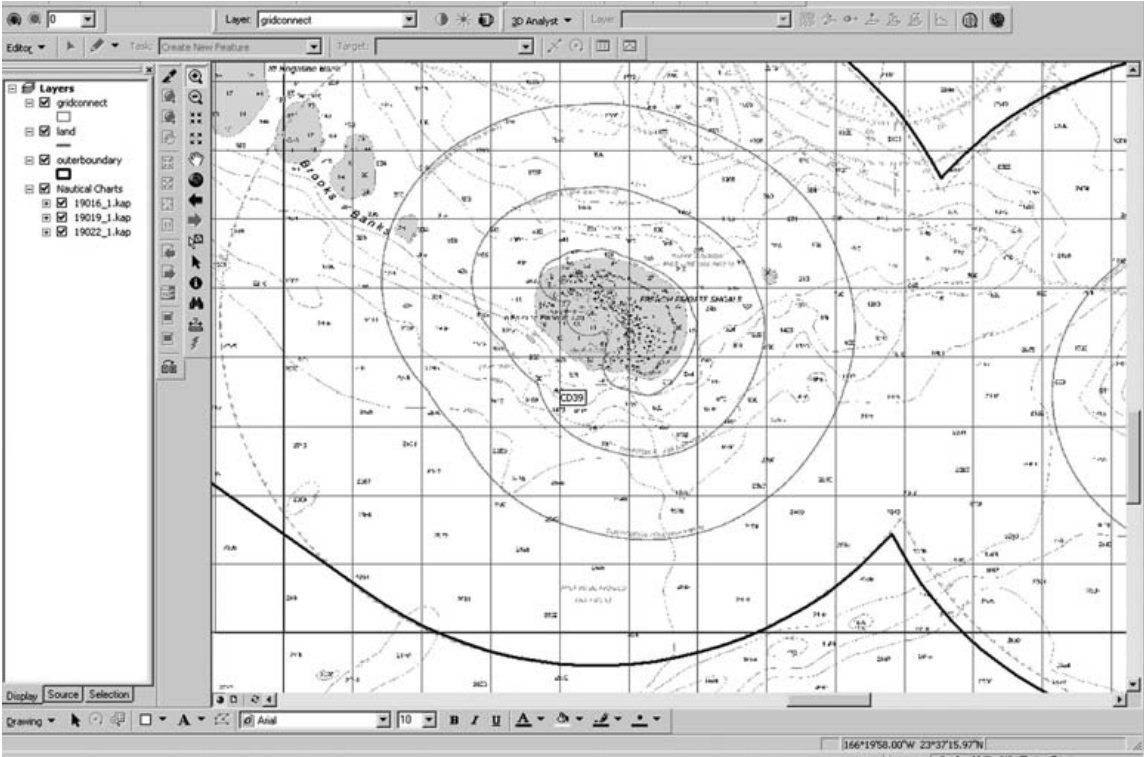
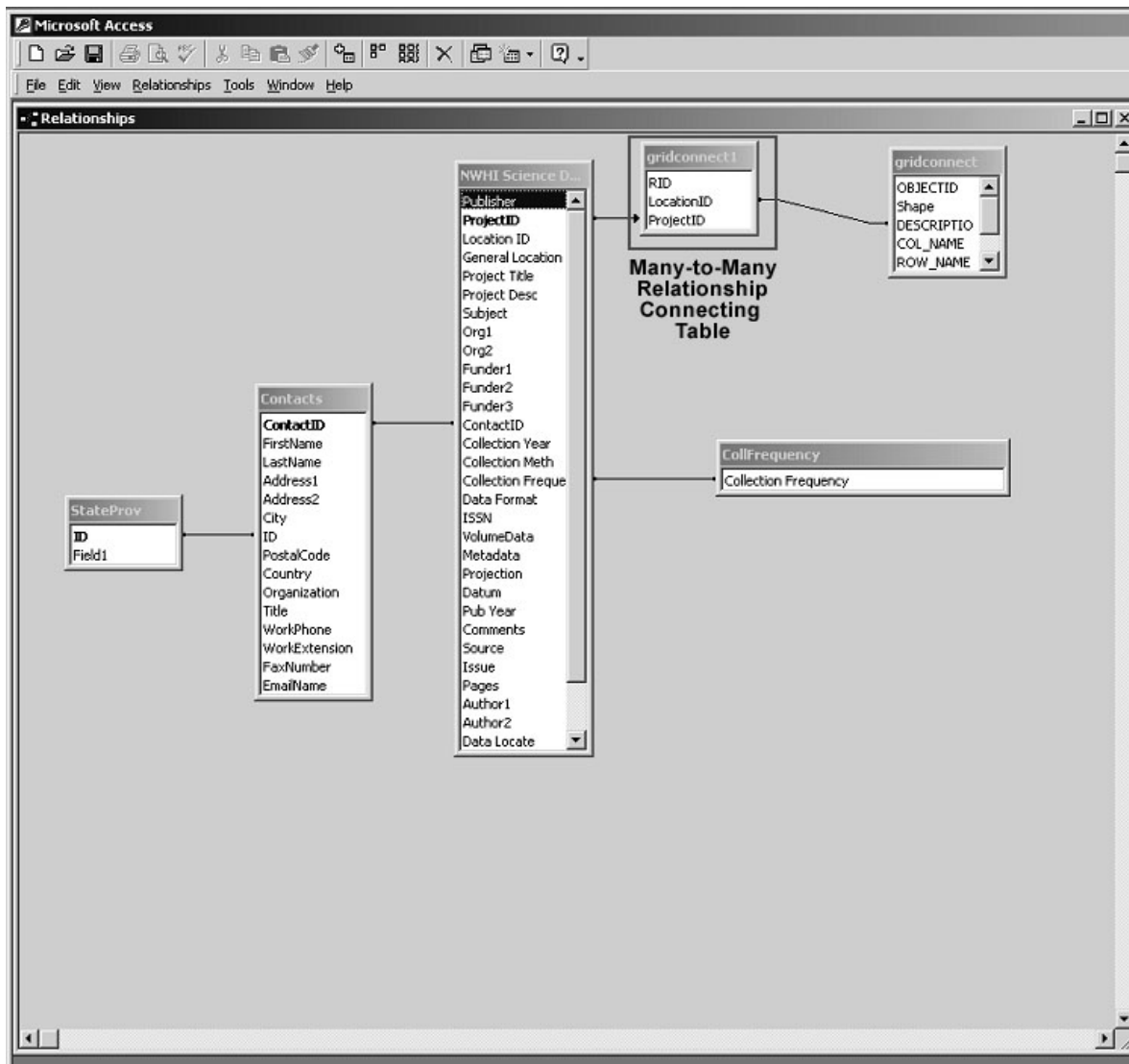**Figure 2.** French Frigate Shoals with overlying 100-sq.-nm grid in ArcMap 9.0

**Figure 3.** The relational database table linkages in MS Access. The Many-to-Many relational table is in the box labeled "Many-to-Many Relationship Connecting Table."
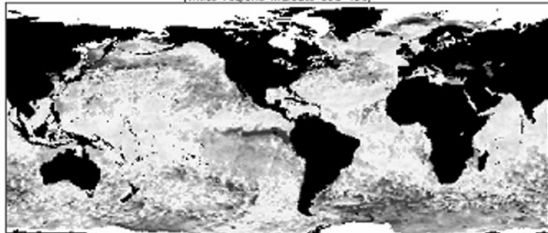
**Figure 4**. View of the MS Access Data input and editing form.

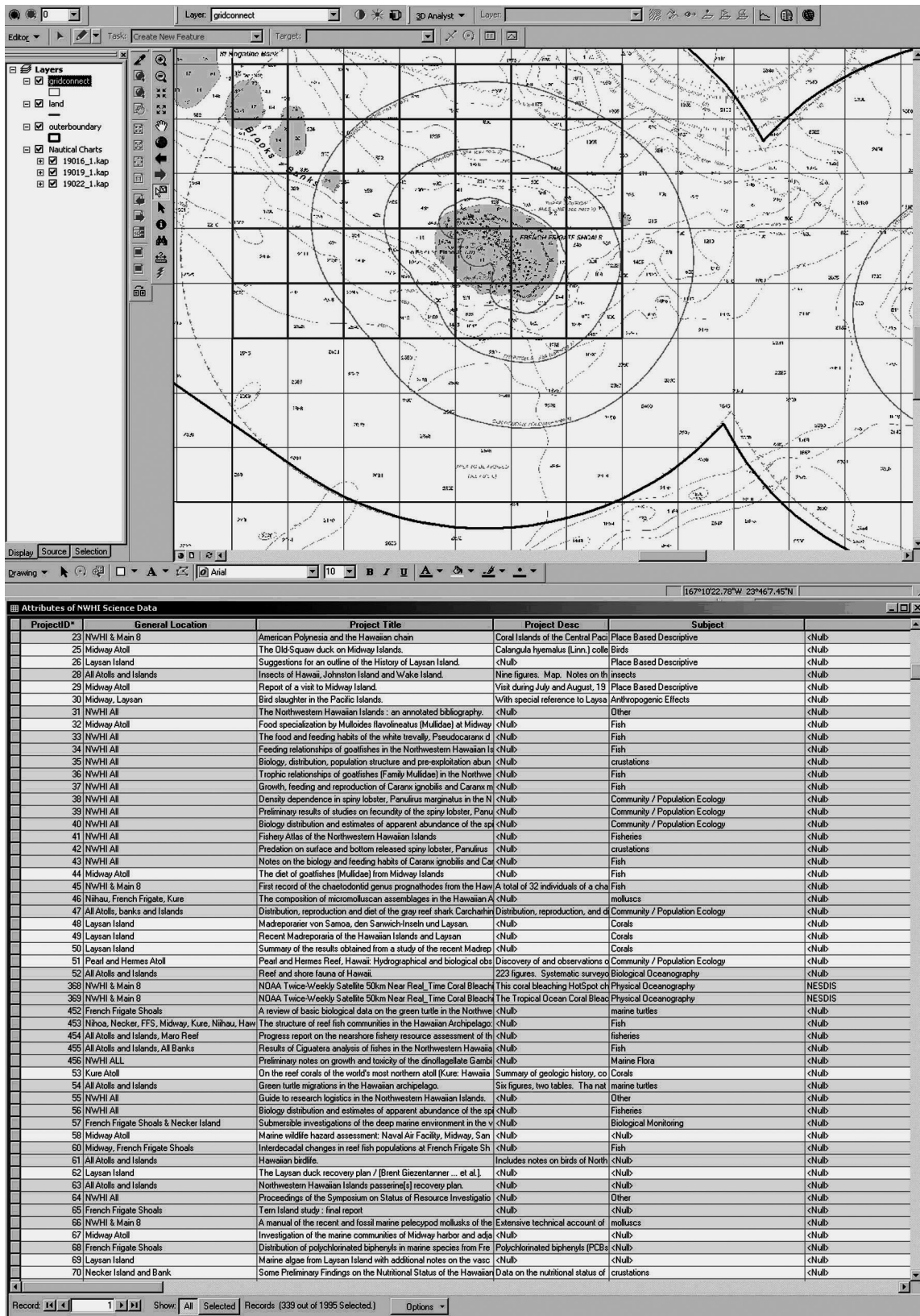| ProjectID* | General Location | Project Title | Project Desc | Subject | |
|---|---|---|---|---|---|
| 23 | NWHI & Main 8 | American Polynesia and the Hawaiian chain | Coral Islands of the Central Paci | Place Based Descriptive | <Null> |
| 25 | Midway Atoll | The Old-Squaw duck on Midway Islands. | Calangula hyemalus (Linn.) colle | Birds | <Null> |
| 26 | Laysan Island | Suggestions for an outline of the History of Laysan Island. | <Null> | Place Based Descriptive | <Null> |
| 28 | All Atolls and Islands | Insects of Hawaii, Johnston Island and Wake Island. | Nine figures. Map. Notes on th | insects | <Null> |
| 29 | Midway Atoll | Report of a visit to Midway Island. | Visit during July and August, 19 | Place Based Descriptive | <Null> |
| 30 | Midway, Laysan | Bird slaughter in the Pacific Islands. | With special reference to Laysa | Anthropogenic Effects | <Null> |
| 31 | NWHI All | The Northwestern Hawaiian Islands : an annotated bibliography. | <Null> | Other | <Null> |
| 32 | Midway Atoll | Food specialization by Mulloides flavolineatus (Mullidae) at Midway | <Null> | Fish | <Null> |
| 33 | NWHI All | The food and feeding habits of the white trevally, Pseudocaranx d | <Null> | Fish | <Null> |
| 34 | NWHI All | Feeding relationships of goatfishes in the Northwestern Hawaiian Is | <Null> | Fish | <Null> |
| 35 | NWHI All | Biology, distribution, population structure and pre-exploitation abun | <Null> | crustations | <Null> |
| 36 | NWHI All | Trophic relationships of goatfishes (Family Mullidae) in the Northwe | <Null> | Fish | <Null> |
| 37 | NWHI All | Growth, feeding and reproduction of Caranx ignobilis and Caranx m | <Null> | Fish | <Null> |
| 38 | NWHI All | Density dependence in spiny lobster, Panulirus marginatus in the N | <Null> | Community / Population Ecology | <Null> |
| 39 | NWHI All | Preliminary results of studies on fecundity of the spiny lobster, Panu | <Null> | Community / Population Ecology | <Null> |
| 40 | NWHI All | Biology distribution and estimates of apparent abundance of the spi | <Null> | Community / Population Ecology | <Null> |
| 41 | NWHI All | Fishery Atlas of the Northwestern Hawaiian Islands | <Null> | Fisheries | <Null> |
| 42 | NWHI All | Predation on surface and bottom released spiny lobster, Panulirus | <Null> | crustations | <Null> |
| 43 | NWHI All | Notes on the biology and feeding habits of Caranx ignobilis and Car | <Null> | Fish | <Null> |
| 44 | Midway Atoll | The diet of goatfishes (Mullidae) from Midway Islands | <Null> | Fish | <Null> |
| 45 | NWHI & Main 8 | First record of the chaetodontid genus prognathodes from the Haw | A total of 32 individuals of a cha | Fish | <Null> |
| 46 | Niihau, French Frigate, Kure | The composition of micromolluscan assemblages in the Hawaiian A | <Null> | molluscs | <Null> |
| 47 | All Atolls, banks and Islands | Distribution, reproduction and diet of the gray reef shark Carcharhin | Distribution, reproduction, and di | Community / Population Ecology | <Null> |
| 48 | Laysan Island | Madreporarier von Samoa, den Sanwich-Inseln und Laysan | <Null> | Corals | <Null> |
| 49 | Laysan Island | Recent Madreporaria of the Hawaiian Islands and Laysan. | <Null> | Corals | <Null> |
| 50 | Laysan Island | Summary of the results obtained from a study of the recent Madrep | <Null> | Corals | <Null> |
| 51 | Pearl and Hermes Atoll | Pearl and Hermes Reef, Hawaii: Hydrographical and biological obs | Discovery of and observations o | Community / Population Ecology | <Null> |
| 52 | All Atolls and Islands | Reef and shore fauna of Hawaii. | 223 figures.  Systematic surveo | Biological Oceanography | <Null> |
| 368 | NWHI & Main 8 | NOAA Twice-Weekly Satellite 50km Near Real_Time Coral Bleachi | This coral bleaching HotSpot ch | Physical Oceanography | NESDIS |
| 369 | NWHI & Main 8 | NOAA Twice-Weekly Satellite 50km Near Real_Time Coral Bleachi | The Tropical Ocean Coral Bleac | Physical Oceanography | NESDIS |
| 452 | French Frigate Shoals | A review of basic biological data on the green turtle in the Northwe | <Null> | marine turtles | <Null> |
| 453 | Nihoa, Necker, FFS, Midway, Kure, Niihau, Haw | The structure of reef fish communities in the Hawaiian Archipelago: | <Null> | Fish | <Null> |
| 454 | All Atolls and Islands, Maro Reef | Progress report on the nearshore fishery resource assessment of th | <Null> | fisheries | <Null> |
| 455 | All Atolls and Islands, All Banks | Results of Ciguatera analysis of fishes in the Northwestern Hawaiia | <Null> | Fish | <Null> |
| 456 | NWHI ALL | Preliminary notes on growth and toxicity of the dinoflagellate Gambi | <Null> | Marine Flora | <Null> |
| 53 | Kure Atoll | On the reef corals of the world's most northern atoll (Kure: Hawaiia | Summary of geologic history, co | Corals | <Null> |
| 54 | All Atolls and Islands | Green turtle migrations in the Hawaiian archipelago. | Six figures, two tables.  Tha nat | marine turtles | <Null> |
| 55 | NWHI All | Guide to research logistics in the Northwestern Hawaiian Islands. | <Null> | Other | <Null> |
| 56 | NWHI All | Biology distribution and estimates of apparent abundance of the spi | <Null> | Fisheries | <Null> |
| 57 | French Frigate Shoals & Necker Island | Submersible investigations of the deep marine environment in the v | <Null> | Biological Monitoring | <Null> |
| 58 | Midway Atoll | Marine wildlife hazard assessment: Naval Air Facility, Midway, San | <Null> | Fish | <Null> |
| 60 | Midway, French Frigate Shoals | Interdecadal changes in reef fish populations at French Frigate Sh | <Null> | Fish | <Null> |
| 61 | All Atolls and Islands | Hawaiian birdlife. | Includes notes on birds of North | <Null> | <Null> |
| 62 | Laysan Island | The Laysan duck recovery plan / [Brent Giezentanner ... et al.]. | <Null> | <Null> | <Null> |
| 63 | All Atolls and Islands | Northwestern Hawaiian Islands passerine[s] recovery plan. | <Null> | <Null> | <Null> |
| 64 | NWHI All | Proceedings of the Symposium on Status of Resource Investigatio | <Null> | Other | <Null> |
| 65 | French Frigate Shoals | Tern Island study : final report | <Null> | <Null> | <Null> |
| 66 | NWHI & Main 8 | A manual of the recent and fossil marine pelecypod mollusks of the | Extensive technical account of | molluscs | <Null> |
| 67 | Midway Atoll | Investigation of the marine communities of Midway harbor and adja | <Null> | Fish | <Null> |
| 68 | French Frigate Shoals | Distribution of polychlorinated biphenyls in marine species from Fre | Polychlorinated biphenyls (PCBs | <Null> | <Null> |
| 69 | Laysan Island | Marine algae from Laysan Island with additional notes on the vasc | <Null> | <Null> | <Null> |
| 70 | Necker Island and Bank | Some Preliminary Findings on the Nutritional Status of the Hawaiian | Data on the nutritional status of | crustations | <Null> |

**Figure 5.** Thirty-five selected grids squares over French Frigate Shoals, and a few of the selected references found for those grids.
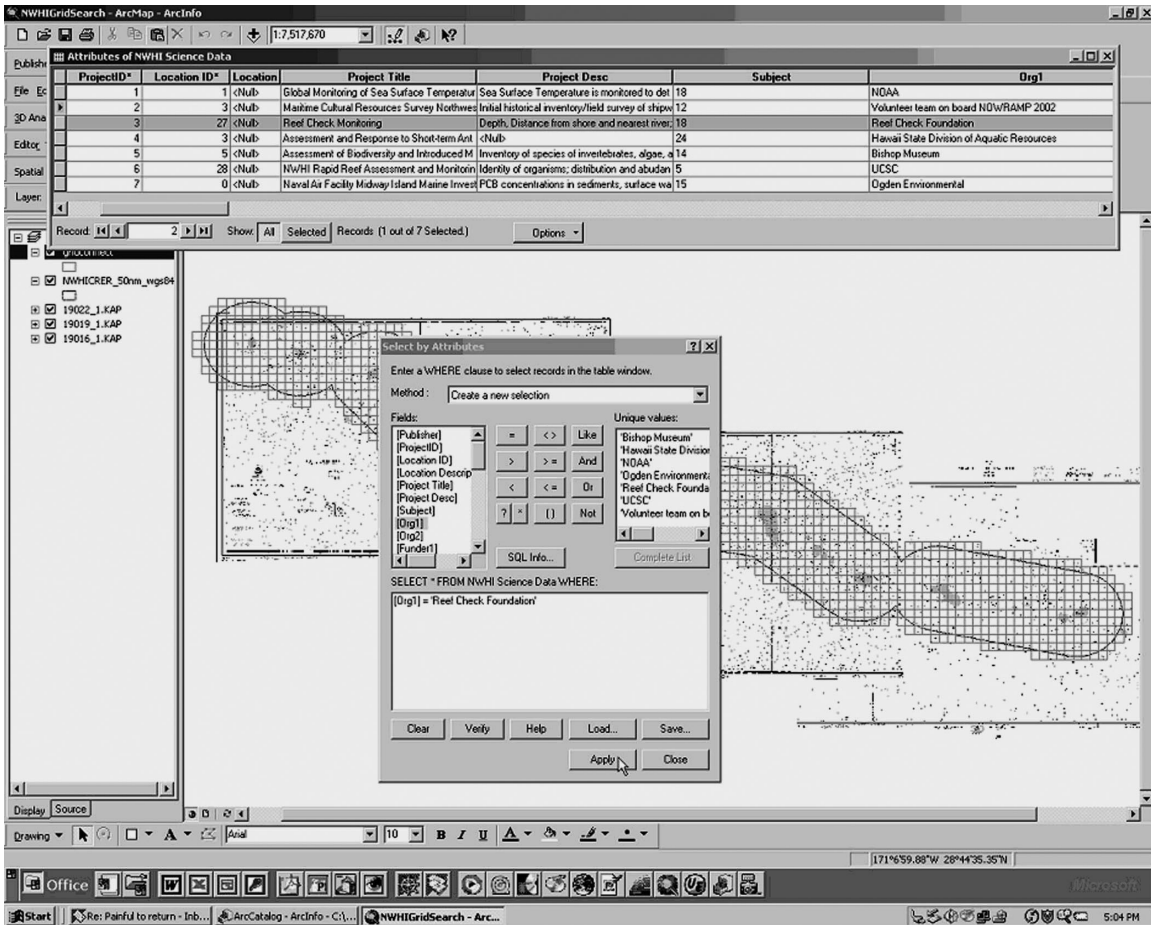
**Figure 6.** References or grids may be selected using attribute query methods alone, or combined with geographic location selections.
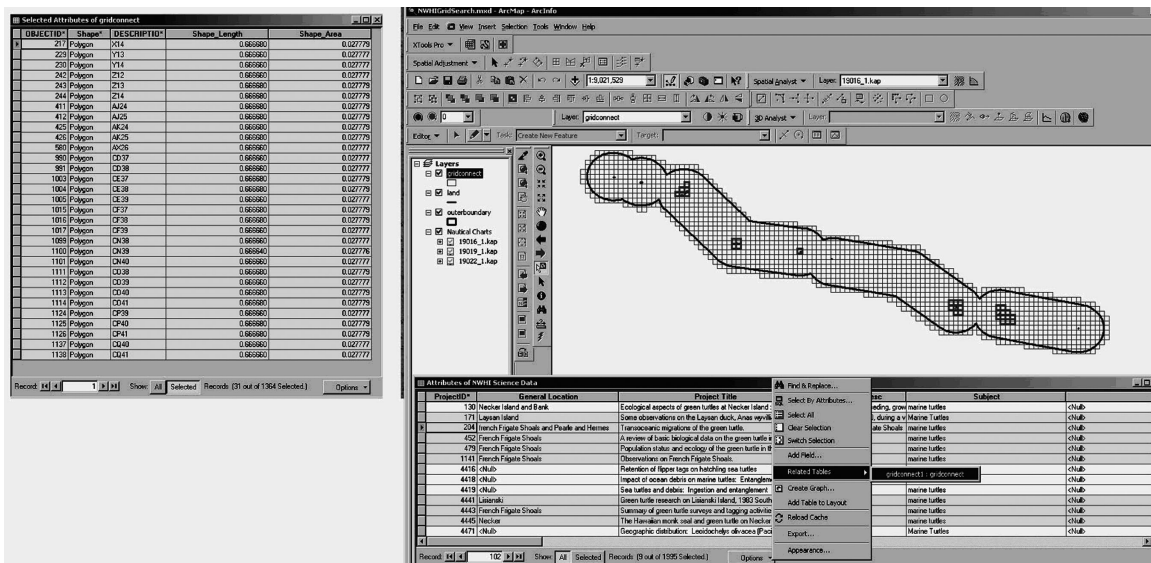


**Figure 7.** Grids may be selected by choosing the references and searching for the related grids.

**Figure 8.** Clicking the left portion of any record allows a user to view the entire record in a window.

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# PROTECTED SPECIES



NOAA Photo by Chad Yoshinaga

# PATTERNS OF GENETIC DIVERSITY OF THE HAWAIIAN SPINNER DOLPHIN (*STENELLA LONGIROSTRIS*)

BY

KIMBERLY R. ANDREWS[1], LESZEK KARCZMARSKI[2], WHITLOW W.L. AU[1], SUSAN H. RICKARDS[3], CYNTHIA A. VANDERLIP[4], and ROBERT J. TOONEN[1]

## ABSTRACT

We used population genetic analyses to investigate the genetic structure of the Hawaiian spinner dolphin (*Stenella longirostris*).  Genetic samples were collected from spinner dolphins at locations across the Hawaiian Archipelago: Kure Atoll (n=34), Midway Atoll (n=57), Pearl & Hermes Reef (n=21), French Frigate Shoals (n=15), Ni'ihau (n=39), O'ahu (n=47), Maui/Lana'i (n=60), and the Big Island of Hawai'i (n=77).  A 429-base-pair region of the mitochondrial DNA control region was used to evaluate genetic diversity and population structure.  Peaks in genetic diversity were found at the Big Island of Hawai'i ($\pi$=0.0082) and French Frigate Shoals ($\pi$=0.0072), and genetic diversity was reduced at the three most northwestern Hawaiian atolls (Kure Atoll $\pi$=0.0025, Midway Atoll $\pi$=0.0019, and Pearl & Hermes Reef $\pi$=0.0017).  Analysis of Molecular Variance (AMOVA) and exact tests of population subdivision indicated significant genetic structure for the spinner dolphin within Hawai'i.  With few exceptions, dolphins at every island were found to be significantly genetically differentiated from dolphins at every other island for one or more tests of population subdivision ($F_{ST}$ or $\Phi_{ST}$ $\geq 0.02$, $p < 0.05$).  Exceptions included dolphins at Kure Atoll, Midway Atoll, and Pearl & Hermes Reef, which together seemed to form one interbreeding group, distinct from the rest of the Archipelago.  Dolphins at O'ahu were also an exception in that they were not differentiated significantly from dolphins at Kure Atoll, Midway Atoll, or Pearl & Hermes Reef.

## INTRODUCTION

The Hawaiian spinner dolphin is a geographically isolated subgroup within *Stenella longirostris*, a species of small cetaceans found in tropical locations worldwide (Perrin, 1998).  Hawaiian spinner dolphins are genetically distinct from spinner dolphins in the eastern tropical Pacific (Galver, 2000), but no genetic data are available comparing spinner dolphins from Hawai'i with spinner dolphins at nearby Pacific islands.  In

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Hawai'i, spinner dolphins are found near islands and atolls, where they use calm, shallow bays and lagoons throughout most of the daylight hours (Norris et al., 1994; Karczmarski et al., 2005).  Although they occur off all of the Main Hawaiian Islands, they seem to be associated with only four of the Northwestern Hawaiian Islands: Kure Atoll, Midway Atoll, Pearl & Hermes Reef, and French Frigate Shoals (Karczmarski et al., 2005) (Fig. 1).  Sightings in offshore waters are not frequent, although some groups of spinner dolphins have been seen in the channels between islands and other offshore waters in the Main Hawaiian Islands (Mobley et al., 2000).  There is little information on offshore distribution in the northwestern Hawaiian region (Barlow et al., 2004), and details on offshore movements at night for any location in the Hawaiian Archipelago remain meager.
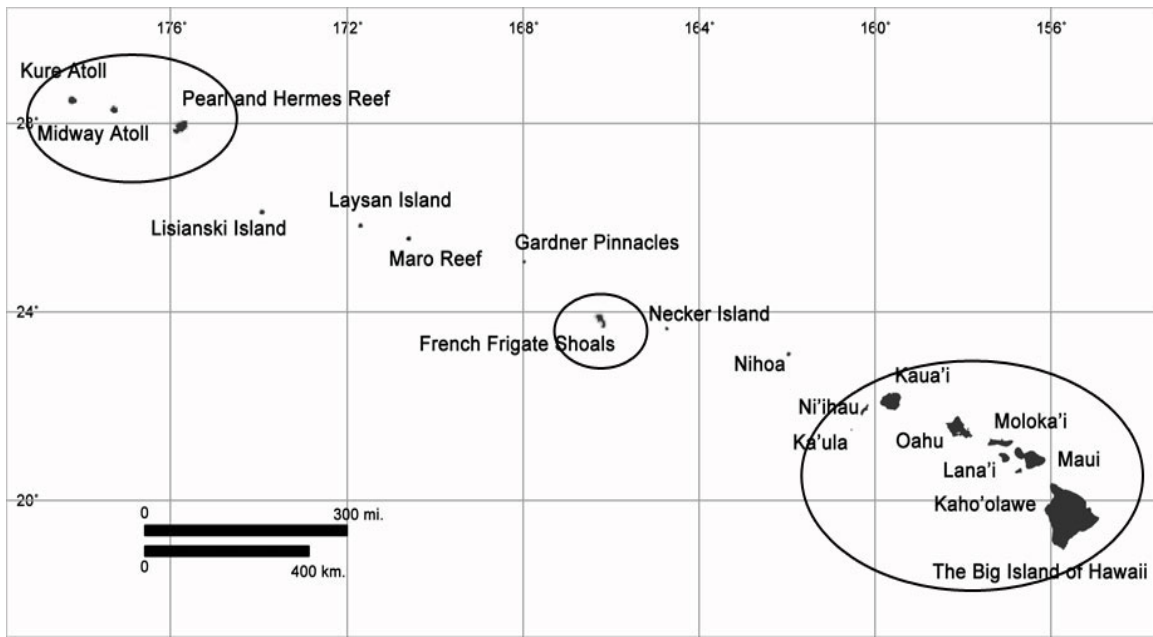


**Figure 1.**  Map of the Hawaiian Archipelago.  Circles indicate islands and atolls where spinner dolphins are regularly sighted.

Little is known about the amount of movement of the Hawaiian spinner dolphins between islands.  Because spinner dolphins have a capacity for high mobility, relatively high rates of movement throughout the Archipelago might be predicted.  A recent study in far northwestern Hawai'i documented movement between Midway and Kure Atolls (Karczmarski et al., 2005) and, seemingly to a much lesser degree, between Pearl & Hermes Reef and Midway (and possibly between Pearl & Hermes Reef and Kure) (L. Karczmarski and S.H. Rickards, unpublished data).  However, the overall pattern suggests that such movements are relatively infrequent, and groups show generally high geographic fidelity to their specific atoll (Karczmarski et al., 2005).

These distribution and movement data provide limited information to predict population structure of the spinner dolphin throughout the Archipelago.  The fact that some spinner dolphin groups are found in the channels between the Main Hawaiian

Islands (Mobley et al., 2000) may suggest that the spinner dolphins in the Main Hawaiian Islands form one genetically homogeneous group, with considerable interbreeding between islands. Although the observed movements between Midway Atoll, Kure Atoll, and Pearl & Hermes Reef were infrequent, we would expect that these amounts of movement, if associated with successful interbreeding, would still be sufficient to result in genetic homogeneity among these three atolls. The large geographic distance between the Main Hawaiian Islands and French Frigate Shoals, and between French Frigate Shoals and the three atolls at the far-western end of the Archipelago, might limit movement and interbreeding of individuals between these locations.

To gain insight into population structure, we conducted a population genetics study using tissue samples collected from free-ranging spinner dolphins throughout the Hawaiian Archipelago. We report on preliminary analyses using the mitochondrial DNA (mtDNA) control region. Because population genetic techniques can provide valuable information for the determination of stock structure and vulnerability under the Marine Mammal Protection Act (Dizon et al., 1992; Wade and Angliss, 1997; Dizon et al., 1997), these data will have direct application to the management of the Hawaiian spinner dolphin.

**METHODS**

Tissue samples were collected from spinner dolphins throughout the Hawaiian Archipelago. Three sampling techniques were used: biopsy with a Paxarms air rifle (Krützen et al., 2002), biopsy with a Hawaiian sling (in which elastic propels a pole with attached biopsy tip), and a skin-swabbing technique (Harlin et al., 1999). Biopsy with a Hawaiian sling and skin swabbing involved sampling of animals riding the bow wake of a small boat, and biopsy with an air rifle involved sampling of animals between 5 and 20 meters from a boat. Skin-swab samples consisted of flakes of sloughed skin, and biopsy samples consisted of cylindrical plugs of skin and blubber about 5 mm in diameter and about 5 mm long. In addition, some extracted genomic DNA samples were provided by the National Marine Fisheries Service, Southwest Fisheries Science Center (SWFSC), including accession numbers 7185-7202, 15510, 17432, 30411-30420, 30449, 30512-30516. Numbers of samples from each location included in this study, and years samples were collected, are listed in Table 1.

Genomic DNA was extracted from tissue samples using Qiagen DNEasy extraction kits. For each sample, a polymerase chain reaction (PCR) was carried out to amplify a 489-base-pair fragment of the 5' end of the mtDNA control region. Primers used were KRAdLp 1.5t-pro modified from Pichler et al. (2001) plus an added 5' M13 tail (5'-TGTAAAACGACAGCCAGTACACCCAAAGCTGGAATTC-3') and dLp5 (5'-CCATCGWGATGTCTTATTTAAGRGGAA-3') (Pichler et al., 2001). PCR reactions were 50μl volumes containing 1X Reaction Buffer (Promega Corporation), 200μM of each dNTP, 2.0mM $MgCl_2$, 0.5 units *Taq* DNA polymerase (Promega Corporation), and 0.2μM each primer. Cycle conditions were: 95 °C for 1 min, followed by 40 cycles of 94°C for 30 sec, 54 °C for 30 sec, and 72°C for 30 sec, followed by a final 72 °C extension

for 15 min.  PCR products were visualized on a 1.5% agarose gel containing ethidium bromide and were cleaned prior to sequencing using Qiaquick PCR Cleanup Kits (Qiagen Corporation).  Each PCR product was cycle-sequenced with both forward and reverse primers on an ABI 3730 automated sequencer.  The forward and reverse sequences were aligned for each individual using Sequencher v.4.2 (Genecodes Corporation).  Removal of primer sequences and ambiguous sequence resulted in a 429-base-pair consensus fragment.  The resulting consensus sequences were aligned for all individuals using Sequencher v.4.2.

The computer program Arlequin v.2.000 (Schneider et al., 2000) was used to calculate standard variance components including haplotype and nucleotide diversities

Table 1. Numbers of genetic samples collected at different locations in different years and standard measures of genetic diversity of Hawaiian spinner dolphins at different locations within the Hawaiian Archipelago.  The Big Island of Hawai'i is referred to as "Big Island."

| Location | 1997 | 2000 | 2001 | 2002 | 2003 | 2004 | Total Sample Size | Nucleotide Diversity ($\pi$) | Haplotype Diversity (h) |
|---|---|---|---|---|---|---|---|---|---|
| Kure Atoll | | | | 34 | | | 34 | 0.0025 | 0.3993 |
| Midway Atoll | | | 47 | 10 | | | 57 | 0.0019 | 0.4023 |
| Pearl & Hermes | | | | | | 21 | 21 | 0.0017 | 0.1810 |
| French Frigate | | | | 1 | | 14 | 15 | 0.0072 | 0.5333 |
| Ni'ihau | | | | 28 | 11 | | 39 | 0.0065 | 0.6802 |
| O'ahu | | | 23 | 6 | 10 | 8 | 47 | 0.0037 | 0.5402 |
| Maui/Lana'i | | 1 | | 9 | 50 | | 60 | 0.0042 | 0.4729 |
| Big Island | 17 | | | 3 | 57 | | 77 | 0.0082 | 0.7163 |

(Nei, 1987).  Haplotype diversity is calculated without taking into account the genetic distance between haplotypes, whereas nucleotide diversity does take genetic distance into account.

Arlequin was used to test for the presence of reproductively isolated subgroups at different Hawaiian islands and atolls using Analysis of Molecular Variance (AMOVA) (Excoffier et al., 1992), treating each island or atoll as an *a priori*-defined group.  The Tamura and Nei model (Tamura and Nei, 1993) was found to be the best-fit model available using Modeltest v3.6 (Posada and Crandall, 1998), and this model was used to estimate genetic distances.  The statistics $F_{ST}$ and $\Phi_{ST}$ were used to evaluate the level of reproductive isolation among groups; these values range from 0 to 1 and represent

measures of the amount of genetic variation within groups versus among groups.  A value of 0 indicates no genetic structure among groups, a value of 1 indicates that groups are completely reproductively isolated, and values between 0 and 1 indicate intermediate levels of isolation (Wright, 1951).  The significance of $F_{ST}$ and $\Phi_{ST}$ was evaluated using 100,000 random permutations.  In addition, exact tests of population subdivision (Raymond and Rousset, 1995) were carried out with Arlequin, using 100,000 steps of a Markov chain to test for the presence of genetic structure.

## RESULTS

Nucleotide and haplotype diversities for the spinner dolphin varied across the Hawaiian Archipelago (Table 1, Fig. 2).  Two peaks in nucleotide diversity were observed: one at the Big Island of Hawai'i (hereafter referred to as "Big Island") and one at French Frigate Shoals.  Whereas the peak in nucleotide diversity at the Big Island was due to a large percentage of individuals having unique or divergent haplotypes, the peak in nucleotide diversity at French Frigate Shoals was due to two individuals (out of a sample size of 15) that had a unique haplotype sequence which was highly divergent from any other sequence in the Archipelago. With the exception of French Frigate Shoals, nucleotide diversities at the Northwestern Hawaiian Islands were lower than at the Main Hawaiian Islands.
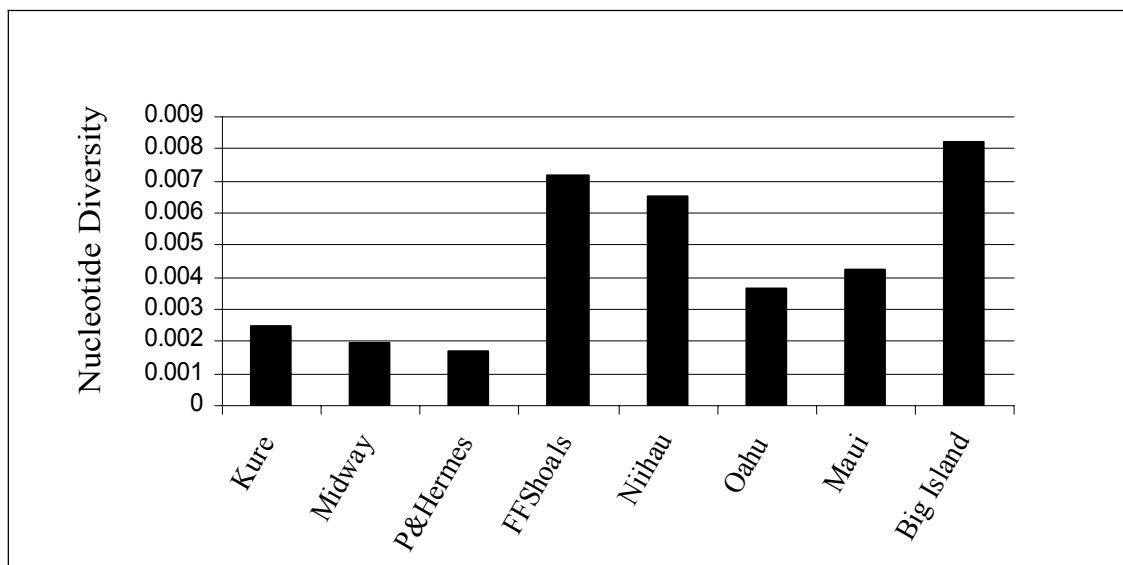


**Figure 2.** Nucleotide diversities at the mitochondrial DNA control region of spinner dolphins at locations across the Hawaiian Archipelago.  The Big Island of Hawai'i is referred to as "Big Island."

Three tests (AMOVA pairwise $\Phi_{ST}$ using genetic distance, AMOVA pairwise $F_{ST}$ using conventional F-statistics, and exact test of population subdivision) were used to test for the presence of reproductively isolated subgroups. With few exceptions, dolphins at every island were found to be significantly genetically differentiated from dolphins at every other island for one or more tests of population subdivision ($F_{ST}$ or $\Phi_{ST}$ $\geq 0.02$, $p < 0.05$). Exceptions included dolphins at Kure Atoll, Midway Atoll, and Pearl & Hermes Reef, which together seemed to form one interbreeding group, distinct from the rest of the Archipelago. Dolphins at Oʻahu were also an exception in that they were not differentiated significantly from dolphins at Kure Atoll, Midway Atoll, or Pearl and Hermes Reef.

## DISCUSSION

High genetic diversity at a neutral genetic locus can generally be attributed to: 1) large population size; and/or 2) intermixing of populations from more than one source. In this study, two peaks in genetic diversity of Hawaiian spinner dolphins were observed: one at the Big Island and one at French Frigate Shoals. The peak in genetic diversity at the Big Island is likely explained by population size, estimated at roughly 1,000-2,000 or more individuals (Norris et al., 1994; Östman, 1994). Although no population size estimates are available at any of the other islands, the population size at the Big Island is likely larger than populations at the other Main Hawaiian Islands because a greater amount of daytime resting habitat is available at the Big Island compared to the other Main Islands (availability of resting habitat is thought to have strong influence on population size in Hawaiian spinner dolphins; Norris et al., 1994; Karczmarski et al., 2005). Population sizes at Midway and Kure Atolls, estimated at 260 and 110 respectively (L. Karczmarski and S.H. Rickards, unpublished data), are likely much smaller than at any of the Main Hawaiian Islands. However, the extent to which these populations at Midway and Kure are reproductively closed is unknown. As would be expected from small populations, low genetic diversity was found at Midway and Kure Atolls, indicating that the populations at these atolls are not connected to the Main Hawaiian Islands (or any other potential unknown offshore populations) by ongoing gene flow. Population sizes at Pearl & Hermes and French Frigate Shoals are unknown, but have been observed to be greater than 300 individuals at each location (L. Karczmarski and K.R. Andrews, unpublished data).

Because neither population size nor movement patterns at French Frigate Shoals is known, we are unable to determine whether the high genetic diversity at this location is due to large population size or intermixing of populations. However, increased genetic diversity at French Frigate Shoals is attributed to a highly divergent haplotype in 2 out of a total of 15 individuals, making diversity due to a large population size unlikely. Instead, this pattern suggests that the high genetic diversity is likely a result of migration from another source. The divergent haplotype at French Frigate Shoals was unique among haplotypes in the Hawaiian Archipelago, further supporting the hypothesis of possible migration from outside of the Hawaiian Islands.

The genetic structure found within the Hawaiian spinner dolphin only partially matched the general expectations derived from the limited data available on movements. Whereas the distribution and movement data suggested that the dolphins at the Main Hawaiian Islands were a genetically homogeneous population with considerable levels of exchange (successful interbreeding) between islands, the genetic data reported here do not support that prediction. Rather, the data indicate that limited exchange occurs between dolphins associated with each Main Hawaiian Island. Our findings for the Northwestern Hawaiian Islands, however, did follow the initial expectations. Spinner dolphins at French Frigate Shoals were found to have limited exchange with dolphins from other islands, and dolphins at Midway Atoll, Kure Atoll, and Pearl & Hermes Reef were found to form one genetically homogeneous population that was distinct from the rest of the Archipelago.

The data indicate greater exchange rates between the three most western atolls than between the Main Islands, despite the fact that geographic distances separating these three atolls are greater than are most of the distances separating the Main Islands. These differences in exchange rates probably relate to differences between the Main Islands and the northwestern atolls in factors including population sizes and social structure (for details see Karczmarski et al., 2005), and oceanographic and physiographic features such as remoteness of habitat and availability of suitable resting sites (Karczmarski et al., 2005). These higher exchange rates may be an expression of intrinsic mechanisms related to inbreeding avoidance and preservation of genetic fitness of insular, small populations, although more research is needed to test this hypothesis.

More research is currently underway, including the collection of more tissue samples and more detailed analyses of additional genetic loci, specifically including microsatellites. These additional data will further elucidate the patterns of genetic diversity throughout the Hawaiian Archipelago for the spinner dolphin, and will provide valuable information for the determination of stock structure and vulnerability for effective conservation and management planning.

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# HAWAIIAN MONK SEAL (*Monachus schauinslandi*): STATUS AND CONSERVATION ISSUES

BY

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## ABSTRACT

The authors detail pertinent information on the history, current status, and conservation of the endangered Hawaiian monk seal (*Monachus schauinslandi*). The present population is estimated at about 1,200 to 1,300 seals, a decrease of 60% since the 1950s. Counts declined about 5%/yr from 1985 to 1993, remained relatively stable through the year 2000, and then declined again from 2001 to 2003. Population trends have been variable at the six main reproductive subpopulations in the Northwestern Hawaiian Islands (NWHI). Over the last few decades, pup production has averaged about 200, but overall juvenile survival has declined at most sites. The largest subpopulation is at French Frigate Shoals, where counts have dropped by 60% since 1989 and the age distribution has become severely inverted as a result of high juvenile mortality over the last decade. Overall demographic trends and parameters suggest that the total population will likely continue to decline, at least in the short term. Monk seals appear throughout the Hawaiian Archipelago, and although most are found in the NWHI, a small but increasing number haul out and pup in the Main Hawaiian Islands (MHI). Monk seals typically use isolated beaches for resting, molting, parturition, and nursing offspring; and forage on demersal and epibenthic prey. Past and present sources of anthropogenic impacts to monk seals include hunting (during 1800s and early 1900s), disturbance (e.g., prior military activities beginning in WWII), entanglement in marine debris, and fishery interactions. Primary natural factors affecting monk seal recovery include predation by sharks, aggression by adult male monk seals, and reduction of habitat and prey associated with environmental change. Identification and mitigation of these and other possible factors (e.g., disease) limiting population growth represent ongoing challenges and are the primary objectives of the Hawaiian monk seal conservation and recovery effort.

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**OVERVIEW**

Early History

      Although it is not clear when monk seals first reached the Hawaiian Archipelago (Repenning and Ray, 1977), archeological research indicates that Hawaiian monk seals were present in the Main Hawaiian Islands (MHI) prior to European contact at about 1400-1760 AD (Rosendahl, 1994).  Several primitive monk-seal skeletal characteristics (Ray, 1976; Barnes et al., 1985) indicate that their early ancestors may have been present 14-15 million years ago (mya) (Repenning et al., 1979), and mitochrondial and nuclear DNA studies show the species first split from its Monachinae ancestors between 11.8-13.8 mya (Fyler et al., in press).

      The natural history of the monk seal is inextricably linked to the biogeographic setting of the Northwestern Hawaiian Islands (NWHI).  The monk seal population may be characterized as a classic metapopulation (Hanski and Gilpin, 1991), with semi-isolated subpopulations distributed along the chain.  The historic distribution and abundance of the species are unknown, but we can surmise that early monk seals resided in an environment quite different from today's Archipelago, and it may have been capable of supporting many more monk seals than exist today.  The extant islands and atolls that comprise the Archipelago range in age from 7.5 to 30 million years old (MacDonald et al., 1983), and many have undergone major changes during the time of monk seal habitation.  Some islands have subsided to form seamounts, some have become remnants of their former mass, and some new landmasses have emerged.  As these geologic changes have occurred, the monk seal population has undoubtedly also fluctuated in numbers and distribution.

Range

      Monk seals are found throughout the NWHI including the population's six main reproductive sites: Kure Atoll (KUR); Midway Atoll (MID); Pearl and Hermes Reef (PHR); Lisianski Island (LIS); Laysan Island (LAY); and French Frigate Shoals (FFS).  Small numbers also occur on Necker and Nihoa Islands, where a few pups are born each year, and monk seals have been observed at Gardner Pinnacles and Maro Reef.  Although most monk seals can be found in the NWHI, monk seals are also found throughout the Main Hawaiian Islands (MHI), where documented births and sightings suggest that numbers are increasing (Baker and Johanos, 2004).  Monk seals are observed occasionally at Johnston Atoll, and one birth was reported there in 1969.

**LIFE HISTORY AND HABITAT USE**

Terrestrial Habitat

Haul-out areas for parturition, nursing, molting, and resting are primarily sandy beaches, but virtually all substrates, including emergent reefs, are used. If available, monk seals also use the vegetation behind the beaches as a shelter from solar radiation, high surf, wind, or rain; for resting at night; and possibly to avoid disturbance from other seals.

Parturition has been observed in diverse settings and substrates; but on each atoll, certain beaches are preferred for pupping. These areas, typically sandy beaches with protective reef that limit shark access and provide shelter from large surf (Westlake and Gilmartin, 1990), are often shared by multiple females, with some individuals pupping in the same locale each year. Other females seem to favor more isolated beaches where disturbance from other mother-pup pairs is less likely. Births can occur year round but are most common from February through August, with peak parturition in March and April (Johnson and Johnson, 1980; Johanos et al., 1994). Females give birth to a single offspring and remain on shore with their pup for about 6 weeks. Weaning occurs when the mother abandons her pup and returns to the sea to feed. She will mate about 3-4 weeks after weaning her pup, and will haul out again for 10-14 days or more to molt about 5-6 weeks later. Nonparturient adult females usually molt about a month earlier than parturient females (Johanos et al., 1994).

Marine Habitat

Monk seals' primary habitat is the marine environment, where they spend approximately two-thirds of their time (National Marine Fisheries Service (NMFS), unpublished data). In general, monk seal aquatic behaviors include thermoregulatory cooling, resting, playing, mating, and foraging. Mating behavior is aquatic and rarely witnessed, occurring 5 m to 1 km or more from shore when observed (Johnson and Johnson, 1981; Shallenberger, personal communication). Video camera deployments on adult male monk seals have indicated that while in the water seals spend 34% of their time resting, 9% interacting socially, and 57% of their time foraging and traveling (Parrish et al., 2000).

Most foraging occurs near the sea floor (Goodman-Lowe et al., 1998), where they search for food on substrate composed of talus and sand on marine terraces of atolls (Parrish et al., 2000, 2002, 2005). Monk seal feeding has been observed in reef caves that also appear to be used for resting and refuge from predators (Taylor and Naftel, 1978). Parrish et al. (2002) reported that monk seals forage in or near precious coral beds at subphotic zones at depths below 300 m.

Monk seals forage on a wide variety of prey species that are usually found in benthic and demersal habitats (Rice, 1964; MacDonald, 1982; Goodman-Lowe, 1998; Parrish et al., 2000). Through the analysis of identifiable hard parts found in regurgitate and fecal material, Goodman-Lowe (1998) reported that fishes appeared most frequently

(78.6%), followed by cephalopods (15.7%), and crustaceans (5.7%). Out of 31 different families, Labridae, Holocentridae, Balistidae, and Scaridae were the most commonly identified. Cephalopod prey included 7 species of octopus and 19 species of squid. Some prey species are not represented accurately from scat analysis (e.g., lobster) because of differential digestion and passages of identifiable hard parts (Goodman-Lowe et al., 1999), and other methods (including fatty acid analysis) are currently being evaluated to investigate monk seal diet.

Monk seal movement and diving patterns were characterized by deploying satellite-linked radio transmitters on 147 seals (42 adult males, 35 adult females, 29 juvenile males, 14 juvenile females, 12 weaned male pups, 15 weaned female pups) at the six breeding colonies in the NWHI (Abernathy and Siniff, 1998; Stewart 2004a,b; Stewart and Yochem, 2004a,b,c). Data from these deployments indicated that monk seals foraged extensively around the fringing atoll lagoons and outer slopes at FFS, PHR, MID, and KUR, and seaward of LAY and LIS. Locations obtained along the submarine ridges between those atolls and islands, and at virtually all nearby seamounts, suggested that those areas were also used for foraging. Dives of 150 m or less were most common, but secondary diving modes were registered at various depths (though rarely exceeding 500 m.). Individual seals displayed unique patterns in dive depths, distance traveled, and apparent foraging locations, with some of the variability perhaps owing to sex and age of seals. Foraging ranges of instrumented seals varied from less than 1 km up to 322 km (Abernathy, 1999; Stewart, 2004a,b; Stewart and Yochem, 2004a,b,c).

Another technology that has provided valuable insights into monk seal foraging ecology is the CRITTERCAM. Parrish et al. (2000) attached these devices to 24 adult and subadult male monk seals at FFS to learn more about the habitat depth and substrate at locations where monk seals captured prey items. They found that most diurnal foraging of adult males occurred at the 60-m isobath.

More recently, CRITTERCAMS were used to characterize juvenile monk seal habitat use and foraging behavior at FFS. Footage from that research indicated juvenile seals foraged in the same habitats commonly used by adults, but they may have lacked the size and strength to forage as successfully as their adult counterparts (Parrish et al., 2005). The dive patterns of 13 weaned pups, instrumented with time-depth recorders (TDRs) at FFS in 1999 and 2000, indicated that most dives occurred at depths less than 200 m, but occasionally exceeded 200 m. As with other size classes of seals, there was substantial variability among the pups in depth, duration, and temporal patterns of dives (NMFS, unpublished data).

## ABUNDANCE AND POPULATION TRENDS

Most of the data used to estimate population size and composition, demographic rates, migration rates, and other key aspects of the monk seal's life history are derived from annual resightings of permanently identified seals. Individual seals may be permanently identified either by natural markings (primarily scars and distinctive pelage patterns) or by tags (Harting et al., 2004). In the NWHI, flipper tags have been routinely applied to weaned pups since the early 1980s. These "cohort-tagged"

seals are particularly important for estimating vital rates because their age is known. Survival rates are estimated for all six NWHI subpopulations using standard Jolly-Seber methodology (Seber, 1982, as described in Craig and Ragen, 1999 and Harting, 2002). Reproductive rates are estimated for those sites where field effort is of sufficient duration to observe most births or nursing pairs.

Population Size and Trend

Table 1 shows minimum estimates of abundance at the six main reproductive sites in the NWHI. In some cases, these likely represent total enumeration, although at those sites with shorter field seasons, estimated probabilities that known-aged seals are identified during a given field season suggest that certain age groups could be underestimated by as much as 10-20% (Harting, 2002). Efforts are underway to more precisely determine abundance of NWHI monk seals (e.g., Baker, 2004). The best estimate of the population size in the year 2003 is 1,244 seals (Carretta et al., 2004), but their total numbers likely range between 1,200 and 1,300 individuals. These data can also be used to determine a minimum population estimate ($N_{min}$) for the total population that accounts for the statistical uncertainty in the abundance estimates, as is done for Stock Assessment Reports required by the Marine Mammal Protection Act (Wade and Angliss, 1997). Using that procedure, the minimum population size for the main reproductive islands is equal to the best estimate of the minimum population size at those sites. The minimum population size for the total population is the sum of these estimates (Table 1).

Direct enumeration provides the most reliable estimate of population size for recent years but cannot be used for characterizing long-term historical trends because the current level of field effort in the NWHI was initiated only within the last two decades (varying by site). Instead, long-term population trends can be inferred from the results of range-wide beach count[1] surveys that began in the 1950s. Although the methods for the earliest counts were not standardized, complete beach counts are approximately comparable.

The historic timeline of range-wide beach count surveys begins in the late 1950s (Kenyon and Rice, 1959; Rice, 1960), with additional counts conducted at MID in 1956-1958 (Rice, 1960), at KUR in 1963-1965 (Wirtz, 1968), and elsewhere throughout the 1960s and 1970s. Data from these surveys suggest that the species declined by about 50 percent between the late 1950s and the mid-1970s (Kenyon, 1973; Johnson et al., 1982). If only non-pups are included (juveniles, subadults and adults), the population declined by approximately 60% from 1958 to 2001 (Fig. 1).

In more recent years, standardized beach counts suggest that the nonpup population declined rapidly from 1985 to 1993, prior to becoming relatively stable (Fig. 2). A broken-line regression (two regression lines joined at a break point optimized to minimize the sum-of-squares error) fitted to the 1985-2003 data (Carretta et al., 2004)

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[1]A beach count consists of a complete enumeration of all the seals present on all accessible beaches. Beginning in 1983, standardized protocols were established for conducting these counts, which typically number eight or more per season and include all islets within an atoll. The mean number of seals observed on all beach counts in a season is used to assess long-term trends.

estimates that the total counts declined 4.2% per year until 1993, and then declined by 1.9% per year thereafter (95% CI = - 3.0% to - 0.9% per year).

Combining the count data for all of the main NWHI sites (Figs. 1 and 2) conceals the diversity of trends in the individual subpopulations (Fig. 3). There has been considerable variability in the population dynamics at the different locations, with the current demographics of each site probably reflecting a combination of different histories of human disturbance and management (Gerrodette and Gilmartin, 1990; Ragen and Lavigne, 1999), and varying environmental conditions (Polovina et al., 1994; Craig and Ragen, 1999). Although the population decline since 1958 was common to most subpopulations, the degree and duration of that long-term decline, as well as the trend in more recent years, has differed among the sites. The pattern at FFS was unlike that of the other atolls: this subpopulation grew rapidly from the early 1960s to the late 1980s, and then collapsed, with nonpup beach counts declining by 70% during 1989-2001. While LAY and LIS have remained relatively stable since approximately 1990, LAY has tended to increase slightly while LIS has decreased slowly. The three westernmost atolls (KUR, PHR, and MID) all experienced a period of recent growth. The subpopulation at KUR grew at an average rate of 5% per year after 1983, largely as a result of decreased human disturbance, increased survival of young seals, and the introduction of rehabilitated female juveniles. Similarly, the subpopulation at PHR increased at approximately 7% per year during 1983-1999, an annual growth rate that is regarded as the best indicator of the maximum net productivity rate ($R_{max}$) for this species (Carretta et al., 2004). The intensive military presence at MID rendered this atoll largely unavailable to monk seals until relatively recently. Aided by protective management policies and immigration from PHR and KUR, the small MID seal population has increased since 1990. Population growth at these three sites has declined in recent years primarily because of decreased juvenile survival (see Juvenile Survival Rates section).

Because of inaccessibility, systematic enumeration and regular population monitoring has not been possible for Necker and Nihoa Islands. Data from a limited number of brief monitoring efforts indicate that seal counts at those islands tended to increase from approximately the year 1970 to 1990. The observed increase may have been a result of an influx of seals from FFS, which was growing during that same period. In 1993, 14 tagged seals marked as pups at FFS were sighted at Necker Island during a 7-day period (Finn and Rice, 1994). Twelve tagged seals were also sighted at Nihoa Island during the same period, including 10 tagged at FFS (Ragen and Finn, 1996).

Systematic surveys of monk seals were not conducted prior to 2000, so historical abundance data for the MHI are limited. However, the monk seal population in the MHI appears to have increased during the 1990s. One indication of a growing population is the increased number of observed births in the MHI. Prior to and during the 1990s, the number of births observed annually in the MHI was usually zero and never exceeded four. In contrast, beginning in 2000, monk seal births observed in the MHI became more frequent, with 7, 12, 4, and 10 births recorded in 2000, 2001, 2002, and 2003, respectively (Baker and Johanos, 2004; NMFS, unpublished data).

Reproductive Rates

Pup production varies by island and year, but over the last two decades, approximately 200 Hawaiian monk seal pups have been born annually system-wide.   Reproductive data are most complete at LAY and LIS where field observations typically encompass the entire birthing season.  At these sites, an average 68% of known reproductively mature females pup each year (Johanos et al., 1994).

Monk seal females usually give birth for the first time between the ages of 5 and 10.  Fitted reproductive parameters indicate substantial variability among the three subpopulations having sufficient data to estimate age-specific fecundity (FFS, LAY, and LIS). Maturation occurs approximately 1-4 years earlier at LAY than at the other two sites.  In pinnipeds, the onset of sexual maturity usually coincides with the attainment of some percentage of final body size (Laws, 1956), suggesting that the observed delay at both FFS and LIS may be indicative of poorer nutritional conditions for immature seals at these sites.  The smaller weaning sizes observed at both of those sites (Craig and Ragen, 1999; NMFS, unpublished data) is consistent with that theory.  The maximum fecundity attained by mature females at LAY is also higher than at the other sites (Fig. 4). Sample sizes for older females (ages 15 and older) are very small, but the data indicate a senescent decline in fecundity beginning somewhere between 10 and 15 years at both LAY and FFS (Fig. 4).  That pattern is not yet evident at LIS.  Data are not sufficient to fit age-specific reproductive schedules for the other three subpopulations (PHR, MID, and KUR); however, based on the number and age of females at those sites and the total number of pups produced, it appears that fecundity is somewhat lower than at LAY but probably not as low as at FFS.

Less is known about sexual development in males, but their size and behavior suggest that they reach maturity at approximately the same age as females.  Copulation is rarely observed, and hence the reproductive success of individual males is difficult to evaluate without detailed genetic analysis of the population.  Limited observations indicate that males mount the female by biting her back and grasping her sides with their foreflippers.  Females are often observed with bite marks and other wounds on the dorsum, providing evidence of possible mating.  These injuries are observed most frequently around 26 days after the female has weaned a pup (Johanos et al., 1994).

Juvenile Survival Rates

Juvenile survival is a key component of monk seal demography, because of its vital role in determining the trajectory for each subpopulation.  Like many other pinnipeds, the ability to make the transition successfully from weaning to nutritional self-sufficiency represents a critical stage in their early survival (e.g., Bowen, 1991). Although there is considerable annual variability in survival rates, all six major breeding subpopulations have experienced conspicuous declines in juvenile survival and recruitment in the last 10 years (Fig. 5).  The factors underlying this variability are not known with certainty, but there is some evidence that El Niño events or other oceanographic phenomena may influence juvenile survival (Polovina et al., 1994,

Antonelis et al., 2003).  With an intrinsic growth rate of less than 1.0 at all sites except LAY in recent years (NMFS, unpublished data), the demographic rates must improve, or most subpopulations are likely to continue declining.

An imbalance in the age/sex structure of some subpopulations is another aspect of monk seal demography that is a cause of concern.  A succession of poor cohort survival at some sites (especially at FFS, and, more recently, in the three westernmost sites) has led to a pronounced age structure imbalance in which young adult seals are severely under-represented (Fig. 6).  At FFS, the paucity of young seals means that there will be few new females reaching reproductive maturity in coming years, so that annual pup production is expected to drop, and the subpopulation will continue its downward trend.


## PROTECTIVE LEGISLATION

In 1909, President Theodore Roosevelt created the Hawaiian Islands Reservation that included all islands of the NWHI except Midway.  The Reservation was later renamed the Hawaiian Islands National Wildlife Refuge (HINWR), and as a Federal Refuge, was placed within the jurisdiction of the U.S. Fish and Wildlife Service (USFWS). In 1952, KUR was given to the State of Hawaii and was designated a State Wildlife Refuge. A rapid decline in beach counts of monk seals from the late 1950s to the mid-1970s led to the Hawaiian monk seal's designation as "depleted" under the Marine Mammal Protection Act (MMPA), and as "endangered" under the Endangered Species Act (ESA) in 1976. In 1980, the NMFS initiated efforts to define critical habitat for monk seals through an environmental impact statement (EIS), and by 1986, critical habitat designation was assigned from haul-out beaches out to the 20-fathom isobath around KUR, MID (except Sand Island), PHR, LIS, LAY, Maro Reef, Gardner Pinnacles, FFS, Necker Island and Nihoa Islands. In 2000, the waters from 3 to 50 nm around the NWHI were designated the NWHI Coral Reef Ecosystem Reserve by Presidential Executive Order 13178, which provides specific restrictions on human activities permitted within the Reserve.


## CONSERVATION AND EFFORTS TO ENHANCE POPULATION GROWTH

Food Limitation

Recent survival trends (observed to varying degrees at several of the NWHI monk seal subpopulations) indicate that food limitation may be playing a primary role in regulating population growth. Food limitation was first associated with poor juvenile survival at FFS during the early 1990s (Craig and Ragen, 1999).  Subsequently, range-wide decreases in juvenile survival have occurred in early 2000 along with relatively low age-specific reproductive rates (including delayed maturity) at FFS and LIS.  The conclusion that food limitation is having a significant influence on population decline is reinforced by indications of relatively poor body condition in various juvenile age

classes. Further, although the cause of a die-off of about 11 seals throughout the NWHI in 2001 was not determined, necropsies of six carcasses indicated emaciation with no evidence of disease (Antonelis et al., 2001). Subsequent juvenile survival has remained low at most sites (see survival section), and oceanographic changes resulting in low productivity have been postulated as a potential overriding factor.

NMFS initiated two capture-and-release programs in the 1980s, that were designed to increase female recruitment in the then-depleted KUR monk seal population. The Head Start Project (1981-1991) involved the capture and protection of weaned female pups from KUR during the transition phase from weaning to independent feeding. Recognizing that food limitation was most likely limiting juvenile survival at FFS, NMFS also initiated the Rehabilitation Project in 1984. From 1984 to 1995, undersized, weaned female pups from FFS were brought into captivity for 8-10 months on Oahu to increase weight and released back into the wild at either KUR (all years except 1992) or MID (1992), where they had a higher probability of survival. In some years, undersized juvenile females were also collected at FFS, brought into captivity on Oahu for varying amounts of time, and released at either KUR or MID. Of the 104 immature monk seal pups that were handled for the head-start or rehabilitation programs, 68 were released into the wild and another 22 died in captivity (NMFS, unpublished data). The survival prospects of 14 of the handled seals were deemed insufficient for release, and they were therefore transferred into public aquaria and oceanaria for research.

Fishery Interactions

Fisheries can potentially interact with monk seals in multiple ways that may be broadly classified into two categories: direct and indirect interactions. Under direct interactions, seals become hooked or entangled in active fishing gear, feed on fishing refuse, remove bait or catch from fishing lines, or become entangled in derelict fishing gear. Indirect interactions are those which operate through fishery impacts on monk seal prey or habitat. No indirect interactions have yet been documented; however, some prey species (e.g., lobster) have been commercially fished. The diet and foraging habits of monk seals are being carefully evaluated and monitored to determine the importance of such species to monk seals and better assess the nature and magnitude of indirect interactions. In contrast, some examples of direct interactions are known. Direct interactions were documented between the Hawaii-based longline fishery and monk seals in the late 1980s and early 1990s (Lavigne, 1999), and in most cases the interactions involved serious injuries to seals. Direct but rare interactions have also been reported for the bottomfish fishery and the lobster fishery (presently closed) operating in the NWHI. Based on data collected by observers in 1990-1992 from bottomfish vessels fishing around Nihoa Island and Kaula Island, Nitta and Henderson (1993) estimated that monk seals removed bottomfish from fishing lines at a rate of one interaction event per 34.4 hours of fishing. The observers did not record any interactions involving hooking or entanglement. More recently, from October 2003 through the end of June 2004, fishery observers were placed on bottomfish vessels and, having completed 10 bottomfish cruises to date, no monk seal interactions have been observed (NMFS Pacific Islands Regional

Office, Bottomfish Quarterly Status Reports). The recent lack of interaction in this fishery is probably a result of modification in fishing techniques voluntarily initiated by the fishers.

During the last few years, an increasing number of monk seal hookings have occurred in the MHI, apparently associated with state-regulated, shore-based recreational fisheries. These MHI incidents probably represent less of a threat to monk seals than had they occurred in the NWHI, because of the greater opportunity for detection and successful intervention (dehookings) in the MHI. The nearshore gillnet recreational and commercial fisheries in the MHI are also known to interact with monk seals. Since 1982, only one monk seal was found dead in a gillnet associated with these fisheries (NMFS, unpublished data).

In 1991, NMFS and the Western Pacific Regional Fishery Management Council established a permanent Protected Species Zone (PSZ) to reduce the probability of direct interaction between the Hawaii-based longline fishery and monk seals. The PSZ extends 50 nm around the NWHI and the corridors between the islands, and all longline fishing was prohibited in the Zone. No interactions with the longline fishery have been documented since establishment of the PSZ.

Several studies have shown overlap between the foraging habitat of some monk seals and certain types of deep-water precious corals (Abernathy and Siniff, 1998, Parrish et al., 2002). Thus, removal of corals from these habitats could affect monk seals indirectly if the abundance of coral-associated seal prey was reduced. President Clinton's Executive Order 13178 established the NWHI Coral Reef Ecosystem Reserve which precludes precious coral harvest within 50 nmi of the NWHI.

Male Aggression

Single- and multiple-male aggressions that severely injure or kill adult females and immature seals have been recorded since the 1970s (e.g., Johnson and Johnson, 1981; Alcorn and Henderson, 1984; Johanos and Austin, 1988; Hiruki et al., 1993). Although evidence of male aggression has been observed at all major breeding sites, the intensity of the problem varies by location and year.

From 1984-1994, a total of 37 adult males were captured on Laysan and either transported to Johnston Atoll or the MHI, or brought into permanent captivity in an effort to balance the sex ratio and reduce multiple-male aggression. At French Frigate Shoals, three individual adult males were observed repeatedly attacking and killing pups; one male was euthanized in 1991 (Craig et al., 1994), and two males were captured and relocated to Johnston Atoll in 1998 (Craig et al., 2000). None of the relocated males have returned to their site of capture. Such actions have successfully reduced deaths as a result of male aggression and will be continued in the future, as necessary.

Entanglement in Marine Debris

Monk-seal entanglement in marine debris continues to affect monk seals despite international law prohibiting the intentional discard of debris from ships at sea (MARPOL[1], Henderson, 2001).  Monk seals have one of the highest documented rates of entanglement of any pinniped species (Henderson, 1984, 1985, 1990, 2001).  The number of annual entanglements has varied over the last 21 years, but, to date, a peak in the number of entanglements occurred in 1999, when 25 incidents were reported (Henderson, 2001). The sources of debris come from fisheries and other maritime activities around the Pacific Rim (Donohue et al., 2001), and current studies indicate there is no sign of this problem abating in the future (Boland and Donohue, 2003).

Since the inception of the NMFS Marine Mammal Research Program (MMRP) beach debris removal program in 1982, the incidence of entangled monk seals at breeding sites of the NWHI has been well documented, and the field staff has actively worked to disentangle seals and remove potential entangling debris from haul-out beaches.  From 1982 to 2003, a total of 238 monk seals were disentangled from marine debris.

In 1996, the severity of the problem was quickly discovered, and a large-scale, multi-agency cleanup effort was initiated in 1998.  In 1999, the Coral Reef Ecosystem Division of the NMFS Pacific Islands Fisheries Science Center (PIFSC) was designated to lead the cleanup effort. Currently, approximately 440 metric tons of potentially entangling marine debris have been removed from the coral reefs and beaches of the NWHI (Boland et al., 2006). In addition to the cleanup efforts, national and international agreements are needed to stop the generation of debris in the marine environment.

Shark Predation

Most mature monk seals are scarred from earlier encounters with sharks, and shark predation has been directly witnessed on several occasions (Bertilisson-Friedman, 2002; Wirtz, 1968; Taylor and Naftel, 1978; Balazs and Whittow, 1979; Johanos and Kam, 1986; Alcorn and Kam, 1986).  Prior to the late 1990s, shark predation was thought to be a relatively minor component of the overall mortality, with most predation incidents assumed to be from tiger sharks.

Beginning in the late 1990s, there was a significant increase in shark predation on monk seal pups prior to or near the time of weaning at FFS.  Initially, the problem was detected only at the Trig/Whaleskate Island complex, where from 1997 to 1999, 18-28 pups were apparently killed each year by Galapagos sharks patrolling the shoreline[2]. Since that time, the number of apparent mortalities at Trig has declined to three to nine pups each year, but the incidence of shark attacks and mortalities of pups prior to or near

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[1]The MARPOL Convention is the main international convention covering prevention of pollution of the marine environment by ships from operational or accidental causes. It is a combination of two treaties adopted in 1973 and 1978, respectively, and updated by amendments through the years.

[2]Many of the mortalities attributed to shark predation are not directly observed but are inferred based on the disappearance of a pup, plus the presence of patrolling sharks and/or the absence of any other compromising survival factor.

the time of weaning at other sites in the atoll has increased.  From 2000-2003, the proportion of pups born at FFS believed to be attacked by sharks (including confirmed attacks and mortalities and inferred disappearances) has ranged from 18 to 30% of the annual cohort.  It is suspected that the high predation rate is an unusual behavior involving a limited (possibly small) number of Galapagos sharks at FFS.  The conspicuous lack of Galapagos shark predation on monk seal pups at the other five breeding sites is consistent with this view.

Although nonlethal shark deterrents were preferable to lethal removal, attempts to haze sharks away from pupping beaches in 2000-2001 proved unsuccessful and made sharks wary and more difficult to catch.  During those same years, six Galapagos sharks were removed using hook and line and harpoon, and another four sharks were removed in 2002-2003.  These efforts have greatly enhanced pup survival at Trig Island (within FFS), by reducing the number taken by sharks (including both confirmed and inferred losses) from 28 to 3 in 1997 and 2003, respectively.  To further enhance post-weaning survival, pups were relocated from Trig Island to other sites in the atoll (e.g., Gin Island) where little or no shark predatory behavior had been previously observed.  Beginning in 2003, Galapagos shark predation on preweaned pups was detected at several other islets in the atoll, indicating that mitigation efforts should be expanded to include those sites.  The objective of the subsequent expanded program was to reduce the likelihood of this shark behavior spreading to other sites at FFS and possibly throughout the Archipelago.  To date, mitigation efforts to reduce Galapagos shark predation on pups prior to and near the time of weaning have reduced the total estimated shark predation at FFS from 31 in 1997 to 11 in 2003.

Human Disturbance

Monk seals avoid beaches where they are often disturbed, and the consequence of disturbance ultimately equates to a reduction of available habitat and population size (Kenyon, 1972; Gerrodette and Gilmartin, 1990).  Chronic disturbance may cause seals to abandon haul-out sites and preferred sites for parturition.  Such behavior may lead to increased vulnerability to shark predation, especially for recently weaned or preweaned pups (Ragen, 1999).  Although the closure of all military base and navigation aid stations in the NWHI eliminated one of the primary threats of human disturbance, the relatively low level of ongoing human activities in the NWHI must still be carefully regulated, monitored, and assessed to ensure there are no deleterious effects (e.g., Baker and Johanos, 2002; Littnan et al., 2004). Additionally, monk seals in the MHI have probably grown in numbers (Baker and Johanos, 2004), resulting in an increased likelihood of human interactions in that expanding population.

Public outreach and education remain the single most powerful tools for reinforcing a stewardship ethic that promotes the conservation of the Hawaiian monk seal and the habitat in which it occurs.  As monk seal numbers increase in the MHI, so does the importance of increasing educational efforts to systematically include all potential stakeholders.

Habitat Loss

Critical habitat loss from erosion is a serious concern for monk seals in the NWHI.  At FFS, the attrition of terrestrial habitat over the last two decades has reduced the availability of beaches for parturition by more than 50% at most sites (Table 2).  The disappearance of Whaleskate Island in 1998-99 is particularly noteworthy because it led to a dramatic increase in the density of mother-pup pairs at Trig Island in 1999.  Concurrently, high levels of shark predation on preweaned pups at Trig Island were documented, suggesting that the high density of seals and frequent female/female interactions led to the separation of mothers and pups and facilitated the high predation level by Galapagos sharks.  Additional loss of island habitat at FFS and possibly at other sites in the NWHI, as a result of a combination of potential environmental factors and changes in oceanographic conditions (e.g., frequency of storms, rate of coral-reef growth, sea-level rise, and prevailing currents), could exacerbate this problem.

In 2004, a conspicuous decrease in the size of all islands in FFS is apparent when compared to previous information collected in 1923, 1942, and 1963 (Table 2).  In a few instances, there was a slight increase from 1923 to 1963 (e.g., East Island), and, in one instance, there was a large increase in the size of Tern Island because of the construction of a runway for the Navy in 1942.  However, in most cases, the islands sizes at FFS were at least 50% smaller in 2004 than in 1963. Future studies are needed to assess the rate of loss and the capacity of monk seals and other protected species to spatially adapt to the disappearance of habitat critical for their reproductive success.

One mitigation option is to evaluate the efficacy of habitat restoration to increase available haul-out sites for monk seals.  Such an endeavor could also increase nesting habitat for Hawaiian green sea turtle (*Chylonia mydas*) and numerous seabirds.  The benefits of such mitigation can be inferred from observing the increase in available habitat for breeding monk seals, turtles, and seabirds associated with the enlargement of Tern Island by the Navy.

Infectious Diseases

Exposure to known pathogens has been serologically observed in all subpopulations.  The impacts of these pathogens in causing disease or inhibiting recovery are unknown.  To date, no epidemics of infectious disease have been positively identified in monk seal populations, but the immunologically naive population is very vulnerable to many exotic diseases.  Although the probability of any particular disease being introduced into the population is unknown, disease in seal populations can be and has been devastating (e.g., Osterhaus et al., 1997).

Reducing the risk of disease introduction is an ongoing effort, with support of quarantine, vector control, and comprehensive stranding response.  Further, baseline serological surveys and continual surveillance will enhance response and control of observed pathogens.  Vaccination and translocation are being explored to reduce potential impacts of pathogens.

Biotoxins

The role of biotoxins in the morbidity and mortality of monk seals is unclear because of the lack of specific and sensitive assays to test seal tissues for these compounds and their metabolites, the lack of data on the distribution of biotoxins in monk seal prey, and knowledge about temporal variation in background levels of biotoxins in the monk seals' environment. Scientific advancement in detection of sodium channel-blocking biotoxins and potentially harmful algal blooms will improve our understanding of the effects of intoxication and improve our response toward the conservation of seals. Vessel groundings that result in damage to coral reefs and trauma to reefs associated with such events have been implicated in biotoxin outbreaks that may have a secondary effect on monk seals.

Contaminants

Historic human use of the NWHI has resulted in the deposition of a number of contaminants in monk seal habitat (e.g., polychlorinated hydrocarbons). Many of the contaminants found in the NWHI result from the past use of this area by the military and/ or for navigational aid stations. Extensive remedial cleanup has been undertaken at FFS, MID, and KUR, but some contaminant sources (both known and suspected) remain in those environments. The effects of these compounds on monk seal health, reproduction, and survival are unknown, but are presently not believed to represent a significant risk to recovery.

## FUTURE CONSERVATION EFFORTS

Previously, an assortment of science-based recovery efforts were implemented to address specific mortality sources, stabilize declining populations, or catalyze the recovery of severely depleted monk seal subpopulations. The conspicuous slowing of the overall rate of the population decline in the mid-1990s (Fig. 2) should be viewed as a success by providing more time to refine our enhancement techniques and identify new recovery strategies based on ongoing scientific investigations.

While the status of the species would undoubtedly be far worse had none of these interventions been applied, the population is now at its lowest level in approximately five decades. Further, multiple indicators (beach counts, population estimates, age/sex structures, and demographic rates) suggest that, at most sites, the prognosis for imminent improvement is poor.

It is apparent that the ultimate goal of reversing overall population decline will hinge on a comprehensive, scientifically sound characterization and mitigation of natural and anthropogenic factors limiting population growth. We must also anticipate and plan for those factors not currently constraining population growth, but likely to become threats at some future time (e.g., morbilliviruses). Certainly, some of these limiting factors (such as a declining forage base associated with oceanographic phenomenon) cannot be directly mitigated through management intervention. The task is, then, to

identify a suite of mitigations that are achievable, cost-effective, and likely to maximize the biological return (in terms of growth potential) until such time as natural conditions allow us to scale back the level of direct intervention. There is much to learn before our understanding of monk seal ecology is complete enough to know precisely all of the possible interventions and how they should be implemented. But with the aid of rapidly evolving technologies (e.g., satellite transmitters, CRITTERCAM, fatty acid analysis) we are gaining new insight into aspects of the monk seal's world that could not have been anticipated a decade ago. We are optimistic that these advances will motivate creative solutions to mitigate the primary factors now limiting monk seal recovery.

## ACKNOWLEDGEMENTS

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Table 1. Estimated 2003 monk seal abundance for each population segment ($N_{min}$), calculated according to the methods of Wade and Angliss (1997).

| Site | Estimation Method | N | Std Dev | $N_{min}$ |
|------|-------------------|-----|---------|-----------|
| FFS | Direct enumeration | 311 | NA | 311 |
| LAY | Direct enumeration | 272 | NA | 272 |
| LIS | Direct enumeration | 150 | NA | 150 |
| PHR | Direct enumeration | 209 | NA | 209 |
| MDY | Direct enumeration | 63 | NA | 63 |
| KUR | Direct enumeration | 92 | NA | 92 |
| Necker | Corrected beach counts | 48.3 | 19.6 | 35 |
| Nihoa | Corrected beach counts | 47.2 | 21.2 | 33 |
| Main HI | Aerial survey | 52 | NA | 52 |
| TOTAL | | 1,244.5 | | 1,217 |

Table 2. Changes in size (acres) of emergent islets at French Frigate Shoals. (1923 to 1966: Amerson, 1971).

| | YEAR (month) | | | | |
|---|---|---|---|---|---|
| LOCATION | 1923(Jun.) | 1942(Aug.) | 1963(Jun.) | 1966(Jan.) | 2004(Sept.)* |
| Bare Island | 0.1 | | 0.1 | | <0.1 |
| Disappearing Island | | | 6.2 | | 0.4 |
| East Island | 9.6 | | 11.3 | | 6.2 |
| Gin Island | | | 3.2 | | 2.1 |
| Little Gin | | | 5.1 | | 2.3 |
| Mullet Island | 0.4 | | 0.5 | | <0.1 |
| Near Island | | | 0.1 | | <0.1 |
| Round Island | 1.6 | | 0.5 | | <0.1 |
| Shark Island | 1.1 | | | 0.8 | 0.1 |
| Tern Island | 11 | 11 | 56.8 | | 25.5 |
| Trig Island | 5.3 | | 9.9 | | 1.1 |
| Whale-Skate | 8.3 | | 16.8 | | <0.1 |

* 2004 island acreages derived from GPS perimeter measurements.
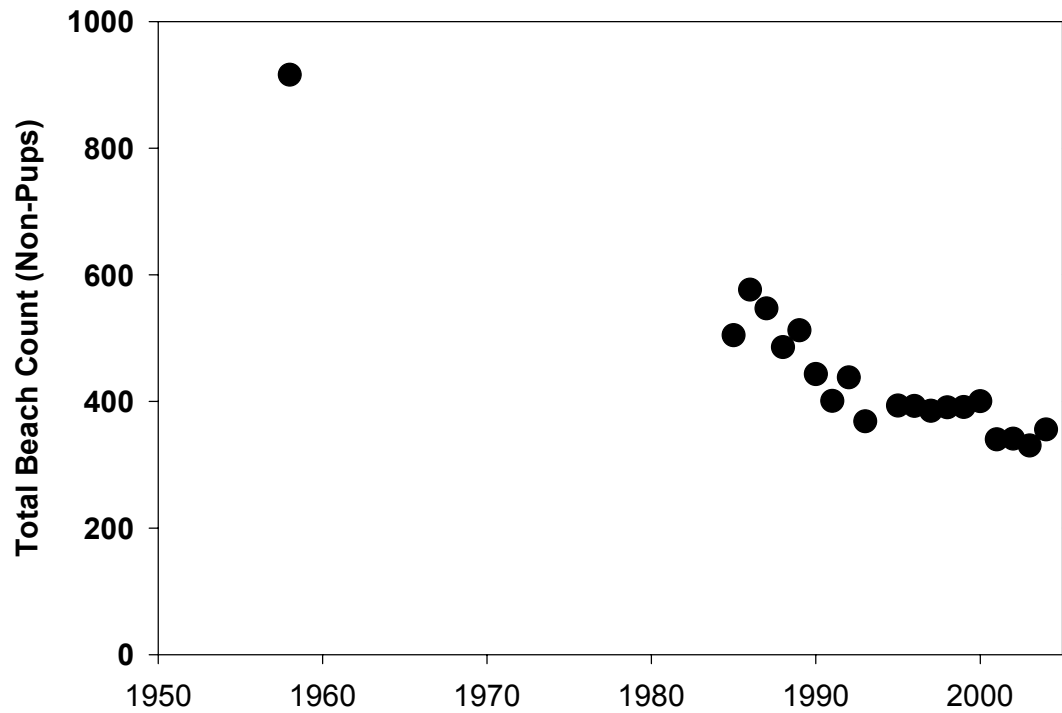
**Figure 1**. Historical trend in mean beach counts (nonpups) of Hawaiian monk seals at the six main subpopulations.
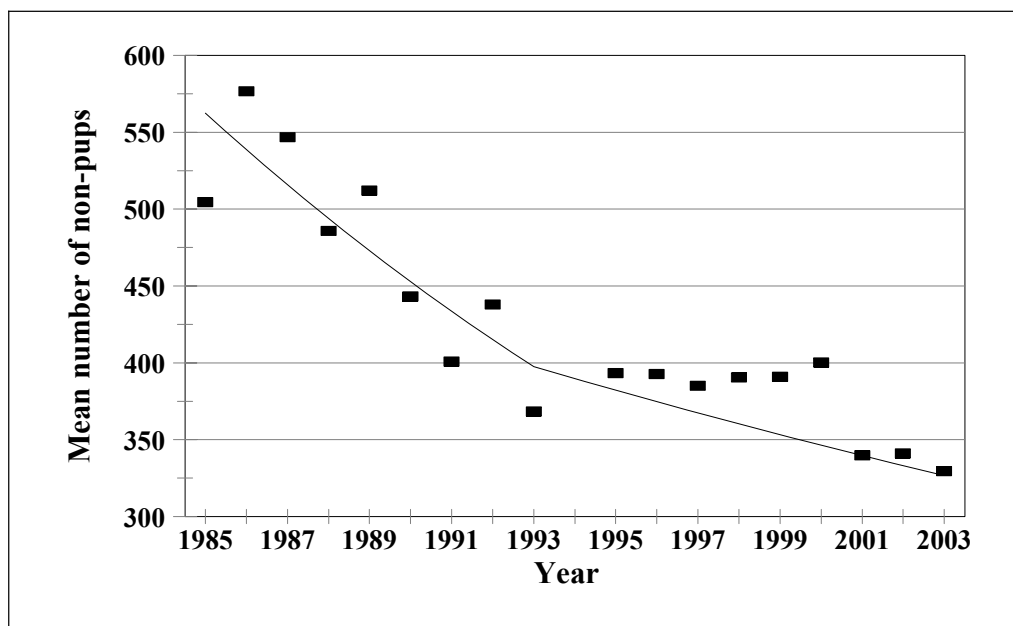


**Figure 2**. Recent (1985-2003) trend in monk seal population abundance in the NWHI. Plotted values are the mean number of nonpups observed during standardized beach counts at all six of the primary breeding subpopulations.
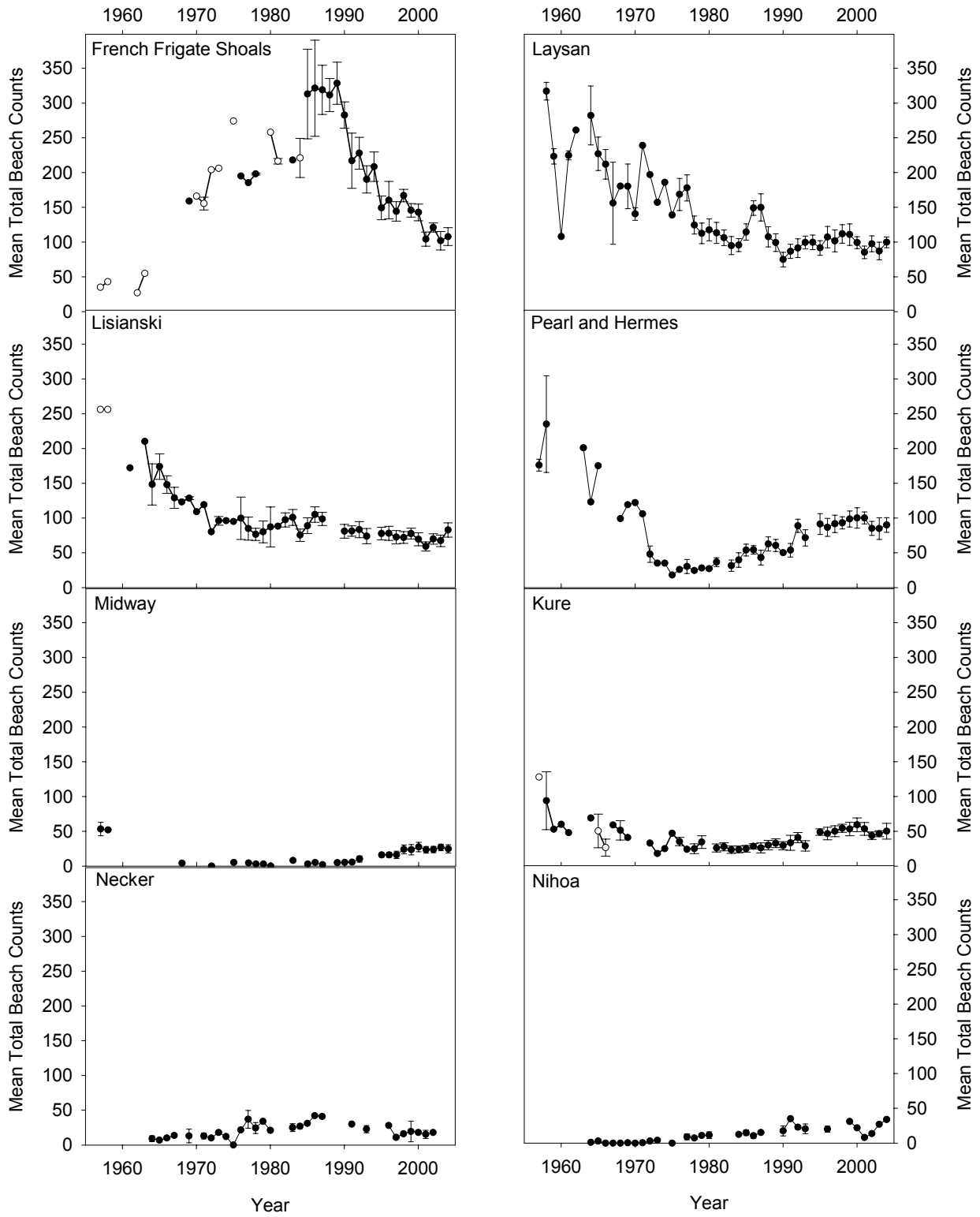
**Figure 3.** Population trend index (mean beach counts) for individual NWHI subpopulations (--○-- indicates less reliable historical counts).
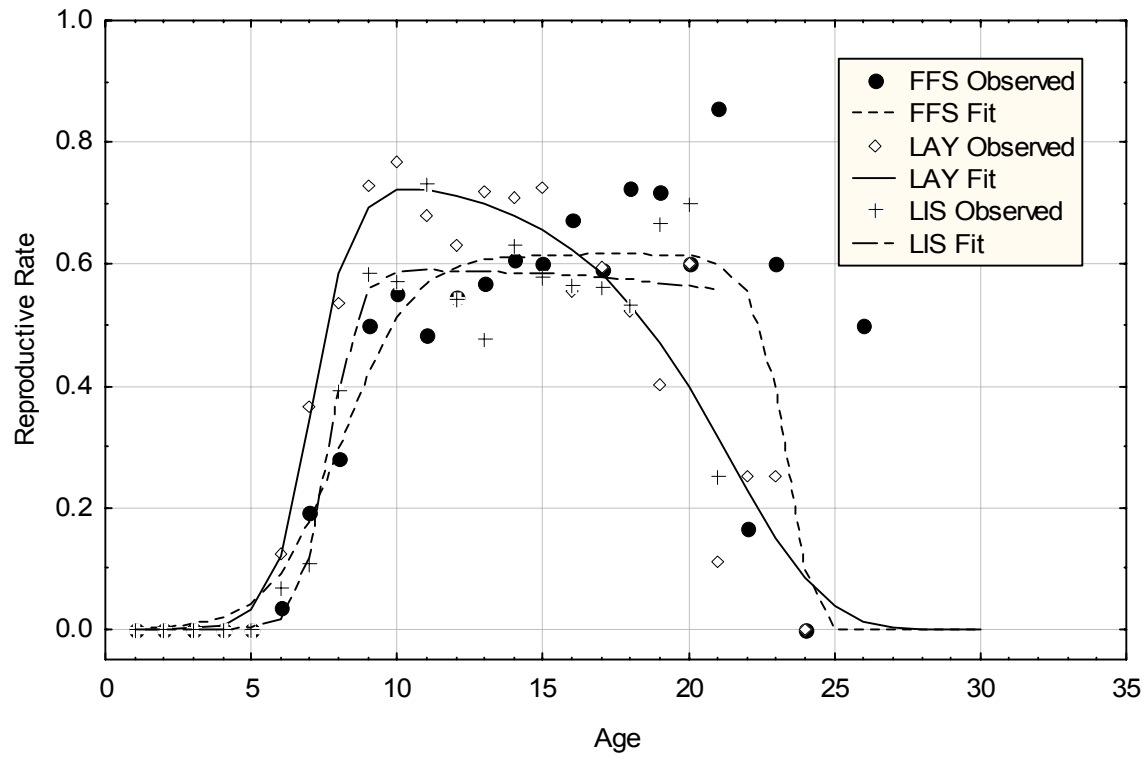
**Figure 4.** Comparison of age-specific reproductive rates for Hawaiian monk seals at FFS, Laysan Island, and Lisianski Island. Curves are fitted reproductive functions to observed reproductive frequencies for known-age seals pooled over all years.
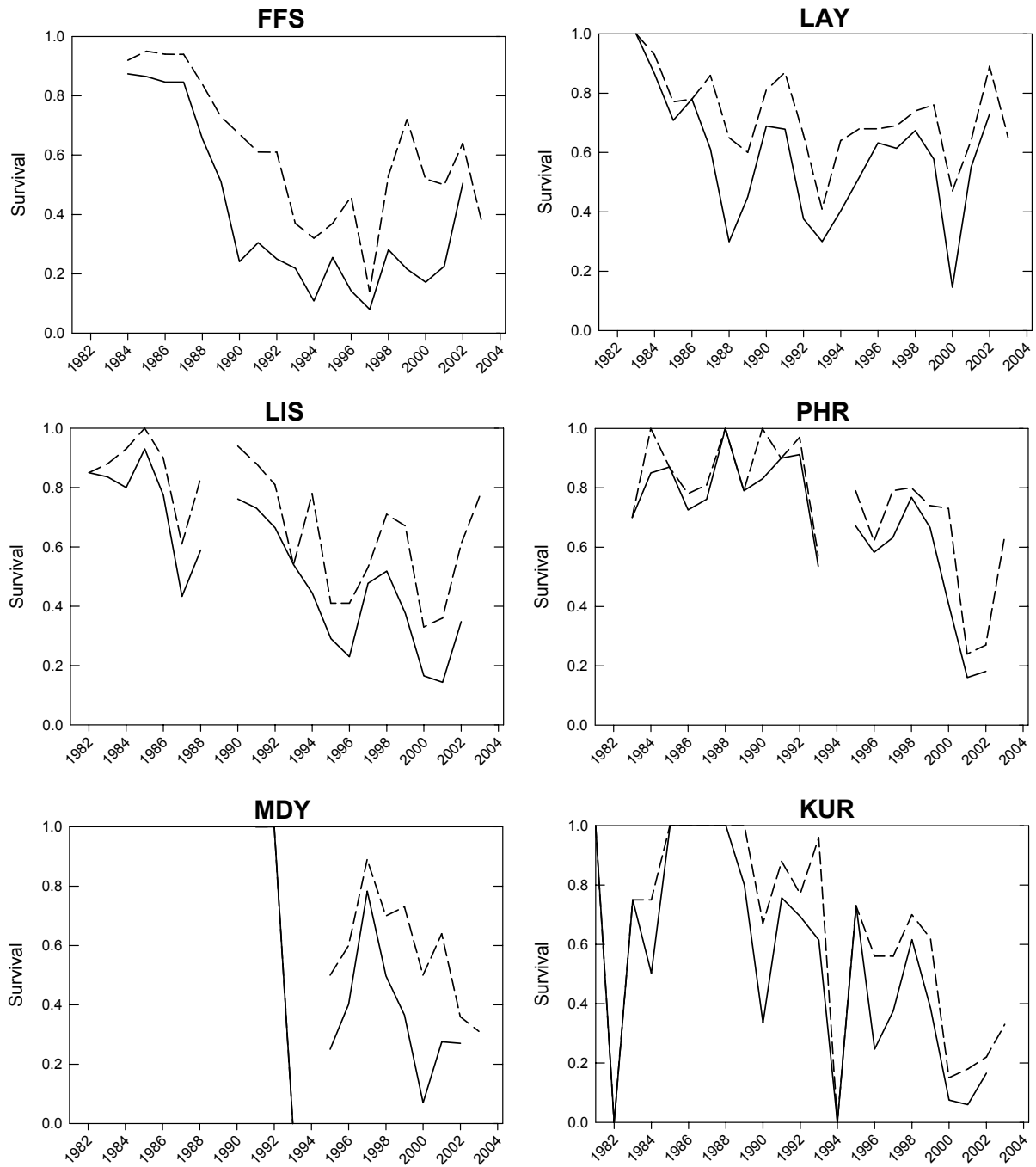
**Figure 5.** Cohort survival (weaning to age 1 and weaning to age 2) for the six primary breeding subpopulations (----- Survival to 1 year of age, ——— Survival to 2 years of age).
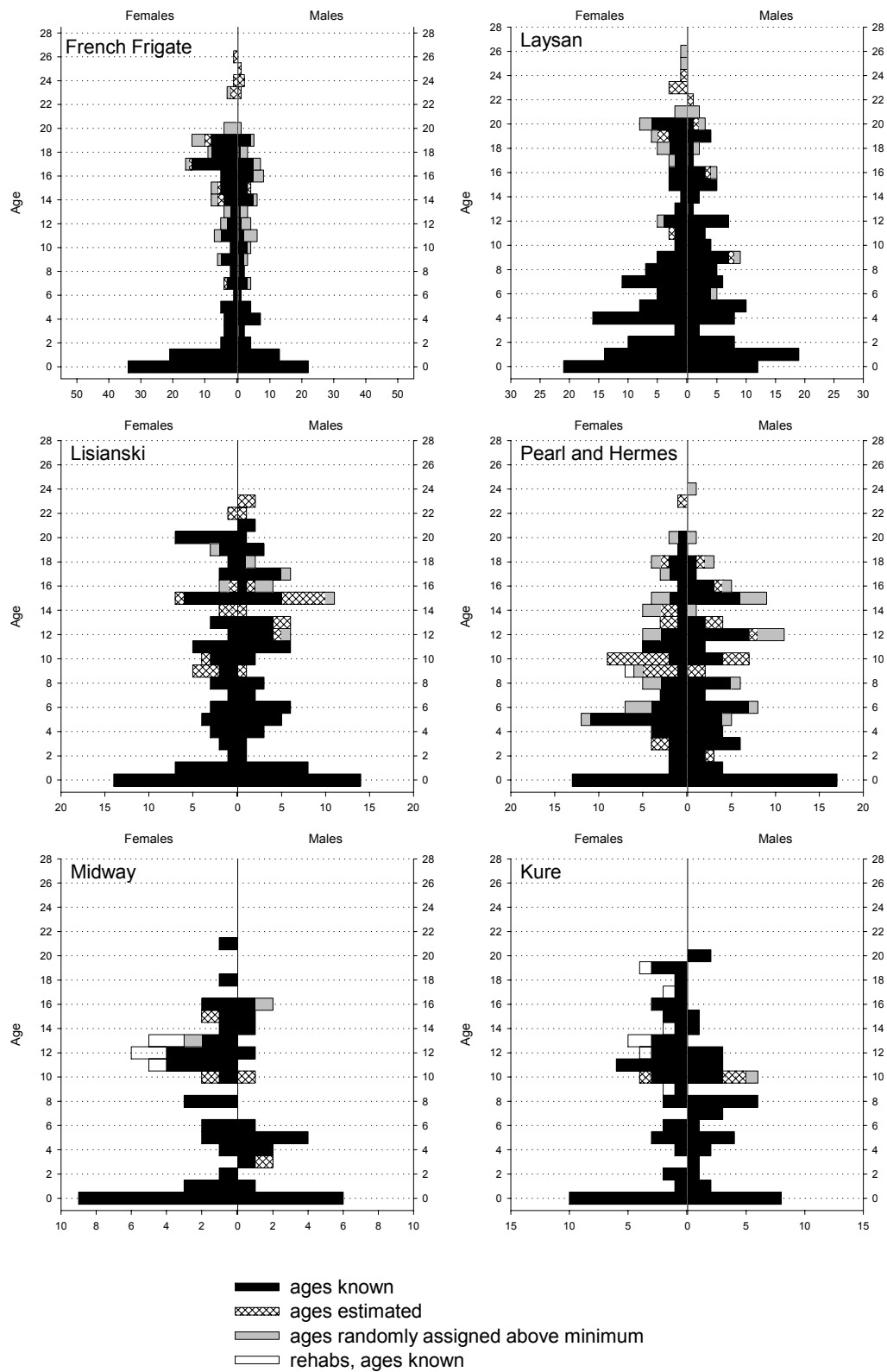
**Figure 6.** Current (2003) monk seal age structure for the six primary breeding subpopulations in the NWHI. Females are shown on the left and males are shown on the right. Patterns indicate different levels of certainty for the true age of each seal (see legend).

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# INCREASING TAXONOMIC RESOLUTION IN DIETARY ANALYSIS OF THE HAWAIIAN MONK SEAL

BY

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## ABSTRACT

We examined otoliths found in regurgitate samples (spews) of Hawaiian monk seals, *Monachus schauinslandi*, to identify fish prey, and report for the first time that these seals eat morid cods typically found at subphotic depths.  Dietary information was used to build a comparative skeletal collection and create a digital image database to aid foraging ecologists in the efficient, species-level identification of fish remains.  We suggest that high-resolution dietary analysis will significantly enhance understanding of monk seal foraging behavior and food requirements, and that previous assumptions that Hawaiian monk seals forage largely in shallow coral-reef habitats are in need of revision.

## INTRODUCTION

The total population of the endangered Hawaiian monk seal, *Monachus schauinslandi*, is composed of approximately 1,300 individuals living mainly on six reef systems in the Northwestern Hawaiian Islands (Antonelis et al., 2006).  The emaciated condition of some pups and adults suggests that starvation may be a threat to the species (Ragen and Lavigne, 1999; Parrish et al., 2000).  Population biologists report declines in birth rates and survival rates of pups and juveniles, and increases in age of first reproduction of females (Stewart, 2004).  A reduction in prey is most likely a significant factor influencing these trends (Parrish, 2004).  Such a reduction could be caused by natural prey fluctuations or competition for prey resources (Goodman-Lowe, 1998).  For these reasons, understanding the diet and foraging habits has been identified as a key component for successful conservation of the Hawaiian monk seal (Stewart, 2004).  Such information can help resource managers evaluate concerns of user groups (lobster, finfish, and precious coral fisheries) and efforts to enhance juvenile survival (*e.g.*, translocation) when making management decisions for the conservation and recovery of monk seals.  However, what and where monk seals eat must be fully understood (Ragen and Lavigne, 1999; Parrish, 2004) before assessments of prey availability and abundance can be made.

Early studies on the diving behavior of seals, combined with dietary analyses, led to the inference that seals forage mainly within the shallow coral-reef habitat.  DeLong et al. (1984) used depth recorders to describe the diving behavior of six animals and

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reported that the majority (59%) of dives were shallower than 40 m. Kenyon and Rice (1959), DeLong et al. (1984), and Goodman-Lowe (1998) used a variety of techniques to describe the diet of seals at family-level taxonomy and reported that nearly all prey could be classified as reef-associated.

Since then, a variety of telemetry studies have provided cause to question whether seals feed primarily within the reef habitat. Seals routinely travel between the islands, banks, and seamounts of the Northwestern Hawaiian Islands (Parrish, 2004) and may travel up to 160 km from their haul-out location (Abernathy, 1999). More recent depth recorder data shows seals spend a large portion of their dive time between 50 and 300 m (Stewart, 1998). Furthermore, some seals routinely dive to subphotic depths. Parrish (2004) summarized telemetry data and found that, of 37 adults tagged (Abernathy, 1999; Stewart 2004; Stewart & Yochem, 2004 a and b), 47% dove to at least 300 m. Combined, these telemetry data suggest seals forage at the edges of atolls and banks, in the slope habitat (Parrish, 2004).

Seal-mounted video cameras further show that most time in shallow water (>50%) is spent sleeping and socializing (Parrish et al., 2000). Other shallow dives (<20 m) are prolonged midwater swims as seals travel to foraging grounds at remote locations (Parrish et al., 2002). Thus, shallow-water activity does not coincide with prey capture. In fact, seal-mounted video cameras show that, although most time is spent in the shallow waters of the atoll, most prey are captured at depths of 50-100 m (Parrish et al., 2000). Seals ignored shallow-water reef fishes and fed on fishes from low-relief habitats in deeper water (Parrish et al., 2000).

By increasing taxonomic resolution in dietary studies, we will obtain a more detailed picture of food resource use by monk seals and an increased probability of detecting relationships between prey resources and monk seal demography. Although nearly all fishes eaten by monk seals belong to a reef-fish family (Kenyon and Rice, 1959; DeLong et al., 1984; Goodman-Lowe, 1998), most reef-fish families have deep-water members. For instance, all dietary analyses indicate that conger eels are an important part of seal diets. Kenyon and Rice (1959) noted that these eels are abundant within the atolls, and DeLong et al. (1984) state that the family prefers shallow, benthic habitats. A plot of the depths where the 10 Hawaiian congrids occur (Fig. 1) shows that the distribution of these eels is more complicated. A similar pattern can be found for nearly all fish families important (prevalent) in the monk seal diet. Species-level dietary analysis can be combined with known patterns of habitat use (depth and bottom type) by prey species to infer where seals successfully capture food.

We performed preliminary dietary analysis on Hawaiian monk seals, and used the information to describe seal prey use, to infer foraging behavior, and to guide the expansion of a comparative collection of fish skeletons. With access to the information housed in such a comparative collection, most foraging ecologists can conduct species-level dietary analysis and contribute to a better understanding of seal food resource use. We describe a prototype photographic database (virtual collection) designed to give researchers remote access to the collection and to identify fish remains to species more efficiently.
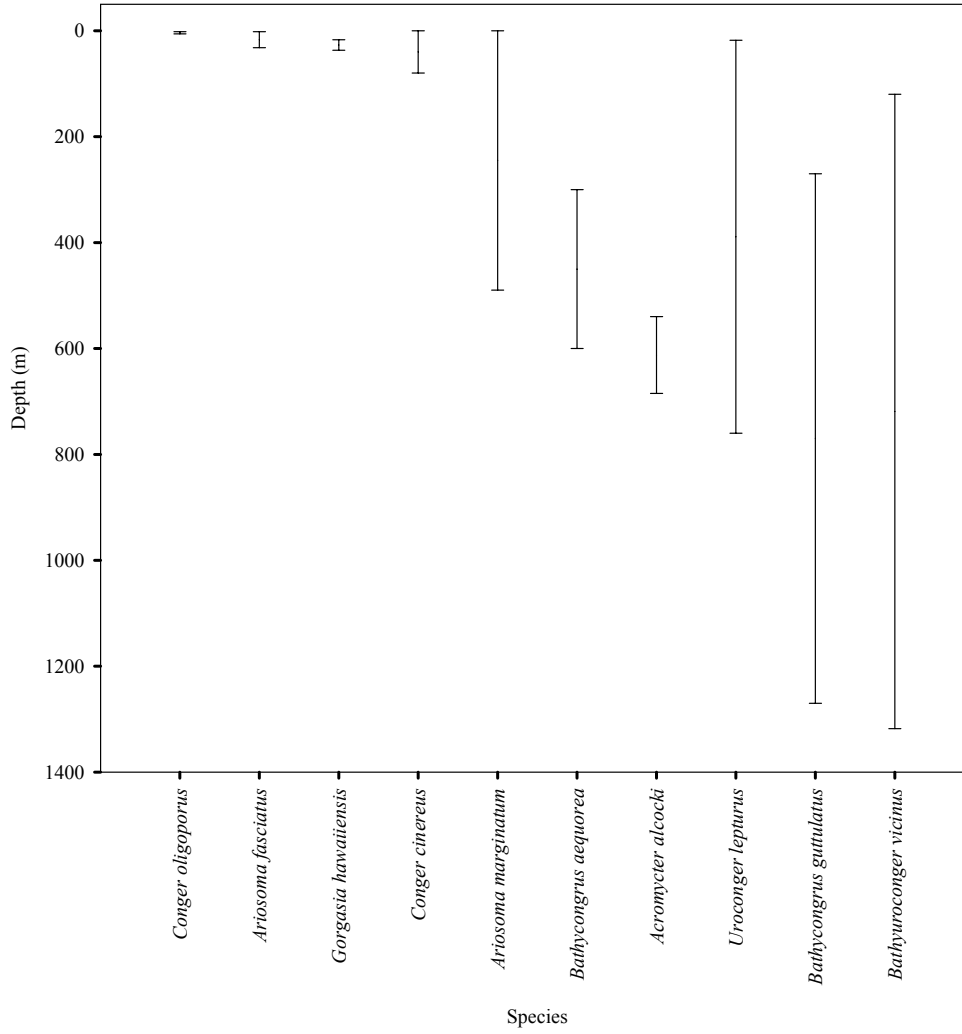
**Figure 1**. Depth distribution of 10 Hawaiian congrid species.

**METHODS AND MATERIALS**

Overview

Our methods were an iterative process. Preliminary dietary analyses were performed on seal regurgitate samples (spews), and this information, combined with results from past dietary studies (DeLong et al., 1984; Goodman-Lowe, 1998), was used to compile a list of fish families important in seal diets. These families were then targeted for collection, with the intention of building a comparative skeletal collection of all Hawaiian species in those families. Diagnostic bones were photographed and incorporated into an image management program to aid rapid identification of fish remains. These physical and virtual comparative collections were then used to re-examine samples, to examine other spew samples, and eventually to examine fecal samples (scats). More prey species or families will be added to the collection as necessary.

Dietary Analysis

Spews were used for the preliminary analysis because fish prey tends to be less digested than in feces; thus the likelihood of identifying prey was increased. Spews were collected from the Northwestern Hawaiian Islands (NWHI), during the 1996-2001 National Marine Fisheries Service (NMFS) summer field camps. Samples were sent to the lab, washed with fresh water, dried, and stored in plastic bags for processing. Otoliths were the primary structures used to identify fish prey because the otolith literature most fully represents Hawaiian fish families. We used the otolith atlases of Smale et al. (1995), Rivaton and Bourret (1999), and Dye and Longenecker (2004) as identification guides. We also used, when appropriate, a comparative collection of fish skeletons housed at the Bishop Museum to identify bones.

Physical Comparative Collection

Species from fish families important in the diet of monk seals were collected during NMFS cruises, and frozen until processing. Fishes were identified to species, measured, and photographed. A disarticulated skeleton does not possess the features typically used for taxonomic work; therefore, any deviations from the species description were noted.

Scales were sampled from six locations (Casteel, 1974) on each specimen: the nape, dorsally on the flank, ventrally on the flank, posterior to the dorsal fin, dorsally on the caudal peduncle, and ventrally on the caudal peduncle. These were mounted in a standardized order between glass slides. Skeletons were prepared by eviscerating, skinning, and removing most muscle from the specimen; drying the carcass; and cleaning it with dermestid beetles (see Sommer and Anderson, 1974 and Bemis et al., 2004 for details and variations of techniques). Skeletons were further cleaned and partially disarticulated by cold-water maceration (Hildebrand, 1968).

Virtual Comparative Collection

Structures incorporated into the virtual collection (i.e., photographic database) are those commonly found in seal spews (personal observation) and described as useful taxonomic indicators by Wheeler & Jones (1989). These structures are [following the terminology of Rojo (1991)]: saggitae (saccular otoliths), premaxilla, maxilla, dentary, angular, quadrate, hyomandibular, prevomer, parasphenoid, basioccipital, supraoccipital, pterotic, frontal, opercle, preopercle, three precaudal vertebrae, three caudal vertebrae, and the six scales collected as described above. The three vertebrae selected for the precaudal and caudal series represent the range of conditions for each vertebral type. Because the neurocranium of fishes is often found relatively intact in seal spews, images were included for each species.

Structures were photographed from several aspects (typically lateral and medial, or dorsal and ventral) on a dissecting microscope at the highest magnification that included the whole structure in the field of view. Images were incorporated into the photo management program, SuperJPG. This program allows images to be linked to keywords (e.g., family name, genus name, species name, bone name, and features found on each bone). An extensive review of phylogenetic literature provided the terminology used to describe bone features. An illustrated glossary of these terms (Longenecker, 2004) was produced to accompany the virtual collection.

## RESULTS

Dietary Analysis

Thirty-one spews from the 1996-2001 field collections were examined for preliminary dietary analysis. The majority of spews (22) were collected at Laysan, six were from Lisianski, one from Seal-Kittery Island at Pearl and Hermes Reef, and one each from Disappearing Island and Little Gin Island at French Frigate Shoals. In Table 1, we present fishes eaten, by family. Not all prey items were identified. However, the percent number (number of prey from a given taxon divided by the total number of identified prey, expressed as a percentage) and percent frequency of occurrence data do give an estimate of which families are most important in the monk seal diet. Moridae and a tentatively identified Cynoglossidae are reported as monk seal prey for the first time.

Some fishes were identified beyond family level. Thirty-five of the 47 congrids were *Ariosoma marginatum*. One of the labrids was a razor wrasse (*Iniistius*). Both holocentrids were *Myripristis* species (soldierfish).

Parts of crustaceans and molluscs were also found. Of the crustacea, one was a stomatopod and another was a lobster.

Table 1.  Family-level identification of fishes from 33 spews of Hawaiian monk seals collected 1996 – 2001 from Laysan Island, French Frigate Shoals, Lisianski Island, and Pearl and Hermes Reef.  Eighty-eight individuals were identified.

| Family | % Number | % Frequency of Occurrence |
|---|---|---|
| Congridae | 53.4 | 25.8 |
| Tetraodontidae | 22.7 | 6.5 |
| Labridae | 6.8 | 9.7 |
| Scaridae | 4.6 | 3.2 |
| Holocentridae | 2.3 | 6.5 |
| Priacanthidae | 2.3 | 3.2 |
| Moridae | 1.1 | 3.2 |
| Ophidiidae | 1.1 | 3.2 |
| Scorpaenidae | 1.1 | 3.2 |
| Acanthuridae | 1.1 | 3.2 |
| Monacanthidae | 1.1 | 3.2 |
| Balistidae | 1.1 | 3.2 |
| Cynoglossidae (tentative) | 1.1 | 3.2 |

Table 2.  Fish families important in the monk seal diet ($\geq$3% Frequency of Occurrence as reported in Goodman-Lowe, 1998), the approximate number of Hawaiian species, and the number of species in the comparative skeletal collection.

| Family | # Hawaiian species | # species in collection |
|---|---|---|
| Congridae | 10 | 3 |
| Tetraodontidae | 14 | 4 |
| Labridae | 41 | 13 |
| Scaridae | 7 | 5 |
| Holocentridae | 18 | 5 |
| Priacanthidae | 4 | 2 |
| Ophidiidae | 4 | 0 |
| Acanthuridae | 23 | 15 |
| Monacanthidae | 9 | 4 |
| Balistidae | 10 | 5 |
| Muraenidae | 40 | 4 |
| Synodontidae | 15 | 2 |
| Mullidae | 11 | 10 |
| Kyphosidae | 5 | 1 |

Physical Comparative Collection

The comparative skeletal collection currently houses 515 specimens representing 177 species.  Our collection is far from complete; approximately 1,000 fish species are known from the Hawaiian Islands.  Even when considering only the subset of families documented from monk seal diets (DeLong et al., 1984; Goodman-Lowe, 1998; Parrish et al., 2000; present study), we have only 34.5% of the species, and no family is complete. Table 2 is a list of fish families important in the monk seal diet, the approximate number of species in Hawaii, and the number of species in the collection.

Virtual Comparative Collection

The digital image database currently contains 414 images representing 21 species from 7 families.  These are linked to descriptors (key words) which can be used to sort images and display only those structures with specific character(s).  Each image is linked to the family, genus, species, and structure (bone name or otolith) it represents. Structures are being linked to character states used in phylogenetic analyses.  For example, the dentaries are linked to 24 character states that can be selected singly or in combination.  The sorting power of the database is illustrated in Figure 2; an investigator attempting to identify a bone can display all images of bones from one or more taxa, all images of a single bone type with one or more characters, or all images of a single bone type from a given taxon.

## DISCUSSION

Dietary analysis using spews and scats is inherently biased.  Because seals may travel up to 160 km from their haul-out location (Abernathy, 1999), prey eaten at distant locations may be voided before the seal returns to a beach.  Thus, spews and scats may mostly represent prey taken in nearby locations (Parrish, 2004).  Variation in digestion rates of prey parts may lead to over- or under-representation of prey.  Spew analysis may present unique problems.  Goodman-Lowe (1998) suggests eels are more likely to be regurgitated than other prey.  Similarly, fishes likely to be ciguatoxic may be over-represented in spews.  Despite these potential drawbacks, scat and spew analysis remains the most direct way to determine what seals eat.  This low-technology, low-cost method can potentially generate large amounts of information from the abundant deposits (thousands have been collected) left by seals on beaches.

Our work represents the first report of morid cods (Moridae) in the diet of Hawaiian monk seals.  Nine morid species occur in Hawaii, and all are found in depths greater than 95 m.  The family is characteristic of the subphotic fish community (Parrish, 2004).  The morid was found in a spew collected on Laysan.  This finding is consistent with recent telemetry studies showing most seals at Laysan (80%) dove at least to depths of 100 m, and all adult females dove beyond 300 m (Stewart and Yochem, 2004b).

We found at least four congrid eel species in seal spews.  As these are identified to less-inclusive taxonomic groups (genus and species), we will gain increasingly
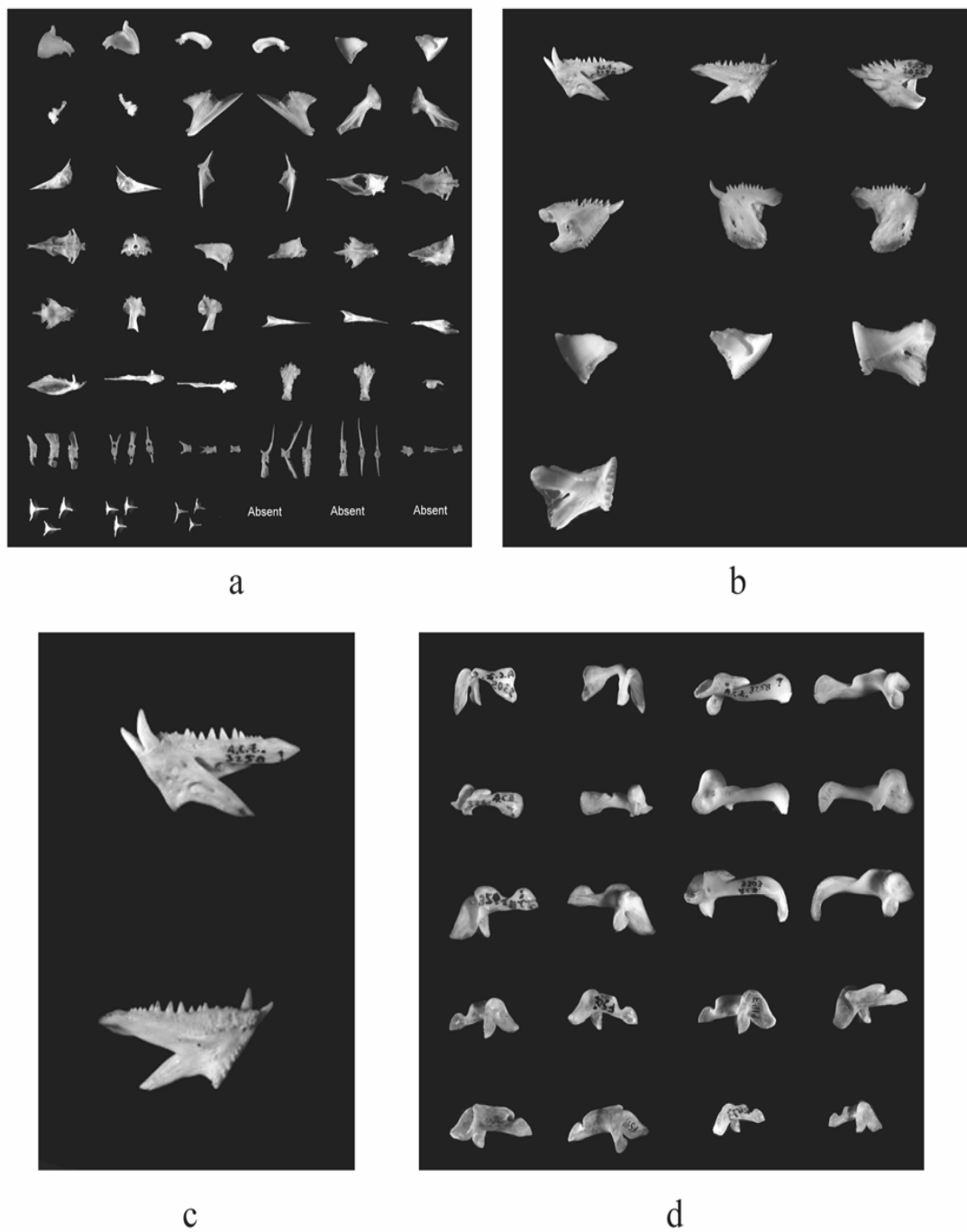
**Figure. 2.** Examples of the sorting power of the virtual comparative collection. (a) all structures from *Canthigaster jactator* ("absent" represents scale-less locations), (b) all dentaries with an interdigitate mandibular symphysis, (c) all dentaries with an interdigitate mandibular symphysis and a pointed ventral process, (d) all labrid maxillae.

detailed knowledge about the foraging habits of monk seals. For instance, the majority of congrids consumed were *Ariosoma marginatum*. This is a sand-dwelling species (Randall, 1996). Of the labrids eaten, one belonged to the genus *Iniistius*. These razorfishes also live over open sand bottom (Randall, 1996). The presence of these prey in spews corresponds with evidence from seal-mounted video cameras that sand bottoms are the second most frequent habitat searched by foraging seals (Parrish et al., 2000).

A current drawback of using fecal and regurgitate samples to describe monk seal foraging behavior is an inability to match a scat or spew found on the beach to a single animal. Thus, it is possible that some animals will be sampled repeatedly, and others not at all. Efforts are now underway to match scats and spews to individuals so that bias can be reduced, and sex- and age-based dietary analyses can be performed.

Species-level identification of prey fish previously required access to a large comparative collection of fish bones and an intimate knowledge of its contents. Unfortunately, there are few of these comparative collections, their creation and maintenance is time-consuming and costly, they require a significant amount of space, and accessing them can be difficult. Further, few foraging ecologists have the necessary familiarity with comparative fish osteology to realize the full potential of a comparative osteological collection. The imaging technology we describe will give many researchers unlimited virtual access to a comparative collection and will efficiently guide foraging ecologists toward high-resolution identification of fish remains.

We are currently working to incorporate cephalopod beaks into the image database. These are abundant in scats and spews (Kenyon and Rice, 1959; DeLong et al., 1984; Goodman-Lowe, 1998; present study). Goodman-Lowe (1998) was particularly successful at high-resolution identification of cephalopod beaks. We anticipate that our virtual reference collection will help others perform the same quality of work.

The digital image database described here was designed specifically to aid studies of Hawaiian monk seal foraging ecology. The disarticulated skeletons prepared in this study will be added to a comparative collection begun by archaeologists at Bishop Museum. We anticipate the virtual collection will be useful to a broad range of foraging ecologists, archaeologists, and paleontologists.

## ACKNOWLEDGEMENTS

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through Cultural & Historical Organizations, also known as ECHO, provides educational enrichment to native and non-native children and lifelong learners.  We thank Bud Antonelis and Charles Littnan for comments on the manuscript.  This is contribution #2005-004 to the Hawaii Biological Survey.

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# MOVEMENTS OF MONK SEALS RELATIVE TO ECOLOGICAL DEPTH ZONES IN THE LOWER NORTHWESTERN HAWAIIAN ISLANDS

BY

FRANK A. PARRISH[1] and KYLER ABERNATHY[2]

## ABSTRACT

In the 1990s, adult male and female monk seals (n = 24) at French Frigate Shoals were fitted with satellite tags and their activity monitored (median 87 days). The distribution of their movements was compared with the area and distribution of four ecological zones that were used to classify the summits of the Hawaiian ridge. The zones were defined by depth as reef (<30 m), bank (30-50 m), slope (51-300 m), and subphotic (301-500 m). Geographic Information Systems (GIS) comparisons indicated that the seals moved throughout the region and did not focus their activities in a particular zone or limit themselves to shallow depths or proximity to their haul-out areas. Surveys of fish assemblages in each of the four zones showed an overall decline in biomass with depth. The same fish families were found in all zones except for the subphotic zone, where other families were dominant. The fish survey data were classified into prey-evasion guilds for monk seals, and the percent composition of the four zones then was compared with the monk seal diet data from the literature. The composition of the seals' diet differed significantly from the composition of fish found in each zone. However, on the basis of a dissimilarity index, the composition of the fish guilds in the bank and slope zones deviated the least from the monk seals' diet.

## INTRODUCTION

Where and what monk seals eat is a question that scientists and resource managers of the Northwestern Hawaiian Islands (NWHI) have attempted to address using a wide variety of methods. Monk seals (*Monachus schauinslandi*) (Gilmartin and Eberhardt, 1995) routinely move between the reef systems of the Hawaiian Archipelago and dive to a wide range of depths (Abernathy, 1999). The scale of these movements challenges some long-standing assumptions about monk seal foraging habitat and highlight the need for information about prey distribution in the seals' forage grounds. Studies of foraging behavior of French Frigate Shoals (FFS) seals have included tracking of movements using satellite tags (Abernathy, 1999) and analysis of prey fragments in seal scat (Goodman-Lowe, 1998). In this study, these foraging data are compared with regional surveys of potential prey assemblages.

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All available foraging data (Abernathy, 1999; Goodman-Lowe, 1998; Parrish et. al., 2000, 2002, 2005) indicate that FFS seals feed on benthic and demersal fish species, and thus their foraging grounds are limited to the benthic habitat afforded by the shallow portions (<600 m) of the Hawaiian Archipelago. Modified by a long history of sea-level change (Grigg and Epp, 1989), the habitat of the lower Archipelago is composed of four obvious depth zones. The first zone is the shallow "reef" of FFS (<30 m) that hosts the sand islets where the monk seal subpopulations rest and rear their young. The next most prominent zone consists of the submerged "banks" at 30-50 m that occur SE and NW of FFS. These banks support minimal coral coverage and are covered primarily with sand and algae. At the edge of the reef or bank, the "slope" zone (51-300 m) begins. At the base of the steepest slope segments, often around 60 m deep, talus accumulates, with smaller sizes of rubble sorting below. At 80-100 m, there is often a terrace where sand accumulates, and then the slope continues steeply down to 300 m. Deep-water black corals (*Cirripathes* sp.) often are seen ~200 m deep, growing on the carbonate remnants of prehistoric coral reef complexes or lithified carbonate sand fields. The slope decreases significantly at ~300 m. At this depth, light is well below the level needed for photosynthesis; this fourth zone (301-500 m) will be called "subphotic." Bottom types include carbonate, basalt, manganese crust, and sand with occasional patches of deep-water corals in areas of high current flow.

In this paper we consider seal movements in relation to these four depth zones. We compare the prey base among the habitat zones visited by the seals. Finally, the prey-base data will be evaluated in relation to available monk seal diet data. The following hypotheses will be tested: 1) seals feed more in the nearest habitats and less in distant ones; 2) seal feeding is governed by the structure (body size, numerical density, or biomass density) of the fish community available; and 3) different patterns in seal feeding found among habitats are not related to morphological or behavioral differences in the prey types.

## METHODS

Seal Movement Data

Satellite tags were fitted to 24 adult FFS seals (males and females) between April and July during 1992–94 and 1996-1997 (median 87 days)(Abernathy, 1999). Although the distance and dive characteristics of the seals' movements have been described (Abernathy and Siniff, 1998; Abernathy, 1999), at that time there were no data on seal-prey assemblages with which to compare. Activity patterns for each seal were plotted on a base map in a raster-based geographic information system (GIS)(IDRISI) representing the $600^2$ - km area (0.13 km²/raster cell) section of the Archipelago from Necker Bank to Gardner Bank - the extent of travel documented for the FFS seals. Isobaths from National Ocean Survey charts were used to delineate the four depth/habitat zones, reef (0-30 m), bank (31-50 m), slope (51-300 m), and subphotic (301-500 m) as the primary test categories (Fig. 1).
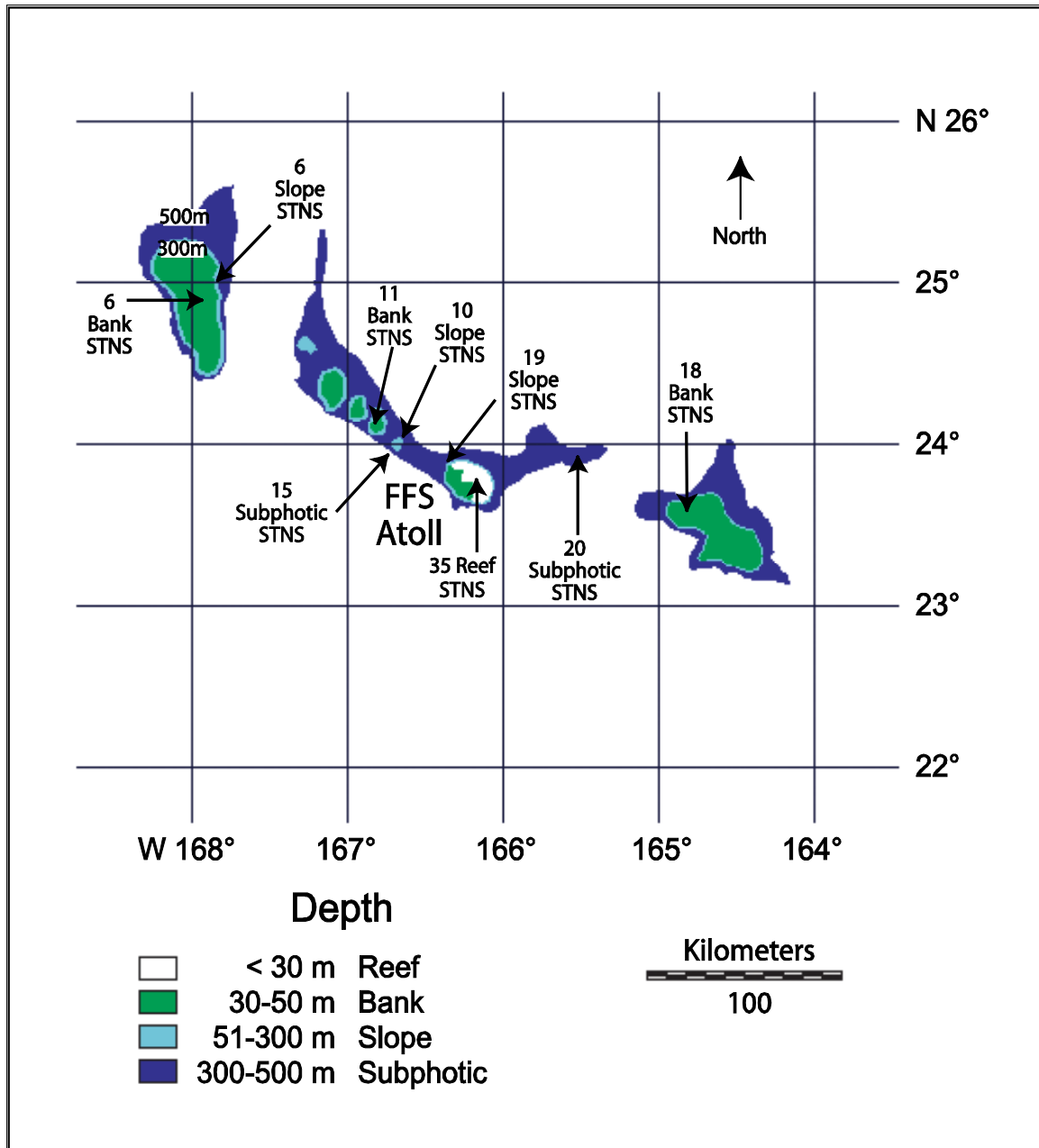
**Figure 1**. Base GIS coverage of the French Frigate Shoals region with each of the four habitat zones represented. Arrows indicate the location of the fish surveys.

Satellite tags can provide positions of seals only if they are on the surface during the daily pass of the orbital ARGOS satellites. Furthermore, some sampling bias may be introduced by the varying degrees of satellite coverage throughout the course of the day. Positional accuracy checked with independent VHF tracking of the satellite tags averaged 16 km ± 13 km (sd). To refine confidence in the seal positions, these data were evaluated using software called "Satel" provided by Loyd Lowry (Alaska Dept of Fish and Game) that calculates the swimming speed required for a seal to travel between consecutive

estimated positions and indicates unrealistic positions given the seal's actual swimming velocity (7.2 km/hr). These poor positions were excluded from further analysis. Finally, even with "good" positions, it should be remembered that these are surface positions and represent seals surfacing from dives, which can be as long as 17 min (Abernathy and Siniff, 1998; Parrish et al., 2002). It was assumed that positions clustered tightly in one or more areas indicated the most reliable focus of the seals' effort over a given habitat. Clusters were defined by eye, with the delineation of the bounding polygons often excluding wide dispersions of points that were likely transits to and from feeding sites or opportunistic searching. Limiting the polygons to exclusively represent the clusters of positions should improve the chances of identifying key foraging habitats. The depth-of-bottom contours at the positional clusters were corroborated by depth-of-dive-activity modes transmitted from the satellite tags. The activity patterns of the 24 seals were overlaid to represent the cumulative area, or "footprint," of their foraging.

Two comparisons were made using the GIS data. First, the amount of overlap between the planar area of each zone and the footprint of the seals' foraging area was compared. Second, a GIS surface was generated with distance values radiating from the seal haul outs at FFS (the six sand islets in the atoll). Distance values then were extracted from each raster cell of the polygons of the four habitat zones and compared to distance values extracted from an overlay of the seals' footprint for each of the four habitat zones.

Fish (Prey) Community Surveys

Fish communities of the four habitat zones were surveyed using a variety of techniques. In each survey the numerical density of taxa and body length (to nearest 5 cm) of a fish assemblage were recorded for a given area for standardized area-based comparisons. Thirty-five visual surveys were made in each of the four habitat zones (Fig. 1), and Table 1 lists the survey methodologies for each of these zones. Survey stations in the FFS reef were established by habitat type using published (NOAA, 2003) benthic maps derived from 4-m resolution IKONOS satellite imagery. For the deeper habitat zones, no such data are available. Bank stations were placed arbitrarily across three banks (Necker, Brooks, and Gardner). The habitat of the slope is determined largely by sorting of talus, rubble, and sand, so the 35 stations were divided to represent the rubble belt, the sand reservoirs, and exposed carbonate bottom. The 35 subphotic stations were conducted from *Pisces* submersibles and included habitats of carbonate, basalt, and deep-water corals.

Length estimates were used with species-specific length-weight coefficients (Friedlander and Parrish, 1998) to obtain an estimate of biomass density. Large apex predators (e.g., jacks, sharks, snappers) were excluded from all the counts because they were too large to be considered seal prey. Trawl specimens from sand bottom were weighed to the nearest gram. No length-weight coefficients are available for subphotic species, so size-specific weights were obtained from historical trawl catch data (unpub. data, Pacific Islands Fisheries Science Center), or the weight of a fish with a similar body shape was used as a proxy. The estimates of prey size, numerical density, and biomass density of the community were then compared across the four zones.

Table 1.  Method, area, number of stations, and other details for fish community surveys made in each habitat zone of the French Frigate Shoals region.

| Zone | Method | Area $(m^2)$ | No. of stations | Years surveyed | Reference for survey methodology used. |
|------|--------|------|-----------------|----------------|------------------------------------------|
| Reef <30 m | Divers | 500 | 35 | 2002 | DeMartini et al. (1996) |
| Banks 30-50 m | Divers | 177 | 35 | 2001-2002 | Bohnsack and Bannerot (1986) |
| Slopes 51-300 m | Divers | 85-250 | 16 | 1998-1999 | DeMartini et al. (2003) |
|  | Trawls | 4000 | 9 | 2002 | Struhsaker (1973) |
|  | Sub | 3600 | 10 | 2000 | Moffitt and Parrish (1992) |
| Subphotic 301-500 m | Sub | 3600 | 35 | 1998-2002 | Moffitt and Parrish (1992) |
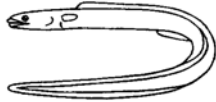
Monk Seal Diet

The value of the fish communities as monk seal prey was derived using data from analysis of scat (Goodman-Lowe, 1998).  The reported frequency of taxon occurrence in the scat data was used as a proxy for prey abundance, and each was classified into one of four guilds reflecting the prey's general evasion tactic, including bottom camouflage, hiding in shelter, fleeing along the bottom, and fleeing through midwater (Table 2). The evasion guilds were used to compare the relative importance of the shallow-reef community, which was best represented in the scat data, to bank, slope, and subphotic fish communities.  After classifying the fish from each of the four habitat zones by evasion guild, their numerical density and biomass density then were compared with the frequency of occurrence of the evasion guild in the seals' diet (Goodman-Lowe, 1998).  We assumed that a high fraction of a particular evasion guild found in the seals' diet meant the seals would target that evasion guild of prey across all four zones. Furthermore, the zone with the fractional makeup that best mirrors the relative fraction in the seals' diet is the zone most used by the seals.

Analysis

The seals' movements were tested in relation to the availability of the four zones using chi-squared comparisons.  The 35 stations per habitat zone provided this study a power of 0.80 to detect large effects at the 0.01 level (Cohen, 1988).  The fish communities of the four zones were evaluated using a Kruskal-Wallis (K-W) analysis of variance (ANOVA) and *a posteriori* Tukey comparisons.  Differences in the evasion guilds were addressed with chi-square using the seals' diet data as the expected values. Finally, the proportions of the evasion guilds in seal prey and the fish communities were converted into distance scores to compare their relative Euclidean distance from the seals diet using a parametric dissimilarity index.

Table 2. Monk seal diet by functional groups derived from analysis of scats (Goodman-Lowe, 1998).

| Evasion Guild | Taxa found in seal scat | Example taxa morphology |
|---|---|---|
| Bottom Camouflage<br><br>BC | *Synodontidae*<br>*Cirrhitidae*<br>*Bothidae*<br>*Scorpaenidae*<br>*Octopodidae* | |
| Bottom Fleer<br><br>BF | *Labridae*<br>*Scaridae*<br>*Acanthuridae*<br>*Muraenidae*<br>*Congridae*<br>*Kuhlidae*<br>*Ophichthidae*<br>*Mullidae*<br>*Lutjanidae* | |
| Bottom Hider<br><br>BH | *Pomacentridae*<br>*Tetraodontidae*<br>*Pomacanthidae*<br>*Chaetodontidae*<br>*Holocentridae*<br>*Pricanthidae*<br>*Apogonidae* | |
| Midwater Fleer<br><br>MF | *Kyphosidae*<br>*Monacanthidae*<br>*Balistidae* | |
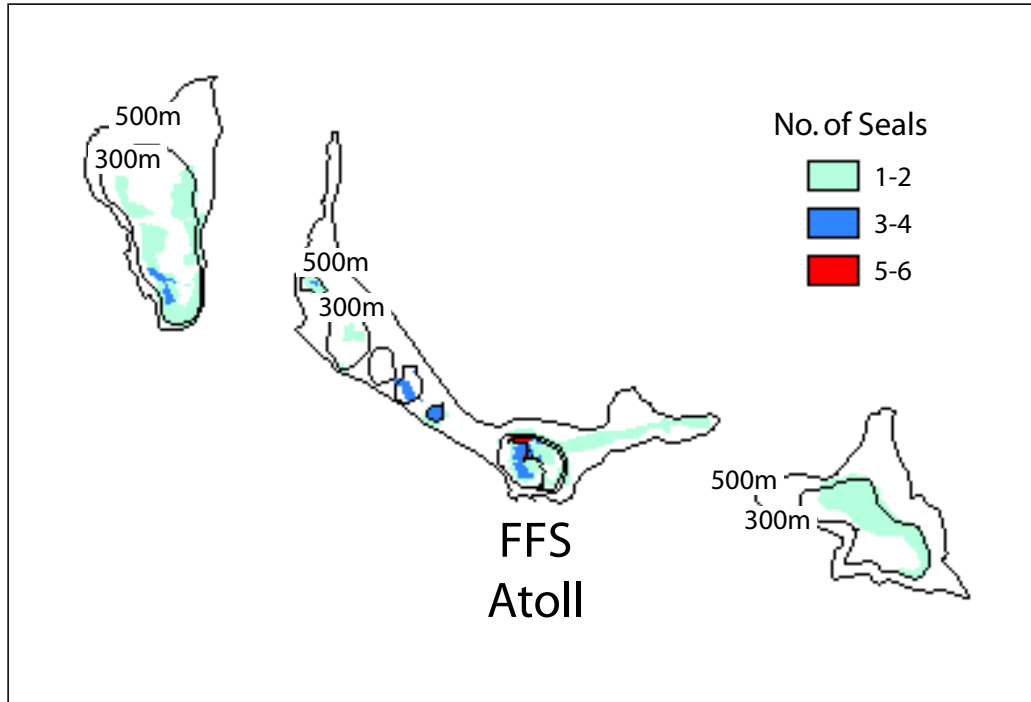
**Figure 2.** Movement of monk seals within the French Frigate Shoals region.

## RESULTS

Seals' Use of Foraging Grounds

The cumulative area or footprint covered by the 24 seals was 24% of the total area available.  The area covered by the movements of a few individual seals made up the bulk of the total footprint (Fig. 2).  Overlap of seal movements was highest closer to the seals' haul outs in the shallows of the island.  However, 25% of the atoll lagoon was left unvisited by the tagged seals.  The median area seals covered in their foraging compared to the area available in each of the zones differed significantly ($\chi^2$=58.9, df=3, P<0.01). The seals used roughly half of what was available in each zone except for subphotic depths, where seals used less than 10% of the available area. The median distance of the four zones compared with the average distance traveled by the seals did not significantly differ ($\chi^2$ =3.19, df=3, P= 0.4), indicating seals generally moved over the full extent of grounds (Fig. 3).
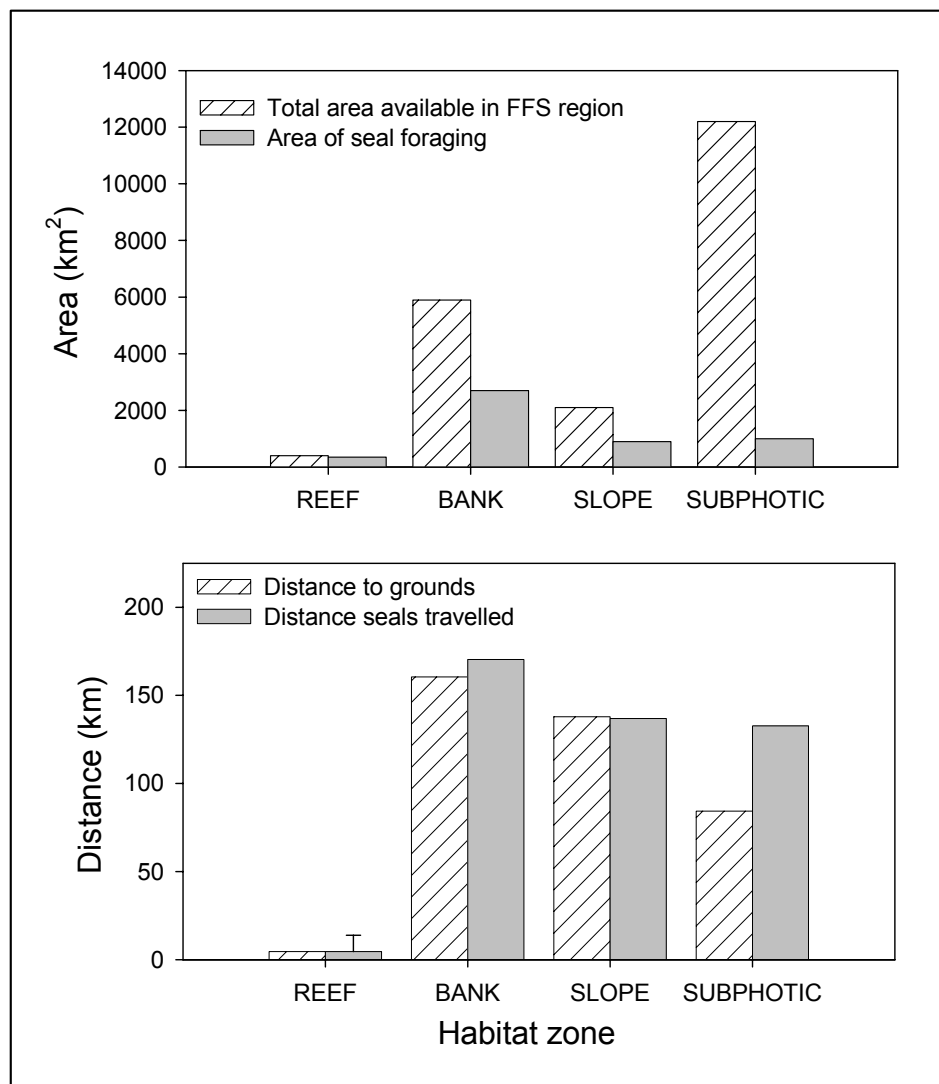
**Figure 3**. GIS derived mean area and distance (from FFS) for each of the habitat zones in the FFS region. The diagonal bars indicate the available habitat and the grey bars are the seals' movements.

Fish Community Structure

Fish size, numerical density, and biomass among stations all were found to differ significantly from a normal distribution (Kolmogorov-Smirnov, Z=2.4 - 4.3, df=139, P<0.01). Significant differences in fish size, numerical density, and biomass density were detected when comparisons were made among the four depth/habitat zones (K-W, $\chi^2$ = 26.6 - 77.5, df =3, P<0.01). Results from the *a posteriori* comparisons using the Tukey tests are detailed in Table 3. As expected, the highest numerical density was in the reef zone, and the lowest occurred at subphotic depths (Fig. 4). However, median fish size exhibited a contrasting pattern, with the largest fish at subphotic depths and the smallest in the reef. Finally, reef biomass density was significantly greater than bank and slope biomass density, which were significantly greater than biomass density in the subphotic zones.

Table 3. Results from K-W analysis of variance of numerical density, body size, and biomass density by habitat zone of the French Frigate Shoals region with results of *a posteriori* comparisons (rf=reef, bk=bank, sl=slope, sp=subphotic).

| Fish Surveys | Median values *Habitat Zone* | | | | | Tukey *a posteriori* comparisons |
|---|---|---|---|---|---|---|
| | Reef (rf) | Bank (bk) | Slope (sl) | Subphotic (sp) | P | 0.05 threshold |
| Density (no./m$^{-3}$) | 0.26 | 0.05 | 0.07 | 0.003 | <0.01 | sp < bk, sl < rf |
| Size (cm) | 8.80 | 10.7 | 8.5 | 13.9 | <0.01 | rf , sl $\leq$ bk $\leq$ sp |
| Biomass (g/m$^2$) | 16.0 | 5.46 | 0.69 | 0.35 | <0.01 | sp < sl, bk $\leq$ rf |
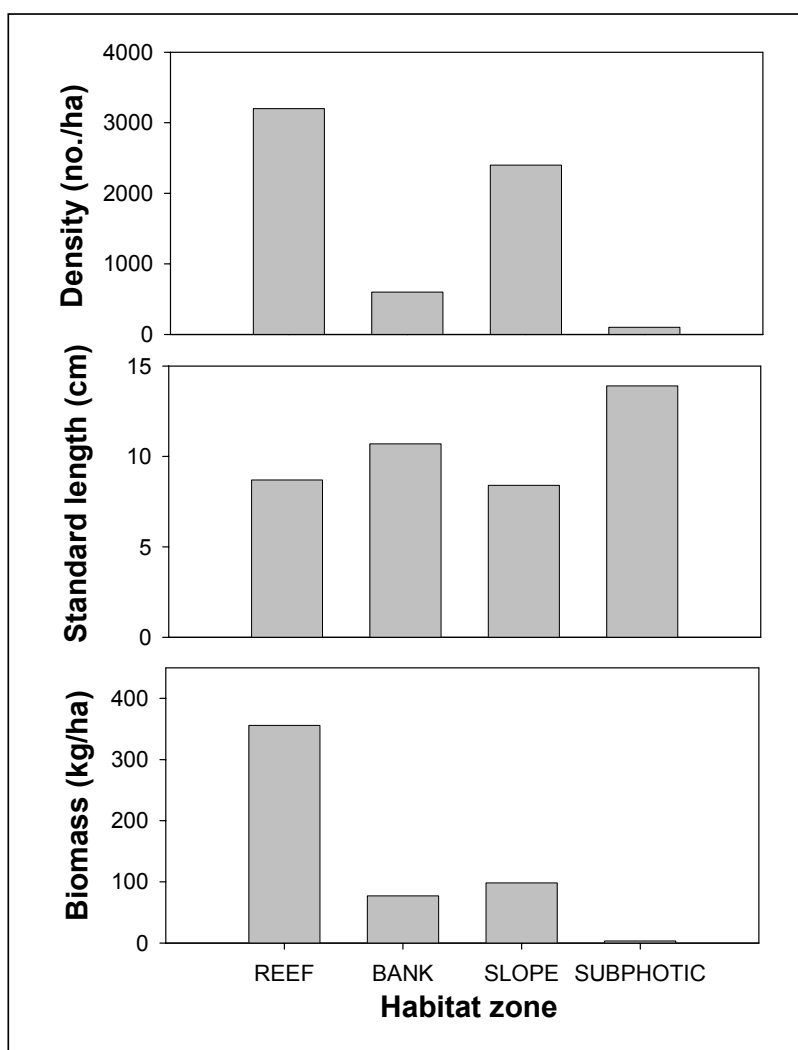


**Figure 4**. Numerical density, standard body length, and biomass density of fish for the four habitat zones in the French Frigate Shoals region.

Prey-Evasion Guilds

Using the frequency of prey items in scat data provided a fractional seal diet of 23% bottom camouflaged (BC), 49% bottom fleers (BF), 26% bottom hiders (BH), and 2% midwater fleers (MF). This diet composition was used as the expected value for all comparisons with the composition of the four habitat zones. Of the four evasion guilds, only the midwater fleers category had a notably low number of families in each of the habitat zones (Table 4). Two dozen prey families were found in each of the four habitat zones. Reef and bank communities were made up of the same families, whereas the slope zone lacked four shallower families and included four deeper ones. The largest difference in family composition was evident in the subphotic zone, where only four families, mostly bottom camouflage, persisted from the shallow atoll depths. Chi-square tests indicated that the observed composition of the evasion guilds for each zone significantly differed from the composition observed in the seals' diet (density $\chi^2$ =37.5-77.6 P<0.001; biomass $\chi^2$ =20.1-73.8 P<0.001). Failing to identify a zone that was not significantly different from the seal diet, we generated scores for numerical density and biomass density using the functional group compositions in a dissimilarity index (Fig. 5). Of these scores, fish biomass density in the bank and slope zones deviated least from the seals' diet. There was no clear pattern in the density data.

Table 4.  Taxa by functional group and habitat zone for the French Frigate Shoals region.
Bold font indicates encountering a new family in a deeper habitat zone.

| Evasion Guild | Reef < 30 m | Bank 30-50 m | Slope 51-300 m | Subphotic 301-500 m |
|---|---|---|---|---|
| Bottom Camouflage BC | *Synodontidae* *Cirrhitidae* *Bothidae* *Scorpaenidae* *Octopodidae* | Same | Same | ***Chlorophthalmidae*** ***Percophidae*** ***Chaunacidea*** ***Lophiidae*** *Bothidae* *Scorpaenidae* *Octopodidae* |
| Bottom Fleer BF | *Labridae* *Scaridae* *Acanthuridae* *Muraenidae* *Congridae* *Kuhlidae* *Ophichthidae* *Mullidae* *Lutjanidae* | Same | *Labridae* *Acanthuridae* *Muraenidae* *Congridae* *Ophichthidae* *Mullidae* *Lutjanidae* | ***Polymixiidae*** ***Moridae*** ***Macrouridae*** ***Berycidae*** *Congridae* ***Ateleopodidae*** ***Triglidae*** ***Squalidae*** |
| Bottom Hider BH | *Pomacentridae* *Tetraodontidae* *Pomacanthidae* *Chaetodontidae* *Holocentridae* *Pricanthidae* *Apogonidae* | Same | *Pomacentridae* *Tetraodontidae* *Pomacanthidae* *Chaetodontidae* *Holocentridae* *Pricanthidae* *Apogonidae* ***Serranidae*** ***Callanthiidae*** ***Caproidae*** ***Symphysanodontidae*** | ***Triacanthodidae*** ***Caproidae*** ***Epigonidae*** ***Symphysanodontidae*** ***Callanthiidae*** ***Owstoniidae*** |
| Midwater Fleer MF | *Kyphosidae* *Monacanthidae* *Balistidae* | Same | *Balistidae* | ***Grammicolepididae*** ***Myctophidae*** ***Zeidae*** |

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**Figure 5.** Scores from a dissimilarity analysis of each habitat's fish density and biomass density in the French Frigate Shoals region. Biomass density of the bank and slope zone differ the least from the seal diet (derived from scats).

## DISCUSSION

Seal Movements

The GIS analysis conducted in this work is imprecise, but given the extensive scale over which the seals' patterns are evaluated, the findings are probably robust. The focus of this work was assessment of the primary area, or the foraging footprint, used by the FFS seal population. Since all seals start their foraging trips from the reef, there is an inherent tendency for a higher foraging overlap closer to the reef. Even so, the fact that 25% of the reef was never visited suggests that seals are not focusing their efforts entirely on the reefs at the atoll. Only 7% of the atoll's seals were tagged, so it is unknown how representative these movement patterns are.

The footprint of seal activities suggests some pattern in selection of foraging grounds. The seals' foraging footprint is found primarily along the edges of the atoll and neighboring banks. In contrast, the subphotic portions of the foraging range occupy the shallow edges and central areas away from the deeper bounding contour of the subphotic

zone. The absence of seal visitation in core areas of the bank summits, and even the central part of the atoll, suggests that the seals are focusing their effort on the transitional habitat of slope. Such a focus would tend to overlap with the adjacent shallower depths and could account for the seals' roughly proportional use of the available area of reef, bank, and slope habitat zones.

Other instrument studies of monk seals similarly have suggested the importance of slope habitats. Studies fitting seals with time-depth recorders show a large portion of effort at depths between 50 and 300 m (Schlexer, 1984; Delong et al., 1984; Stewart, 1998; Baker, unpublished data). Finally, recent work using seal-mounted video cameras or CRITTERCAMS documented seals feeding in a variety of slope habitats (Parrish et al., 2000, 2002, 2005).

Fish Community Structure

As expected, the highest numerical density of fish was found in the shallows of the reef. The median numerical density observed in this study was consistent with values reported from prior studies conducted in NWHI reef systems (DeMartini et al., 2002; Friedlander and DeMartini, 2002). The numerical density was much lower on the bank summits (Parrish and Boland, 2004). In fact, the numerical density estimate of fish on the slope was greater than that on the shallower bank habitat. Greater fish numerical density on deep slopes is consistent with findings of other studies of communities across broad depth ranges (Thresher and Colin, 1986; Chave and Mundy, 1994). Finally, as expected, the subphotic realm supported the lowest numerical density of fish. The length of most fish, regardless of zone, fell in the 10-cm length category. Median fish length was smallest at shallow depths and largest at subphotic depths. The break in size was most evident between the subphotic zone and shallower zones. Despite the larger median lengths of subphotic fish, the low numerical density of the zone resulted in low total biomass density. Biomass density declined steeply with depth from the reefs to the subphotic zone.

Based exclusively on the fish communities, monk seals could be expected to target the shallow reefs to exploit the high numerical density and high biomass density of fish available in that subsystem. If the seals preferred larger prey items, they might opt for subphotic depths. However, the GIS analysis indicated only limited use of the subphotic zone, and diving studies on monk seals (Schlexer, 1984; Delong et al., 1984; Abernathy and Siniff, 1998; Stewart, 1998; Parrish et al., 2000, 2005) also indicate less effort at subphotic depths. The notion that seals are focusing their feeding in the shallow-reef habitats is largely intuitive, given the high composition of reef-related prey identified in scat studies (Goodman-Lowe, 1998). However, recent work using seal-mounted video cameras (Parrish et al., 2000) showed that much of the seals' time in the water (particularly at shallow depths) was not spent feeding, and the minority of time that the seals did feed was on the slopes. Since the surveillance time of the seal-mounted videos is limited to a few days, the findings of longer studies using the satellite tags and monitoring scat contents should be considered more robust.

Prey Preferences

The reliance on scat analysis to represent the seals' diet has shortcomings, but at present there is nothing better to use in its place (Cottrell et al., 1996). The fundamental concern with scat data is the variable resistance of different prey types to digestion (Bigg and Fawcett, 1985; Harvey, 1989; Gale and Cheal, 1992), which ultimately could bias the representation of fragments that pass through the digestive tract. Other problems specific to monk seals include the coarse level of prey identification (family level) in a species-rich prey base. Improved identification of prey fragments could enhance the trends revealed in this analysis. For example, recent CRITTERCAM work indicated that the only wrasses (family *Labridae*) eaten by the seals were sand fish even though most wrasses are thought of as reef fish (Parrish et al., 2005).

Overlap was high between habitat zones in fish families except for the subphotic zone. At subphotic depths, a number of families found only in those depths were present. The persistence of the bottom camouflage families in all zones down to the subphotic depths largely reflects the loss of families associated with herbivory and planktivory, which dominate shallower depths. The chi-square tests of the observed fish numerical density and biomass density against the expected values of the seals diet indicated that all were significantly different. This is not entirely unexpected. Even if we assume no biases associated with deriving the diet from scat data, the movement data suggest the seals are feeding in all the habitat zones, which means that the expected diet used in this analysis is not likely to match the fish community in any one of the zones. By employing a dissimilarity index, each of the habitat zones could be evaluated for its relative agreement with the seal diet. The scores for fish numerical densities showed no trend, whereas the comparison with fish biomass density suggested that the adjacent communities of the bank and slope were most consistent with the seal diet. The reef community was the least similar to the seals' diet, rejecting the intuitive notion that seals feed mostly in the shallows close to their haul-out and pupping areas.

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# FORAGING BIOGEOGRAPHY OF HAWAIIAN MONK SEALS IN THE NORTHWESTERN HAWAIIAN ISLANDS

BY

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## ABSTRACT

The extant population of Hawaiian monk seal (*Monachus schauinslandi*) numbers around 1,300 distributed among six island atolls in the remote Northwestern Hawaiian Islands (NWHI) and at several small, emerging colonies on the Main Hawaiian Islands. Demographic studies have identified poor juvenile survival as the ultimate primary cause of substantial declines at all colonies and of slow recent recovery at some. Variable foraging success may be a key proximate effect, but the knowledge of habitat needs of foraging monk seals has not been adequate to test that hypothesis nor to provide management with the necessary information to address resource conservation issues. We documented the geographic and vertical foraging patterns of 147 Hawaiian monk seals from all six NWHI breeding colonies from 1996 through 2002 to describe the marine habitats that may be key to the species' viability. We found that seals foraged extensively within barrier reefs of the atolls and on the leeward slopes of reefs and islands at all colony sites. They also ranged away from these sites along the Hawaiian Islands Archipelago submarine ridge to most nearby seamounts and submerged reefs and banks. Most dives were less than 150 m deep, though dives of some seals exceeded 550 m. Suitable foraging habitat may be a resource limiting the population of monk seals in the NWHI. Moreover, the foraging biogeography of Hawaiian monk seals may vary spatially and temporally with variation in the extent of physical substrate, prey community composition and species' abundance, and demographic composition of seal colonies.

## INTRODUCTION

The Hawaiian monk seal is endemic to the Hawaiian Island Archipelago. It was listed as "Endangered" in 1976 (U.S. Department of Commerce, 1976) under the U.S. Endangered Species Act (ESA) of 1973[3] owing to substantial declines in abundance during the previous several decades throughout its range in the Northwestern Hawaiian Islands (NWHI). In 2003, the species was estimated to number around 1,300 seals (ca 30% to 40% of recent historic abundance; NOAA Fisheries, unpub. data), virtually all occurring in the NWHI at six breeding colonies (Kure, Midway, and Pearl & Hermes

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atolls, Lisianski and Laysan islands, and French Frigate Shoals; Fig. 1; Ragen and Lavigne, 1999; Baker and Johanos, 2004). These six locations consist of all above-sea-level habitats in the NWHI west of Necker Island (Fig. 1). Movement of seals among colonies is evidently limited (Harting et al., 2002). Consequently, each breeding colony has been considered to be a relatively distinct subpopulation. The greatest affiliations among these colonies are apparently among subpopulations within three regional areas: (1) the western NWHI (Kure-Midway-Pearl & Hermes atolls); (2) the central NWHI (Lisianski-Laysan islands); and (3) the eastern NWHI (French Frigate Shoals). Nonetheless, the demography and trends in abundance of each colony appear to be independent (Harting, 2002). However, the ultimate factor accounting for declines at some colonies and limited or slow recovery at others appears to be poor survival of juvenile seals (e.g., Craig and Ragen, 1999; Harting, 2002; Ragen and Lavigne, 1999). The posited proximate cause of poor survival of juveniles has been poor foraging success[1] from fluctuations or reductions in prey population assemblages. Our strategic objective was to document the geographic and vertical components of foraging habitats of Hawaiian monk seals in the NWHI as a key element in developing conservation and management plans for this critically endangered marine mammal.

## METHODS AND MATERIALS

From 1996 through 2002, we monitored the movements of 147 Hawaiian monk seals (about 10% of the extant species range-wide abundance) for several months or more using satellite-linked radio transmitters that communicated data on their geographic and vertical (dive depth) locations to earth-orbiting satellites (Table 1). The age and sex composition of the instrumented seals was chosen to provide a reasonable sample of males and females in each age category (weaned pups [ca 4 to 6 months old when tagged], juveniles [1 to 4 years old], adults [> 4 years old]) relative to the size of the subpopulation that would allow general characterization of habitat use and permit comparisons among colonies. All transmitters were glued to the seals' dorsal pelage with quick-setting epoxy, and the seals were then monitored remotely through the Argos Data Collection and Location Service (DCLS) until the transmitters were shed in spring and summer when seals molted, the batteries expired, or transmissions ended because of transmitter failure or antenna breakage. Most of the seals were outfitted with transmitters between October and early January (see Stewart and Yochem, 2004a, 2004b, 2004c; Stewart, 2004a) except those at French Frigate Shoals, which were instrumented in spring (cf. Abernathy and Siniff, 1998; Abernathy, 1999).

All satellite-linked radio transmitters that were used consisted of an ARGOS-certified transmitter (PTT = Platform Transmitter Terminal) for determining geographic locations of foraging seals. Most of the transmitters also included a microprocessor-controlled event recorder to monitor use of vertical marine habitats (diving behavior). They (SLDRs = Satellite-Linked Dive Recorders) were capable of either about 20,000

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[1]Poor foraging success of weaned pups and juveniles and perhaps poor provisioning of nursing pups owing to limited body reserves of lactating females. Poor prepartum foraging success may lead to fat deposits insufficient to support lactation.

transmissions (all weaned pups and some juveniles) or about 60,000 transmissions (some juveniles and all adults) because of differences in battery supplies (less battery capacity on the instruments on pups to reduce instrument size and mass). Whenever seals were at sea, transmissions were suppressed when the PTTs and the SLDRs were below the sea surface owing to an electrical conductivity circuit that closed whenever there was continuous saltwater contact between two or three electrodes mounted on the surface of the SLDR. This feature extended tracking duration by conserving power, and it also maximized the probability that adequate transmissions would reach an orbiting satellite when seals surfaced. To further conserve battery power and extend tracking, the SLDRs were programmed to be active only during periods of the day when orbiting ARGOS system satellites were expected to pass within radio view of the NWHI. The SLDRs were also programmed to shift from a transmission rate of around 1/40 s to around 1/90 s once a seal was hauled out constantly for 6 to 10 minutes. Moreover, if the seal remained hauled out for about 70 minutes, transmissions ceased until it reentered the sea for more than 1.5 minutes. The latter feature also ensured that most of the locations that were obtained likely occurred when seals were foraging.

The ARGOS DCLS uses many criteria to generate predictions on the distance error that may be associated with a location, and the DCLS assigns an index of accuracy to each one. The best locations (LC = 1, 2, 3) are predicted to be within a kilometer or less of the true transmitter location. Other locations are made available to wildlife tracking community users (LC = 0, A, B, Z). The Argos DCLS does not provide users with a prediction of the error that may be associated with these locations. The assignment of these indices to locations does not strictly imply that they have large error, only that the criteria used to assign indices with associated predictions of errors were not all satisfied by the transmissions received during satellite passes when the location estimates were made. Of those locations, we considered only locations of LC = 0 and A for analysis. All locations were filtered and outliers were rejected based on knowledge or assumptions about reasonable travel speeds and distances between serial locations.

The SLDRs also recorded and stored information on diving patterns (vertical habitat use). Maximum depth of dive, duration of dive, and time at depth were summarized by 6-hour periods and then transmitted as frequency histograms. The depth of the deepest dive made during each 24-hour period was also recorded and transmitted separately. Locations were determined several times each day by the ARGOS DCLS, as described in detail elsewhere (e.g., Fancy et al., 1988; Harris et al., 1990; Stewart et al., 1989; Stewart, 1997), whenever two or more transmissions reached an orbiting satellite during a single overpass.

We used a probabilistic model (fixed kernel density estimate method; e.g., Kernohan et al., 1996; Worton, 1989) to estimate the extent of monk seal foraging areas. We chose this model because it is relatively assumption free, is less sensitive to outliers, can calculate multiple centers of activity, is relatively robust to sample size variation, and accommodates irregular location distributions relative to other models. In general, it is arguably the most appropriate model for assessing patterns of spatial distribution (cf. Kernohan et al., 1996; White and Garrott, 1990; Worton, 1987, 1989). We calculated 95% and 75% probability distributions as two general estimates of the areas that seals

actually used to forage, out of all locations they visited.  We also calculated the 50% probability distributions to estimate core areas of foraging activity, as have been routinely used in studies of wildlife populations (e.g., Harris and Leitner, 2004; Kernohan et al., 1996; White and Garrott, 1990).

## RESULTS AND DISCUSSION

The median duration of monitoring varied among age and sex classes from 1.3 to 3.5 months overall.  Monitoring of individual seals lasted from 1 to 351 days. Monitoring of seals at French Frigate Shoals (FFS) was substantially shorter than at the other colonies (Table 2), owing primarily to seals at FFS being tagged closer to when they molted.  If patterns of geographic dispersion of seals at the FFS colony are similar during the rest of the year, then the foraging ranges derived from the brief tracking samples should be relatively unbiased indicators of foraging ranges of adult males and females there.  If seals actually disperse less during other parts of the year, then the actual foraging ranges (i.e., probability distributions as measured here) may be more constricted.

Geographic Dispersion of Monitored Seals

Of approximately 54,000 locations that we considered suitable for analysis, 69% were of LC = 0 and LC =A; no error predictions for distance between calculated and true locations are available for those locations.  Most of them were likely determined when seals were actively foraging and consequently spending little time at the surface between dives.

Overall, all seals remained within waters under exclusive jurisdiction of the U.S. (i.e., the U.S. Exclusive Economic Zone [EEZ]; waters from the NWHI and exposed atolls out to 370 km) while foraging during the periods they were monitored.  Virtually all the seals foraged extensively within atoll lagoons or around the island colonies where they were tagged, including the outer slopes of those atolls and islands (Fig. 1).  Core foraging areas (i.e., 50% probability distributions) were generally centered over areas of high bathymetric relief (e.g., submerged banks, seamounts) or focal areas within atoll lagoons (Fig. 1).  When foraging around the colonies, 95% of the locations were within 38 km of the center of the atoll or island, except at French Frigate Shoals where the ranges for adult females extended up to 50 to 58 km (Table 3).  Seventy-five percent of those locations were within 20 km of the colony centers, with minor exceptions (Table 3). The ranges of weaned pups were smaller than those of adults at Kure Atoll and Midway Atoll, but similar at Lisianski Island and Laysan Island (Table 3).

Seals at all colonies also foraged at other extra-colony sites (Tables 4, 5, 6).  There was no consistent pattern of extra-colony site use by adult males, adult females, juveniles, or weaned pups among the colonies.

Overall, seals tagged at Kure Atoll, Midway Atoll, Laysan Island, and French Frigate Shoals used four extra-colony sites near each colony (Table 6).  At Pearl and Hermes Atoll, all but two seals (adult males) foraged exclusively within the barrier reef or on the immediate seaward slopes.

Weaned pups tagged at Kure Atoll and Midway Atoll did not use extra-colony sites. Pups tagged at Lisianski Island used one additional site. Pups tagged at Laysan used two additional sites. Juveniles tagged at Kure Atoll, Midway Atoll, Pearl and Hermes Atoll, and Laysan Island did not use extra-colony sites. Juveniles tagged at Lisianski Island used two extra-colony sites.

The distances from colonies to extra-colony foraging sites varied from around 24.1 to 322 km (Table 3). Those extra-colony sites were at or near shallow reefs and submerged banks (e.g., Maro Reef, St. Rogatien Bank, Raita Bank, Brooks Bank) or seamounts (e.g., Nero, Ladd, Northampton) (Table 4; Fig. 1). Seals oriented near or over the NWHI submarine ridge system when traveling to those sites.

Vertical Dispersion of Monitored Seals: Dive Depth Patterns.

Analyses of frequency-histogram data (6-hour periods for each day; i.e., based on all dives each day) have been reported for Pearl and Hermes Atoll (Stewart, 2004a) and for French Frigate Shoals (Abernathy, 1999). About 90% of dives at Pearl and Hermes Atoll were less than 40 m deep, which correspond to water depths within the atoll lagoon where virtually all seals focused their foraging efforts during the monitoring periods. Most (ca 60% – 80%) dives of seals at French Frigate Shoals were to depths of 4 to 40 m, though there was considerable variation in dive patterns among seals. Many seals dove considerably deeper (e.g., 10% to 25% of dives exceeded 40 m) with additional modal depths of dives at 60 to 80 m, 100 to 120 m, 120 to 140 m, and 140 to 160 m, and a few dives of some seals exceeded 500 m (1,605 ft) (Abernathy, 1999). The maximum depths of dives (i.e., one dive per day) that we report here for seals at Kure and Midway atolls and Laysan and Lisianski islands indicate that a substantially large number of dives were deeper than 40 m, relative to those at Pearl and Hermes Atoll and French Frigate Shoals (Fig. 2). A secondary mode in maximum daily depth occurred at 100 to 150 m at Kure and Midway atolls and at Laysan Island; a third mode occurred at 200 to 400 m at Midway Atoll and Laysan Island; and there was a fourth mode at around 500 m at Kure Atoll.

Generalized Foraging Habitats

The collective patterns of dive depths and geographic dispersion for monk seals throughout the NWHI are partially consistent with the hypothesis that Hawaiian monk seals may often forage in relatively shallow demersal habitats. However, the geographic extent of potential demersal foraging habitats within 500 m of the surface (the maximum vertical extent of virtually all dives) is substantially less than the geographic extent of the dispersion of foraging seals (Stewart, 2004b). This suggests that a substantial number of dives may have been in the water column, rather than to the seafloor, regardless of geographic location. In any event, the information that we collected on diving patterns (6-hour histogram summaries of depth) are difficult to link with more temporally resolved geographic locations of foraging seals and, consequently, with fine-scale bathymetry.

Geographic patterns of foraging were complex and varied among colonies by season and age and sex of seals. For example, seals at Pearl and Hermes Atoll foraged

almost exclusively within the barrier reef of the atoll, compared with other colonies where seals ranged various distances away from islands and atoll lagoons (Table 3). Moreover, core foraging areas within the atoll varied seasonally for some seals but not others. We think that these differences among colonies may reflect important differences in community structure and abundance of prey species, but we recognize that further multidisciplinary research is needed to construct and test these trophic-structure hypotheses.

Because the studies at the six breeding colonies were not conducted simultaneously, we cannot determine whether the variation documented in foraging dispersion among colonies and among adults, juveniles, and pups near colonies, and use of extra-colony sites, might be mostly related to differences in prey availability at and near each colony, colony size and composition, or temporal environmental variability. Foraging ranges and diving patterns are likely dynamic and may vary with environmental conditions, such as abundances and compositions of prey assemblages, and abundances and age structures of monk seal colonies.

## ACKNOWLEDGEMENTS

Table 1. Hawaiian monk seals outfitted with satellite-linked data recorders and transmitters at the Northwestern Hawaiian Islands, 1996-2002[1].

| Colony | Males | | | | Females | | | | TOTAL |
|---|---|---|---|---|---|---|---|---|---|
| | *Adults* | *Juveniles* | *Weaned pups* | *Total* | *Adults* | *Juveniles* | *Weaned pups* | *Total* | |
| French Frigate Shoals[2] *(1996-1997)* | 17 | 0 | 0 | *17* | 10 | 0 | 0 | *10* | **27** |
| Laysan Island[3] *(2001-2002)* | 5 | 5 | 5 | *15* | 5 | 5 | 5 | *15* | **30** |
| Lisianski Island[4] *(2000-2001)* | 4 | 7 | 4 | *15* | 5 | 2 | 4 | *11* | **26** |
| Pearl & Hermes Atoll[5] *(1997-1998)* | 9 | 5 | 0 | *14* | 9 | 1 | 0 | *10* | **24** |
| Midway Atoll[6] *(2000-2001)* | 2 | 5 | 2 | *9* | 3 | 2 | 2 | *7* | **16** |
| Kure Atoll[7] *(2001-2002)* | 4 | 7 | 1 | *12* | 4 | 4 | 4 | *12* | **24** |
| **TOTAL** | **41** | **29** | **12** | *82* | **36** | **14** | **15** | *65* | **147** |

Table 2. Summary of duration of monitoring Hawaiian monk seals at the Northwestern Hawaiian Islands (Laysan Island, Lisianski Island, Pearl and Hermes Reef, Midway Atoll, Kure Atoll = Colony Group 1; French Frigate Shoals = Colony Group 2) from 1996 through 2002.

| Age | Sex | Median monitoring duration (months) | Maximum tracking duration (months) | Number of Seals | Colony Group |
|---|---|---|---|---|---|
| WP | F | 3 | 7.5 | 15 | 1 |
| WP | M | 3.5 | 8.1 | 12 | 1 |
| JUV | F | 5.2 | 8.9 | 15 | 1 |
| JUV | M | 4 | 9.6 | 29 | 1 |
| AD | F | 6.2 | 11.1 | 25 | 1 |
| AD | M | 7.8 | 11.7 | 24 | 1 |
| AD | F | 1.3 | 4.2 | 10 | 2 |
| AD | M | 2.9 | 4.5 | 17 | 2 |

Table 3. Foraging ranges of Hawaiian monk seals from colonies where they were tagged with satellite-linked transmitters.

| Colony | Total number of foraging sites used[1] | 95% of locations (km)[2] | 75% of locations (km)[3] | Distances (km) to extra-atoll/island foraging sites |
|---|---|---|---|---|
| **Kure Atoll** | 5 | | | |
| AD M | 5 | 16 to 20 | 10 to 13 | 62.7, 64.4, 67.6, 133.5 |
| AD F | 1 | 13 to 15 | 8 to 12 | |
| JUV | 1 | 8 to 12 | 3 to 6 | |
| WP | 1 | 5 to 12 | 1 to 3 | |
| | | | | |
| **Midway Atoll** | 5 | | | |
| AD M | 4 | 20 to 30 | 15 to 17 | 66, 74, 96.5 |
| AD F | 2 | 18 to 20 | 12 to 13 | 80.4 |
| JUV | 1 | 6 to 20 | 3 to 10 | |
| WP | 1 | 3 to 8 | 1 to 5 | |
| | | | | |
| **Pearl & Hermes Atoll** | 2 | | | |
| AD M | 2 | 10 to 20 | 5 to 20 | 33.8 |
| AD F | 1 | 8 to 17 | 3 to 13 | |
| JUV | 1 | 5 to 15 | 3 to 12 | |
| | | | | |
| **Lisianski Island** | 7 | | | |
| AD M | 1 | 8 to 20 | 3 to 5 | |
| AD F | 2 | 17 to 28 | 8 to 27 | 56.3 |
| JUV | 3 | 25 to 38 | 20 to 23 | 164.1, 220.4 |
| WP | 1 | 6 to 28 | 3 to 12 | |
| | | | | |
| **Laysan Island** | 5 | | | |
| AD M | 3 | 25 to 30 | 17 to 20 | 80.4, 235 |
| AD F | 2 | 20 to 30 | 15 to 20 | 123.9 |
| JUV | 1 | 20 to 23 | 13 to 15 | |
| WP | 3 | 21 to 27 | 15 to 17 | 54.7, 90.1 |
| | | | | |
| **French Frigate Shoals** | 5 | | | |
| AD M | 3 | 27 to 30 | 17 to 20 | 67.6, 210.8 |
| AD F | 4 | 50 to 58 | 38 to 43 | 115.8, 201.1, 217.2 |

[1] Including colony atoll or island

[2] This is the radial distance from center of colony atoll or island to perimeter boundary that encloses 95% of the locations determined for the seals when they were foraging near the colony atoll or island.

[3] This is the radial distance from center of colony atoll or island to perimeter boundary that encloses 75% of the locations determined for the seals when they were foraging near the colony or atoll.

The centers of the atolls or islands are: Kure Atoll, 28.42°N, 178.31°W; Midway Atoll, 28.24°N, 177.37°W, Pearl & Hermes Atoll, 27.87°N, 175.83°W; Lisianski Island, 26.1°N, 173.97°W; Laysan Island, 25.75°N, 171.74°W; French Frigate Shoals, 28.80°N, 166.21°W.

Table 4.  Generalized radial distances from centers of reefs, banks, and seamounts to the boundaries of zones that encompassed 95% of the foraging locations of Hawaiian monk seals at those sites.

| Extra-colony foraging site[1] | Coordinates of center of zone encompassing 95% of foraging locations at the site | Generalized radial distance (km) from center of zone to zone boundary encompassing 95% of foraging locations at the site |
|---|---|---|
| Un-named Kure seamount 1 (1) | 28.9°N, 179.57°W | 10.1 |
| Un-named Kure seamount 2 (2) | 28.8°N, 178.86°W | 10.6 |
| Un-named Kure seamount 3 (3) | 28.9°N, 178.62°W | 9.3 |
| Nero seamount (5) | 27.96°N, 177.97°W | 16.7 |
| Ladd seamount (7) | 28.55°N, 176.66°W | 26.4 |
| Un-named Pearl and Hermes seamount (9) | 27.73°N, 175.57°W | 2.5 |
| Pioneer Bank (11) | 25.96°N, 173.42°W | 7.2 |
| Northampton seamount W (12) | 25.53°N, 172.41°W | 8.4 |
| Northampton seamount E (13) | 25.37°N, 172.03°W | 8.8 |
| Un-named Laysan seamount (15) | 25.42°N, 171.00°W | 16.6 (merged) and 16.3 (budded) |
| Maro Reef (16) | 25.44°N, 170.61°W | |
| Raita Bank (17) | 25.5°N, 169.46°W | 7.2 |
| Gardner Pinnacles (18) | 24.8°N, 168.01°W | 42.7 |
| St. Rogatien Bank (19) | 24.6°N, 167.29°W | 22.0 |
| Brooks Banks (20) | 24.2°N, 166.85°W | 29.9 |
| Necker Island (22) | 23.46°N, 164.46°W | 48.3 |

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[1] Numbers in parentheses refer to the site locations on Figure 1.

Table 5.  Generalized area (km$^2$) of foraging zone encompassing 95% of foraging locations of Hawaiian monk seals around the center of the island, atoll, reef, bank, or seamount.

| Colony and extra-colony foraging sites[1] | Coordinates of center of zone encompassing 95% of foraging locations at the site | Generalized area of foraging zone encompassing 95% of foraging locations around site center (km$^2$) |
|---|---|---|
| Un-named Kure seamount 1 (1) | 28.9°N, 179.57°W | 321 |
| Un-named Kure seamount 2 (2) | 28.8°N, 178.86°W | 353 |
| Un-named Kure seamount 3 (3) | 28.9°N, 178.62°W | 272 |
| Kure Atoll (4) | 28.42°N, 178.31°W | 878 |
| Nero seamount (5) | 27.96°N, 177.97°W | 876 |
| Midway Atoll (6) | 28.24°N, 177.37°W | 1562 |
| Ladd seamount (7) | 28.55°N, 176.66°W | 2187 |
| Pearl and Hermes Atoll | 27.87°N, 175.83°W | 707 |
| Un-named Pearl and Hermes seamount (9) | 27.73°N, 175.57°W | 20 |
| Lisianski Island (10) | 26.1°N, 173.97°W | 2043 |
| Pioneer Bank (11) | 25.96°N, 173.42°W | 163 |
| Northampton seamount W (12) | 25.53°N, 172.41°W | 222 |
| Northampton seamount E (13) | 25.37°N, 172.03°W | 243 |
| Laysan Island (14) | 25.75°N, 171.74°W | 2240 |
| Un-named Laysan seamount (15) | 25.42°N, 171.00°W | 810 (merged) and 835 (budded) |
| Maro Reef (16) | 25.44°N, 170.61°W | |
| Raita Bank (17) | 25.5°N, 169.46°W | 163 |
| Gardner Pinnacles (18) | 24.8°N, 168.01°W | 5730 |
| St. Rogatien Bank (19) | 24.6°N, 167.29°W | 1521 |
| Brooks Banks (20) | 24.2°N, 166.85°W | 2809 |
| French Frigate Shoals (21) | 23.8°N, 166.21°W | 6420 |
| Necker Island (22) | 23.46°N, 164.46°W | 7331 |

[1] Numbers in parentheses refer to the site locations on Figure 1.

Table 6. Percentages of monitored Hawaiian monk seals at each colony that foraged at various sites in the Northwestern Hawaiian Islands (see Fig. 1 for site locations; WP = weaned pup; J = Juvenile; AM = adult male; AF = Adult female; numbers in parentheses are numbers of seals in each category that were monitored).

| Feature number | Feature name | Kure Atoll | | | | Midway Atoll | | | | Pearl & Hermes Atoll | | | Lisianski Island | | | | Laysan Island | | | | French Frigate Shoals | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | WP (5) | J (11) | AM (4) | AF (4) | WP (4) | J (8) | AM (2) | AF (3) | J (6) | AM (9) | AF (9) | WP (8) | J (9) | AM (4) | AF (5) | WP (10) | J (10) | AM (5) | AF (5) | AM (17) | AF (17) |
| 1 | Un-named Kure seamount 1 | | | 50 | | | | | | | | | | | | | | | | | | |
| 2 | Un-named Kure seamount 2 | | | 50 | | | | | | | | | | | | | | | | | | |
| 3 | Un-named Kure seamount 3 | | | 50 | | | | | | | | | | | | | | | | | | |
| 4 | Kure Atoll | 100 | 100 | 100 | 100 | | 13 | 50 | 33 | | | | | | | | | | | | | |
| 5 | Nero Seamount | | | 25 | 25 | | 13 | 50 | 33 | | | | | | | | | | | | | |
| 6 | Midway Atoll | | | | 25 | 100 | 100 | 100 | 66 | | | | | | | | | | | | | |
| 7 | Ladd Seamount | | | | 25 | | | | 33 | | | | | | | | | | | | | |
| 8 | Pearl & Hermes Atoll | | | | | | | | 33 | 100 | 100 | 100 | | | | | | | | | | |
| 9 | Un-named P&H | | | | | | | | | | 22 | | | | | | | | | | | |
| 10 | Lisianski/Neva Shoals | | | | | | | | | | | | 100 | 100 | 100 | 100 | | | | | | |
| 11 | Pioneer Bank | | | | | | | | | | | | 38 | 22 | 100 | 20 | | | | | | |
| 12 | Northampton W | | | | | | | | | | | | | 11 | 100 | | 30 | 30 | 20 | 40 | | |
| 13 | Northampton E | | | | | | | | | | | | | 11 | | | | | 40 | 40 | | |
| 14 | Laysan | | | | | | | | | | | | | 22 | | 20 | 100 | 90 | 100 | 100 | | |
| 15 | Un-named Laysan 1 | | | | | | | | | | | | | 11 | | | | | | | | |
| 16 | Maro Reef | | | | | | | | | | | | | 22 | | | 70 | 60 | 60 | 80 | | |
| 17 | Raita Bank | | | | | | | | | | | | | | | | 30 | 30 | 40 | 40 | | |
| 18 | Gardner Pinnacles | | | | | | | | | | | | | | | | | | | | 6 | 30 |
| 19 | St. Rogatien Banks | | | | | | | | | | | | | | | | | | | | 12 | 10 |
| 20 | Brooks Bank | | | | | | | | | | | | | | | | | | | | 59 | 30 |
| 21 | French Frigate Shoals | | | | | | | | | | | | | | | | | | | | 100 | 80 |
| 22 | Necker Island | | | | | | | | | | | | | | | | | | | | | 10 |

**Figure 1.** Locations of breeding colonies of Hawaiian monk seals and probability distributions of foraging areas of 147 Hawaiian monk seals. (Lighter to darker shades of green = 95%, 75% and 50% of locations within boundaries; 1= Unnamed Kure seamount 1; 2 = Unnamed Kure seamount 2; 3 = Unnamed Kure seamount 3; 4 = Kure Atoll; 5 = Nero Seamount; 6 = Midway Atoll; 7 = Ladd seamount; 8 = Pearl & Hermes Atoll; 9 = Unnamed P&H seamount; 10 = Lisianski Island/Neva Shoals; 11 = Pioneer Bank; 12 = Northampton seamount W; 13 = Northampton seamount E; 14 = Laysan Island; 15 = Unnamed Laysan seamount; 16 = Maro Reef; 17 = Raita Bank; 18 = Gardner Pinnacles; 19 = St. Rogatien Bank; 20 = Brooks Banks; 21 = French Frigate Shoals; 22 = Necker Island [Mokumanamana])
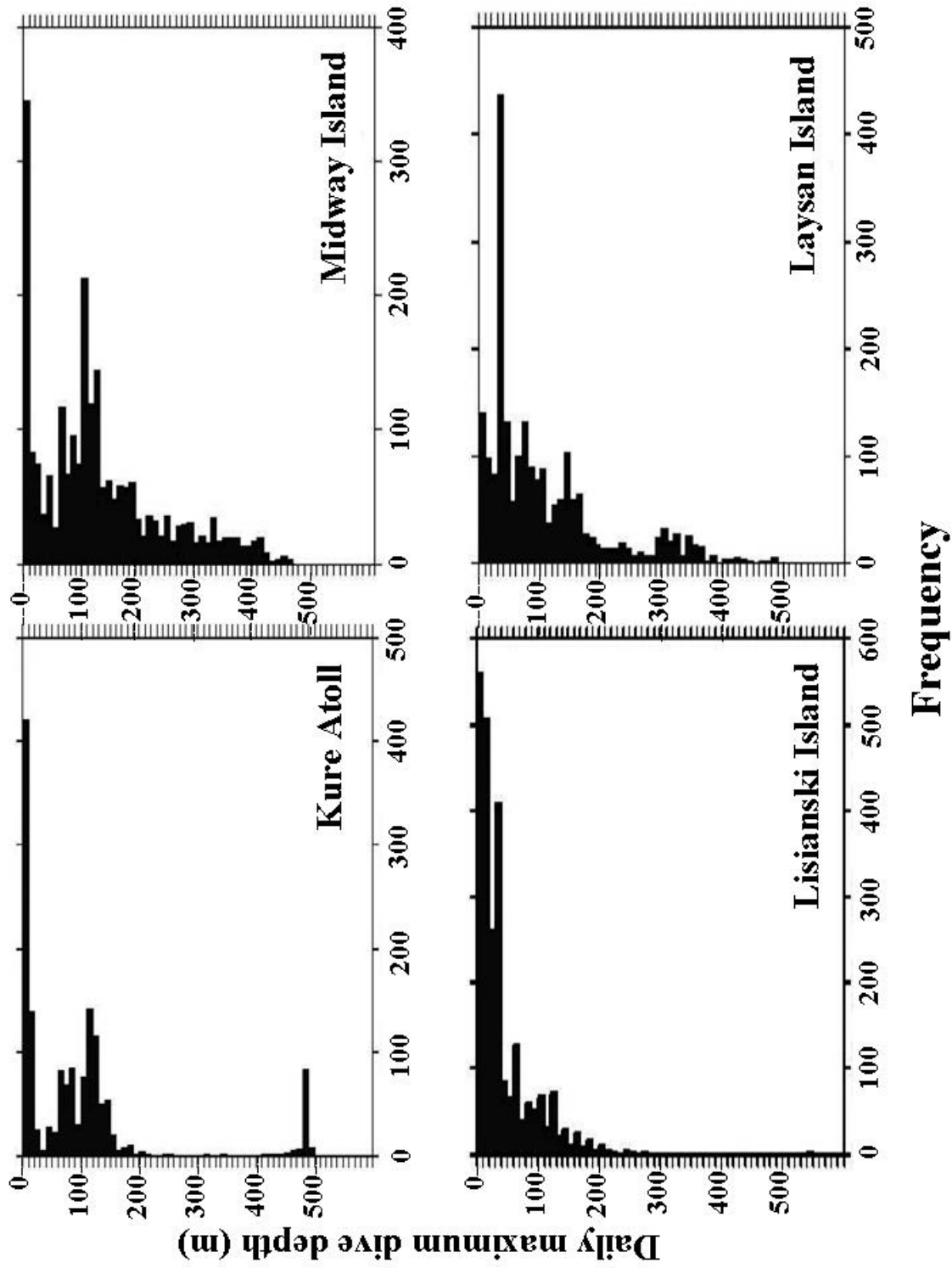
**Figure 2.** Daily maximum depth of dives of Hawaiian monk seals near Kure Atoll, Midway Island, and Lisianski Island, and Laysan Island (histogram intervals = 10m).

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# RECOVERY TREND OVER 32 YEARS AT THE HAWAIIAN GREEN TURTLE ROOKERY OF FRENCH FRIGATE SHOALS

BY

GEORGE H. BALAZS[1] and MILANI CHALOUPKA[2]

## ABSTRACT

The green turtle is one of the long-lived species that comprise the charismatic marine megafauna. The species has a long history of human exploitation with some stocks extinct. Here we report on a 32-year study of the nesting abundance of the green turtles endemic to the Hawaiian Archipelago. We show that there has been a substantial long-term increase in abundance since the 1970s of this once seriously depleted stock following cessation of harvesting. This population increase has occurred in a far shorter period of time than previously thought possible. There was also a distinct 3-4 year periodicity in annual nesting abundance that might be a function of regional environmental stochasticity that synchronizes breeding behaviour throughout the Archipelago. This is one of the few reliable long-term population abundance time series for a large long-lived marine species, which are needed for gaining insights into the recovery process of long-lived marine species and long-term ecological processes.

## INTRODUCTION

The green turtle (*Chelonia mydas*) has a circumtropical distribution with distinct regional population structures (Bowen et al., 1992) and is the most abundant large marine herbivore (Bjorndal, 1997). Globally, the green turtle has been subject to a long history of human exploitation with some stocks now extinct and others in decline (Frazier, 1980; Witzell, 1994). Yet, despite being recognized as globally threatened (National Research Council, 1990), there are few reliable assessments of abundance status and trends of green turtle stocks (Chaloupka and Limpus, 2001). Reliable long-term estimates of population abundance trends are needed to support recovery planning (Foin et al., 1998), and to model sea turtle demography (Chaloupka, 2002), and are essential for developing a better understanding of long-term ecological processes (Inchausti and Halley, 2001).

For sea turtles, population abundance estimates are based preferably on foraging ground capture-mark-recapture programs that can provide more detailed sex- and age-class-specific demographic information (Chaloupka and Limpus, 2001, 2002; Chaloupka et al., 2004; Chaloupka and Limpus, 2005). However, capture-mark-recapture programs in the marine environment for large and highly mobile species, such as sea turtles, are very difficult and expensive to conduct, so are rarely undertaken (Bjorndal et al., 2000;

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Chaloupka et al., 2004). Nearly all assessments of sea-turtle population abundance have been based on trawl-based catch-per-unit-effort estimation, aerial survey-based density and estimation or, more commonly, monitoring the number of females that come ashore each year to nest at stock-specific rookeries (see review in Chaloupka and Limpus, 2001).

Monitoring the nesting is by far the easiest and least expensive means to assess green turtle population abundance, but short-term surveys (< 10 yrs) are inadequate for several reasons (Chaloupka and Limpus, 2001). Most notably, green turtles are long-lived (Zug et al., 2002; Chaloupka et al., 2004; Balazs and Chaloupka 2004b), and females skip several nesting seasons due to nutritional constraints (Bjorndal, 1997). Hence, long-term nesting beach surveys are essential if this form of assessment of green turtle population abundance and trends is to be adopted. The Hawaiian green turtle stock is one of the few sea turtle stocks that has been continuously monitored for several decades and so is suitable for long-term population assessment using nesting beach surveys.

The Hawaiian green turtle genetic stock comprises a spatially disjunct metapopulation with numerous distinct foraging grounds within the Hawaiian Archipelago (Fig. 1). The Hawaiian stock comprises mainly the same mtDNA haplotype (Dutton, 2002) with no difference in mtDNA stock composition between foraging ground populations and females nesting at the regional rookery (Leroux et al., in press). In other words, both the nesters and the turtles resident at various foraging grounds throughout the Archipelago are from the same genetic stock (Leroux et al., 2003), although rarely turtles from the east Pacific stock that nests along the Pacific coast of Mexico are recorded in Hawaiian waters (Balazs, 1976; Dutton, 2002). We report the results of a 32-year study of the nesting abundance of the Hawaiian green turtle stock, thereby extending by two years the trend analysis presented in Balazs and Chaloupka, 2004a. We conclude that this once seriously depleted stock is now well on the way to recovery. This long-term nesting abundance series provides a basis for development of meaningful recovery plans for the Hawaiian green turtle stock.

**METHODS**

Study and Data Description

The principal rookery for the Hawaiian green turtle stock is located on the small sand islands at French Frigate Shoals (Fig. 1), Northwestern Hawaiian Islands, which accounts for > 90% of all nesting within the Hawaiian Archipelago (Balazs, 1976). The main rookery island at French Frigate Shoals is East Island where at least 50% of all the French Frigate Shoals nesting occurs (Balazs, 1976; Niethammer et al., 1997). Tagging and radio telemetry studies have shown that it is rare for a green turtle to nest on East Island in one year and then nest at another island at French Frigate Shoals in subsequent years (Dizon and Balazs, 1982; Niethammer et al., 1997). Thus, there is strong island fidelity within the regional rookery, so that annual nesting trends evident at East Island are not a consequence of permanent emigration.
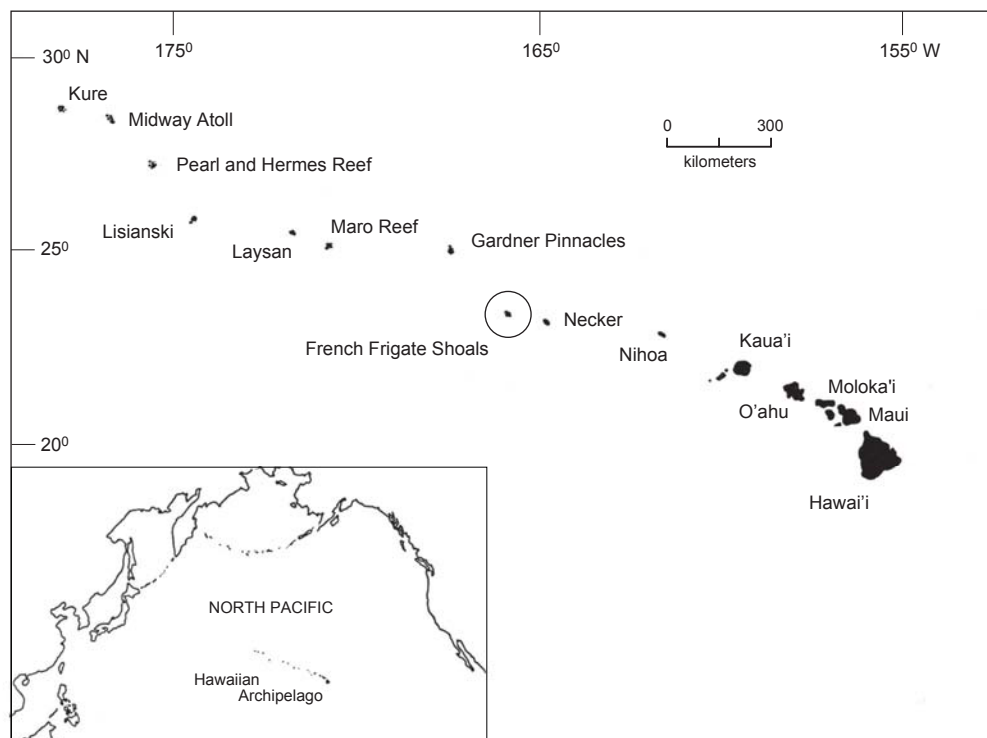
**Figure 1**. The Hawaiian Archipelago. The major rookery of the Hawaiian green turtle stock is at French Frigate Shoals in the Northwestern Hawaiian Islands located at the mid-point of the Archipelago.

Annual surveys of the number of female green turtles coming ashore to nest each night have been conducted at East Island since 1973, initially by the Hawaii Institute of Marine Biology (University of Hawaii) and, from 1981 onward, as a cooperative project between National Oceanic and Atmospheric Administration (NOAA)/ National Marine Fisheries Service (NMFS) and U.S. Fish and Wildlife Service (USFWS) (Balazs, 1976, 1980; Wetherall et al., 1998). During the summer nesting season, females that emerged to nest each night were tagged, and morphometric information was recorded. Double-tagging with alloy tags was used prior to 1996, but double-tagging with passive integrated transponder tags has been used since to identify each individual nester uniquely. Some annual surveys were short, as field personnel were not always able to remain on the island for the entire nesting season due to the remoteness of French Frigate Shoals. Consequently, in some years the survey was an incomplete census of all females that emerged to nest. Therefore, a Horvitz-Thompson type estimator (see below) was used to estimate the total annual number of individual nesters.

Nesting Abundance Estimation

Briefly, the Horvitz-Thompson type estimator was derived as follows: let $N_i = n_i/p_i$, where $N_i$ = estimated number female nesters in the $i$th year, $n_i$ = number of uniquely identified female nesters recorded for the $i$th year and $p_i$ = probability of sighting a female that emerges ashore at the rookery and nests at least once during the $i$th year

given various covariates such as arrival time, nesting frequency, nesting duration, and internesting interval. The sighting probability function ($p_i$) was calibrated using entire nesting season census data derived from the nightly emergence probabilities for >1100 nesters recorded during a 5-year season-long saturation tagging program conducted from 1988 to 1992. An empirical bootstrap approach was used to derive confidence intervals for each annual estimate (Wetherall et al., 1998), but the annual estimates are precise due to the substantial seasonal coverage during most seasons and so were not used here. More details are provided in Wetherall et al. (1998) and a summary of the number of tagged nesters, sighting probability, Horvitz-Thompson estimations, and confidence interval estimates since 1973 are available from the authors upon request.

Nesting Trend Estimation

We estimated the underlying time-specific trend in estimated nester abundance using a generalized smoothing spline regression approach implemented in the R package gss (Gu, 2002). This approach uses the data to determine the underlying linear or nonlinear trend without assuming any specific functional form (Gu, 2002). If the underlying trend was linear or near-linear then we estimated the linear nesting population growth rate using a parametric moving average regression, which accounts for autocorrelated error and temporal fluctuations in observed nester abundance (Chaloupka and Limpus, 2001).

We further investigated the long-term trend and apparent periodicity in the Horvitz-Thompson estimate of annual nester abundance using a procedure known as Seasonal and Trend decomposition using Loess or STL (Cleveland et al., 1990), which decomposes a series using nonparametric smoothing into additive frequency components of variation: (1) trend, (2) cyclical or quasi-periodic, (3) seasonal (if applicable, using for instance a monthly data series) and (4) the residual or remainder. STL was used by Chaloupka (2001) to investigate spatial synchrony in egg productivity at green turtle rookeries in the Southeast Asian region. The STL remainder could reflect environmental variability (Chaloupka, 2001) so we used cross-correlation function analysis with autoregressive model-based prewhitening (Vandaele, 1983) to investigate any relationship with major environmental variables such as regional sea surface temperature (see Chaloupka, 2001 for more details of the STL and cross-correlation procedures and application within an ecological context).

**RESULTS**

Nesting Abundance

The Horvitz-Thompson estimates of annual nesting turtle abundance at the East Island rookery are shown in Figure 2a. The estimated trend in East Island nester abundance shows two main features — a dramatic increase in abundance over the 32-year period and substantial fluctuations in the number of annual nesters. The substantial annual
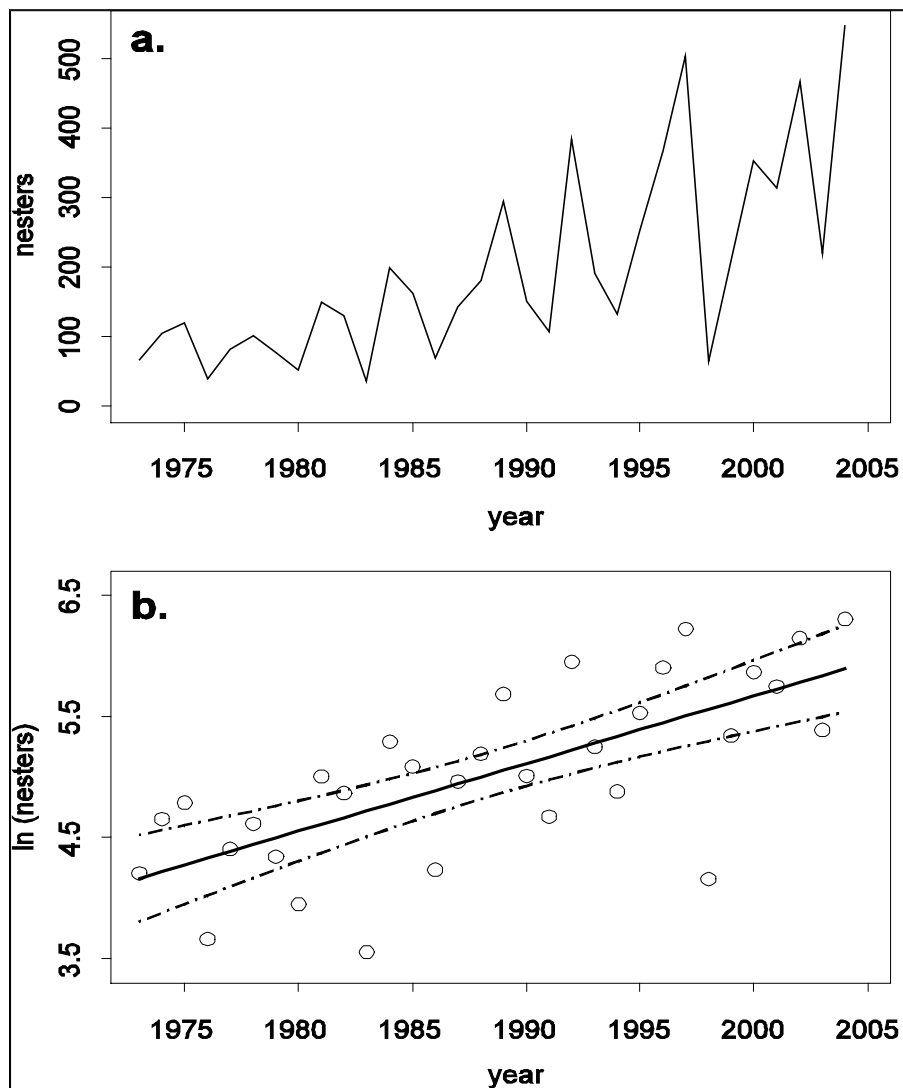
**Figure 2**. Trends in nester abundance. Panel (a) shows a time series plot of the Horvitz-Thompson estimate of the number of female green turtles nesting each year at the East Island rookery (French Frigate Shoals, Northwestern Hawaiian Islands) over the 32-year period from 1973 to 2004. Panel (b) shows the estimated long-term trend in nester abundance derived using a Bayesian smoothing spline regression model (Gu, 2002), which was fitted to the Horvitz-Thompson nester series shown in (a). Solid curve is the posterior mean annual nester abundance derived from the model with a Bayesian 95% credible region shown by dashed curves.

fluctuations in nester abundance for this recovering stock is a characteristic of green-turtle nesting populations due to a variable proportion of females preparing to breed each year in response to strong and spatially correlated ocean-climate variability (Limpus and Nicholls, 1994; Chaloupka, 2001). Other demographic processes of green turtles such as somatic growth are also related to the same regional scale environmental variability (Chaloupka et al., 2004).

Abundance Trends

The estimated underlying long-term trend in the annual nester series is shown in Fig. 2b where it was apparent that this rookery has experienced near-linear increasing annual nester abundance over the last 30 years or more. The underlying linear trend was estimated at ca. 5.7% pa (95% confidence interval: 5.3-6.1), which is consistent with low population growth rates expected for long-lived and late maturing species such as sea turtles (Chaloupka and Limpus, 2001) and one of the reasons why it takes decades for a green turtle population to recover following any major perturbation such as overharvesting or nesting habitat loss (Chaloupka, 2004).

Figure 3 shows the STL decomposition for a 30-year period of the time series realization of estimated green turtle nesting at East Island from 1973-2002. This shows the same series as in Figure 2a but on a log scale to account for the fluctuations in the series (Fig. 3a). The STL-derived long-term trend (Fig. 3b) is very similar to the trend estimated using the Bayesian smoothing spline regression model but there is also a periodic component showing a distinct quasi 3-4 year periodicity in annual nester abundance (Fig. 3c). The bottom panel in the STL plot (Fig. 3d) is the residuals remaining after the trend and quasi-periodicity components have been fitted to the original series shown in the top panel (Fig. 3a.) The remainder accounts for a substantial part of the temporal variability in nester abundance that might reflect temporal variation in sea-surface temperature in the Hawaiian Archipelago. Figure 4 shows a strong cross-correlation between sea-surface temperature in the southern Hawaiian Islands (Koko Head/AVHRR MCSST series) and the STL annual nester remainder — there is in fact a significant 1-year lead and a significant 1-year lag between the two prewhitened series (see Methods) suggesting a significant relationship between annual nesting anomalies and annual sea surface temperature anomalies.

## DISCUSSION

The Hawaiian green turtle nesting population has increased dramatically since protection began in 1978 under the U.S. Endangered Species Act (ESA) and could be approaching the foraging habitat carrying capacity at some locations (Balazs and Chaloupka, 2004b). Prior to 1974, the Hawaiian stock was subject to human exploitation such as turtle harvesting at foraging grounds from the mid-1800s, harvesting of nesters and eggs until the early 1960s, and nesting habitat destruction (Balazs, 1976; Niethammer et al., 1997). Green turtles in United States waters have been protected under the ESA since 1978 (Witzell, 1994). Therefore, the Hawaiian stock has not been exposed to any major human hazards since that time. Moreover, the increase in the abundance of nesting turtles has occurred despite the relatively recent increase in fibropapillomatosis, a tumor-forming disease, which is prevalent in green turtles resident in some Hawaiian foraging grounds (Aguirre et al., 1998; Chaloupka and Balazs, 2005).

The increase in nesting abundance (ca. 5.7% pa) is probably due to increased female nester survival since harvesting of turtles in the foraging grounds was prohibited from the mid-1970s. However, extensive nesting habitat destruction occurred at the French Frigate Shoals rookery during the 1940s (Balazs, 1976; Niethammer et al., 1997).
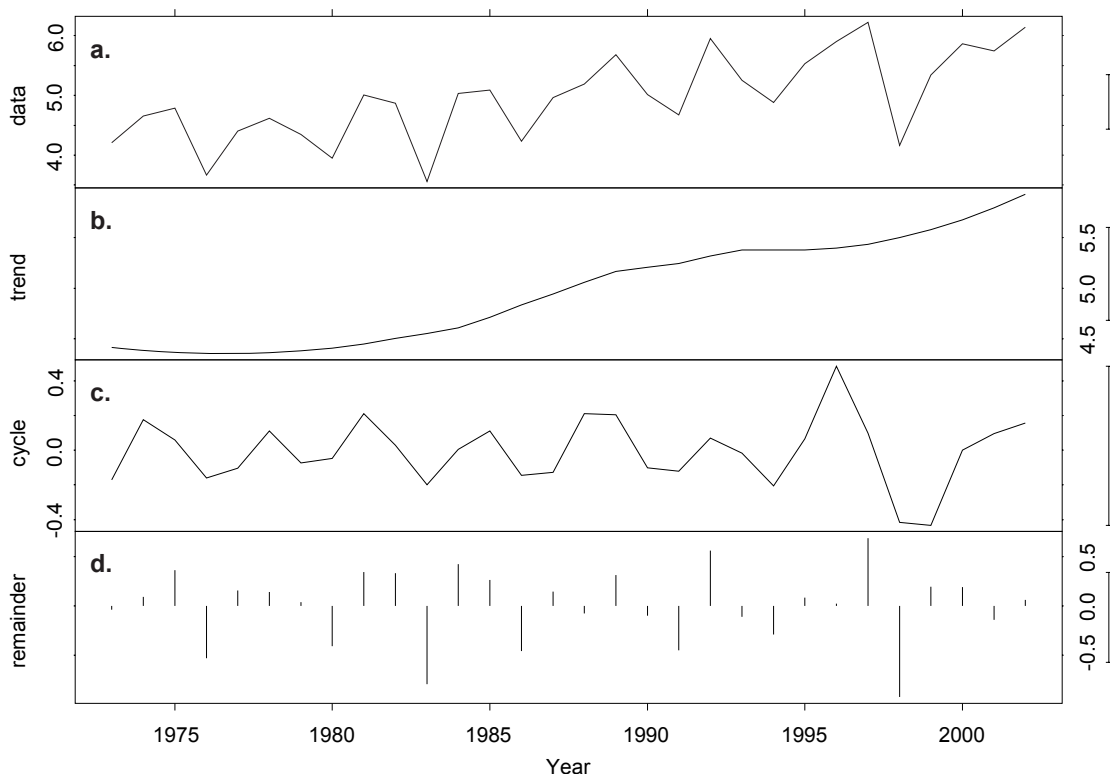
**Figure 3**. STL decomposition plot of the estimated number of female green turtles nesting each year at East Island, French Frigate Shoals over a 30-year period (1973-2002) — note the log scale. Panel (a), Horvitz-Thompson estimates of the annual nesting series. Panel (b), the fitted long-term trend or low-frequency variation in estimated annual number of nesters (bandwidth of trend filter = 17 yr). Panel (c), the fitted 3-4 yr quasi-periodic trend or high-frequency variation in estimated nesters (bandwidth of trend filter = 4 yr). Panel (d), the residual component remaining after trend (b) and quasi-periodicity (c) components have been fitted to the series. The three components shown in (b-d) sum exactly to the series shown in (a). The panel scales are not the same so vertical bar at right of each panel indicates relative variation in scaling among the components and original data series.

Moreover, the Hawaiian green turtle has an approximate 25-35-year generation period (Zug et al., 2002; Balazs and Chaloupka, 2004b) so that it is not possible to attribute the nester increase to just protection of turtles under the ESA since 1978. The increase is most likely a consequence of both the cessation of habitat damage at the French Frigate Shoals rookery from the early 1950s onward, and also protection since the mid-1970s of turtles from harvesting in coastal waters around the main Hawaiian Islands. Moreover, the annual proportion of the recorded nesters comprising previously untagged turtles has declined to a relatively constant level around 32% as the nester population has become extensively tagged. This constant level of apparent new nester recruits suggests that the Hawaiian green turtle population might be approaching carrying capacity, which is indicative of a population well on the way to recovery.
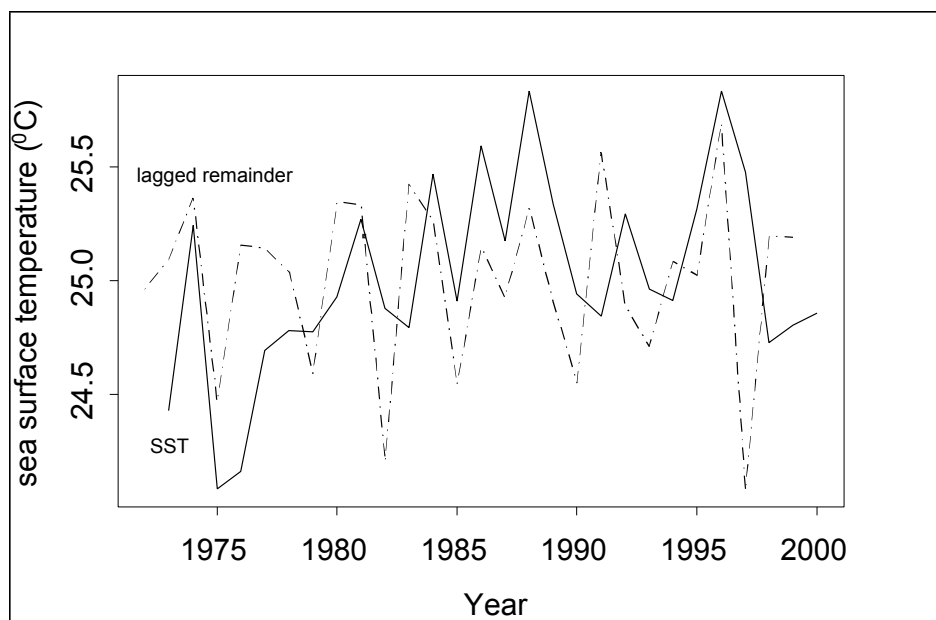
**Figure 4.** Trend in mean annual sea surface temperature recorded near-shore off the southeastern coast of Oahu, (Hawaii) and 1-year lagged STL remainder component shown in Figure 3d. The STL remainder scale shown here has been shifted to reflect the same scale as the sea surface temperature by adding 25 (the sea surface temperature mean) to the STL remainder component (Fig. 3c). The sea surface temperature series was a long-term data series constructed from a combination of measurements determined from near-shore surveys along the southeastern coast of Oahu near Koko Head (Seckel and Yong, 1977) and several different satellite-based time series.

In addition to the recovering nester abundance trend since the mid-1970s, there are also strong environmental forcing effects evident in the Hawaiian green turtle nesting time series. The quasi-periodicity in nester abundance (Fig. 3c) suggests that female green turtles resident in the numerous foraging grounds of the Hawaiian Archipelago migrate to nest at the French Frigate Shoals rookery every 3 or 4 years. The synchronizing agent for this breeding behaviour is not apparent but it might be an environmental forcing function such as a major ocean-climate anomaly, which has been shown to synchronize multistock nesting at Great Barrier Reef green turtle rookeries (Limpus and Nicholls, 1994) and at southeast Asian green turtle rookeries (Chaloupka, 2001). It is possible that the increased nester abundance since the mid-1980s (Figs. 2a, b) could be due to females nesting more frequently (shorter return period between successive nesting seasons) rather than there being more nesters. This is a plausible alternative explanation but unlikely as the nesting frequency has remained constant around 3-4 years over the last 32 years with no indication of any shortening (Fig. 3c).

In addition to the quasi-periodicity (Fig. 3c), there is also some suggestion of an aperiodic environmental effect on nesting abundance that is reflected in the sea surface temperature anomalies (Fig. 4). Solow et al. (2002) have shown recently that sea-surface temperature might be associated with annual fluctuations in the nesting of green turtles at the Tortuguero rookery on the Atlantic coast of Costa Rica. No mechanism was proposed as to why sea-surface temperature would affect such nesting behaviour but a similar sea-surface temperature association is shown here for the Hawaiian green turtle

nesting population (Fig. 4). However, the fact that there were both 1-year lags and leads between the sea-surface temperature and remainder component in Figure 4 indicates that sea-surface temperature is unlikely the causal agent but rather that anomalous nester abundance and anomalous sea surface temperature in the Archipelago's main (southern) Hawaiian Islands are a coincidental consequence of some other long-term environmental forcing function that warrants further investigation.

It is now reasonable to conclude that the Hawaiian green-turtle stock is well on the way to recovery after more than 29 years of protection. What is also clear from our study is that a seriously depleted sea turtle population, such as the Hawaiian stock, can recover following relatively simple and inexpensive policy interventions and in far less time than previously thought (National Research Council, 1990). It is widely held that a seriously depleted green turtle stock could take >100 years to recover, assuming no density-dependent compensatory behaviour, when protected from exposure to anthropogenic hazards (National Research Council, 1990; Chaloupka, 2002). While speculative, the unexpectedly rapid recovery of the Hawaiian stock might be due to density-dependent reproductive behaviour where the proportion of females breeding each year is higher at lower population abundance and lower at higher abundance (Chaloupka, 2004). The green turtle population that nests at Tortuguero (Costa Rica), which is the largest nesting population in the Atlantic, also has increased rapidly since the 1970s following protection of nesting turtles (Bjorndal et al., 1999), while other large nesting populations with a history of habitat protection such as in the Great Barrier Reef are stable or increasing (Chaloupka and Limpus, 2001).

One of the goals of any recovery plan is to revise the risk status of endangered or threatened stocks when there is substantive evidence that an at-risk population or stock fulfils a set of recovery criteria (Foin et al., 1998). The recovery plan for the U.S. Pacific populations of green turtles (NMFS and USFWS, 1998) states that one of the recovery criteria for stocks in U.S. Pacific waters should be a nesting population that is stable or increasing over a 25-year monitoring period. Our 32-year study indicates that the Hawaiian green turtle stock now meets this specific recovery criterion and that the at-risk status of this stock warrants reconsideration in accordance with the procedures specified in the U.S. recovery plan (NMFS and USFWS, 1998).

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# DEMOGRAPHY AND REPRODUCTIVE ECOLOGY OF
# GREAT FRIGATEBIRDS

BY

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## ABSTRACT

Frigatebirds (*Fregata* spp.) differ from most Pacific seabirds in fundamental ways, making it difficult to include them in generalizations about seabird management. We present demographic data on great frigatebirds (*F. minor*) on Tern Island, French Frigate Shoals, in 1998-2000. In terms of mating attempts, males were more likely than females to try to obtain a mate but were much less likely to succeed at pairing, and the variation in pairing success was greater for males than females. Although fledging success was high (63.5%), hatching success was below 30% in all three years of this study. Males end their parental care of fledglings sooner than do females, but parental care by both sexes extends into the pair-formation portion of the next breeding season. Plumage data indicate that females do not breed in years following a successful breeding attempt. For males, the findings are less clear; some males may simultaneously feed 1-year-old offspring and tend new nests. In colony-wide counts of frigatebirds, we detected as many as 1,171 males, 1,053 females, and 691 juveniles on the Island at a time. We estimated that in 1999 there were 2,099 males and 1,615 females that nested, out of a pool of approximately 11,195 males that tried to attract a mate and 1,809 females that evaluated potential mates. Because additional birds did not try to breed at all, the total number of adults in the population is larger than this. Using amplified fragment length polymorphism (AFLP) genetic markers, we found no evidence of spatial genetic structure within the Tern Island colony, confirming previous work showing genetic variation between, but not within, breeding colonies.

## INTRODUCTION

Biological conservation requires a basic understanding of the life history and demography of focal species (Meffe and Carroll, 1994), and sound management may be especially important—and problematic—for species such as seabirds that are clustered into areas of high density during breeding. Frigatebirds (*Fregata* spp.) are colonially breeding seabirds for which detailed reproductive and demographic data are generally lacking for most parts of their range (Metz and Schreiber, 2002), and generalizing

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from other seabird species may be unwise, given that frigatebirds are extreme among seabirds in their sexual dimorphism (Dearborn et al. 2001a), low wing loading (Metz and Schreiber, 2002), thermal-dependent flight (Weimerskirch et al., 2003), short pair bonds (Nelson, 1975), and long parental effort (Nelson, 1975).

Our previous work with great frigatebirds (*F. minor*) breeding on Tern Island (23˚ 45' N latitude, 166˚ 17' W longitude), Hawaii, has shown that these birds are very long-lived (individuals over 40 years of age; Juola et al., in press). They regularly move thousands of kilometers between islands, yet they retain broad-scale genetic differentiation (Dearborn et al., 2003). They typically exhibit a very male-biased sex ratio at the breeding colony (Dearborn et al., 2001a), inbreed slightly when choosing mates (Cohen and Dearborn, 2004), and only rarely exhibit extra-pair paternity (Dearborn et al., 2001a). Finally, reproductive success of frigatebirds on Tern Island is tied to the body condition of the breeding adults (Dearborn, 2001).

Here, we present new data from 1998, 1999, and 2000 to address four basic aspects of reproductive ecology in this Tern Island population of great frigatebirds. First, we compare the pairing success of males and females. Second, we quantify reproductive success at monitored nests. Third, we compare the duration and frequency of breeding of males and females. And finally, we explore the size and structure of the breeding population, based on direct counts, mark-resight data, and spatial analysis of AFLP genetic profiles of breeders.


**METHODS**


Pairing Success of Males and Females


To assess breeding attempts and pairing success of males and females, we banded and wing-tagged unpaired birds at the start of the 2000 breeding season by capturing them in the breeding colony while they were perched in shrubs at night. Between 23 January 2000 and 30 January 2000, we tagged 79 males, 76 of which were in breeding plumage, and 54 females, 51 of which were in breeding plumage. Subsequently, we surveyed the breeding colony three times per day (at 0900, 1330, and 1700) from 23 January through 15 May 2000 to record the reproductive behavior of these marked individuals. An individual was categorized as attempting to mate if a male's gular pouch was inflated or if a female was performing an inspection of a displaying male, either while making stereotypical low-altitude inspection flights or while perched in contact with a displaying male. For tagged birds that eventually built nests, contents of nests were monitored daily. Based directly on these observations of tagged birds, we calculated the proportion of displaying males that obtained a mate and the proportion of mate-evaluating females that obtained a mate.

Reproductive Success

We measured hatching success in 1998, 1999, and 2000 by making daily or twice-daily checks of individually marked nests from the start of egg laying (typically early February) through early summer (July in 1998 and 1999, May in 2000). In 1999, nests were then followed bi-weekly through December to measure fledging success.

Duration of Breeding Cycle and Breeding Frequency Across Years by Males and Females

During the egg-laying period, from the end of January through May or June, many adults are still feeding 1-year-old offspring from the previous breeding season. Although these 1-year-olds can fly, they still rely on colony visits by their parents for most of their food. We recorded all opportunistic observations of adults feeding 1-year-olds from the first of January to early July in 1998 and late January to early May in 1999 and inferred differences in the duration of parental care from temporal patterns in the proportion of feedings made by males versus females. During these feeding observations, we also recorded plumage coloration of the provisioning adult. Comparing their plumage to that of birds currently incubating eggs or brooding new chicks allows an assessment of whether the pool of adults caring for 1-year-olds is different from the pool of adults with new nesting attempts. We assessed the plumage of all males that were incubating eggs or brooding young chicks on Tern Island on 30 March 1999, and we did the same for females on 2 April 1999; we then compared the distribution of plumage coloration in these groups with that of birds that were feeding 1-year-old offspring in 1999.

Breeding Population Size and Spatial Genetic Structure

In 1998 and 1999, we conducted daily counts of the frigatebird colony by following a regular survey route that took us within 50 m of all individuals on the Island (see Dearborn et al., 2001a). During these surveys, we counted individuals in three age classes (1 – 2 year old juveniles, 3 – 6 year old subadults, and adults), two sex classes (for adults only), and three location classes (perched, on nest, and flying). The number of birds on nests at any given time is only a minimum count of the number of nesting attempts and number of birds attempting to nest that year, because the majority of nests fail. To better estimate the number of nesting attempts and the number of adults participating in these attempts, we combined estimates of fledging success at those nests that were monitored during the 1999 season, the number of chicks fledged across the entire colony that season (as revealed in a census made in August), and the frequency of nesting attempts by marked males and females. We calculated the total number of nesting adults in the colony as (# fledged)/(estimate of reproductive success)x(mean # nest attempts for marked males and females). Last, we combined this calculation with our measurement of pairing success for males and females, to yield an estimate of the total number of individuals that attempted to attract a mate (in the case of males) or choose a mate (in the case of females) in that breeding season.

Our previous research on this population had suggested an absence of strong spatial genetic structure to the breeding colony, as assessed with multilocus minisatellite fingerprinting (Cohen and Dearborn, 2004). Here, we use a separate data set to assess the robustness of this finding. In an analysis of population genetic structure among Tern Island, Johnston Atoll, and Christmas Island (Kiribati), we analyzed AFLP data from 117 polymorphic loci (Dearborn et al., 2003), finding significant differentiation among the three islands. Here, we use Spatial Genetic Software v. 1.0c (SGS; Degen et al., 2001) to test for spatial autocorrelation among the Tern Island samples. For each bird that was sampled, we mapped its breeding location on a coordinate grid of the Island and then used SGS to generate eight sets of pairwise combinations of birds whose nests fell into a particular category based on physical distance between the two nests. In this manner, we made sets of all pairs of birds whose nests were within 50 m of each other, within 50-100 m of each other, within 100-150 m of each other, and so forth up to a 350-400m category. Within each distance category, SGS computes the mean of the genetic dissimilarity between each possible pair of sampled birds, using Tanimoto distance for dominant markers such as AFLPs. Plotting the mean genetic dissimilarity ordered across the eight distance categories tests whether there is spatial genetic structure to the population. A 1000-run Monte Carlo permutation test was used to generate confidence intervals for this relationship.

## RESULTS

Pairing Success of Males and Females

Of the 76 tagged males that were in breeding plumage, 64 (84.2%) attempted to attract a mate at some point during the 2000 breeding season, but only 12 (18.75%) succeeded in pairing. Four of the 12 had a nest with a female but no egg, and an egg was laid at the remaining eight nests. None of the marked males nested twice within that breeding season.

Of the 51 tagged females that were in breeding plumage, 28 (54.9%) evaluated the pool of displaying males at some point during the breeding season, and 25 (89.3%) nested (5 of the 25 had a nest with a male but no egg, and 20 laid an egg). Of the 25 females that nested, 8 nested more than once in the season (following nest failure), including 1 that laid an egg on three different breeding attempts within one season.

Individual males were thus much more likely to try to mate than were females (84.2% vs. 54.9%; $X^2 = 13.132$, df = 1, p = 0.0003), but the males that tried to attract a mate were only one-fourth as likely to succeed as females (18.75% vs. 89.3%; $X^2 = 40.307$, df = 1, p < 0.000001). Among those birds that did nest, females were more likely to nest again after nest failure than were males (Fisher exact p = 0.036). For those birds that tried to acquire a mate, there was more within-sex variation in pairing success for males than for females (for number of nesting attempts: male CV = 2.098, female CV = 0.601, and 95% confidence intervals do not overlap).

Reproductive Success

Hatching success was 24.7% (45 of 182 nests) in 1998, 28.4% (74 of 261 nests) in 1999, and 23.5% (4 of 17 nests) in 2000. Using those nests with definitively known lay dates, there was no seasonal change in hatching success in 1998 (logistic regression, n = 118 nests from 25 February to 4 June 1998: Wald $X^2$ = 0.889, df = 1, p = 0.346). In 1999, there was also no significant seasonal change in hatching success (logistic regression, n = 231 nests from 7 February to 30 May 1999: Wald $X^2$ = 2.672, df = 1, p = 0.102). Fledging success was 63.5% (47 of 74 nestlings that hatched) in 1999; thus, overall reproductive success was 18.0% (47 fledglings from 261 nests).

Duration of Breeding Cycle and Breeding Frequency Across Years by Males and Females

We recorded 373 feeding events to 1-year-olds in 1998 and 374 feedings to 1-year-olds in 1999. In January and February, during the early part of the breeding season, roughly one-third to one-half of feedings to 1-year-olds was made by males (Fig. 1). As the new breeding season progressed, however, male effort tapered off, such that nearly all feedings observed in April, May, and June were made by females. This clearly indicates a difference in the duration of parental effort by males and females, though it does not address whether their care for a 1-year-old nestling prohibits them from attempting to start a new nest that same season.
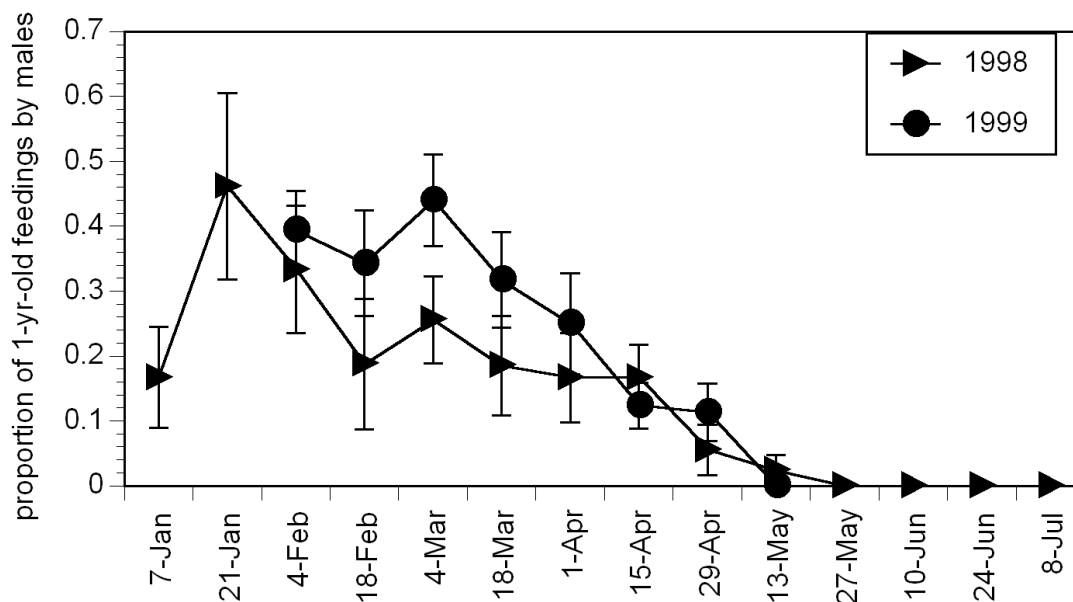


**Figure 1**. Feedings to 1-year-old great frigatebird fledglings made by males and females on Tern Island in 1998 and 1999. Total sample size was 373 and 374 feeding observations in 1998 and 1999, respectively.

Male plumage varied primarily in breast coloration, ranging from black to gray to brown. Based on five categories of breast coloration, we found that the males feeding 1-year-old offspring in 1999 were more likely to be brown than were males on new nests or males trying to attract a mate in that year, and males trying to attract a mate were more likely to have substantial amounts of white in the breast plumage than males who
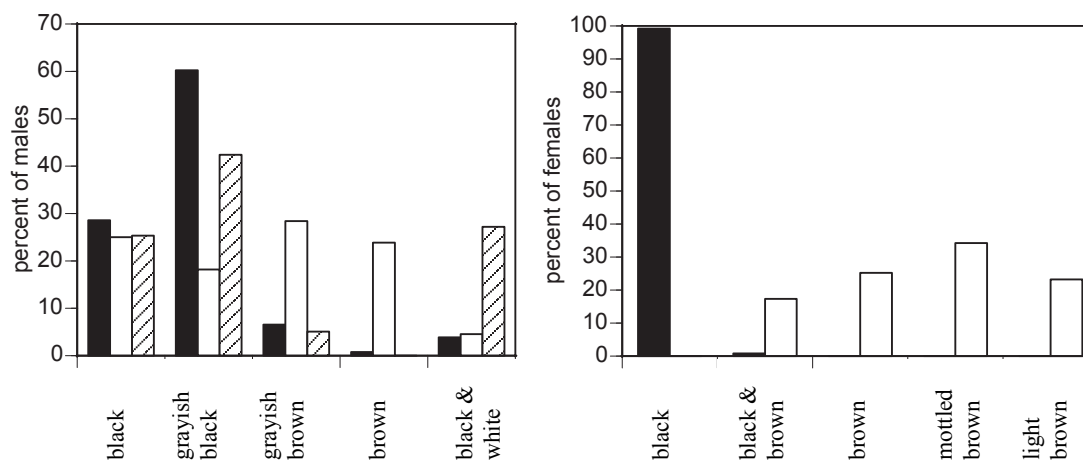
**Figure 2**. Plumage of great frigatebirds feeding 1-year-old fledglings and birds engaged in new breeding attempts on Tern Island in 1999. a) Breast plumage categories of males that were feeding 1-year-olds (open bars) or displaying to attract a mate (hatched bars) or tending a new egg or chick (solid bars). b) Head plumage categories of females that were feeding 1-year-olds (open bars) or tending a new egg or chick (solid bars).

had already been chosen as mates that season ($X^2 = 222.837$, df = 8, p << 0.00001; Fig. 2). This whiter breast plumage is likely indicative of males that are just reaching sexual maturity (Metz and Schreiber, 2002).

Female plumage varied primarily in head coloration, ranging from black to light brown. Based on categories of head coloration, we found that females feeding 1-year-old offspring in 1999 were almost exclusively black-headed, whereas no females on new nests that year were black-headed ($X^2 = 488.343$, df = 4, p << 0.00001; Fig. 2).

Breeding Population Size and Spatial Genetic Structure

Daily counts in 1998 and 1999 revealed as many as 1,171 males, 1,053 females, and 691 juveniles and subadults on the Island at a single time (Fig. 3). In both years, the number of juveniles and subadults was fairly constant over time. In contrast, the total number of adults on the Island fluctuated greatly and generally increased all the way through the pair-formation and egg-laying portion of the breeding season, even though the rate of pairing declined dramatically in May and June. By July, most nests had failed or had reached ages when chicks are unattended except when being fed, and most of the adults on the Island were not engaged in reproductive activity. We previously (Dearborn et al., 2001a) described a seasonal shift in the ratio of males to females that are unpaired and potentially available for mating. This ratio becomes less biased because of a gradual increase in the number of females on the Island (Fig. 3). Here, we apply the plumage criteria described in the previous section to assess whether these females are likely breeders. Plumage-specific daily counts of females were conducted in 1999 only. From January through March of 1999, most of the females on the Island had black head plumage, indicative of current breeders; females with brown or mottled heads were rare, perhaps because they were on the Island only while feeding 1-year-olds. As the number
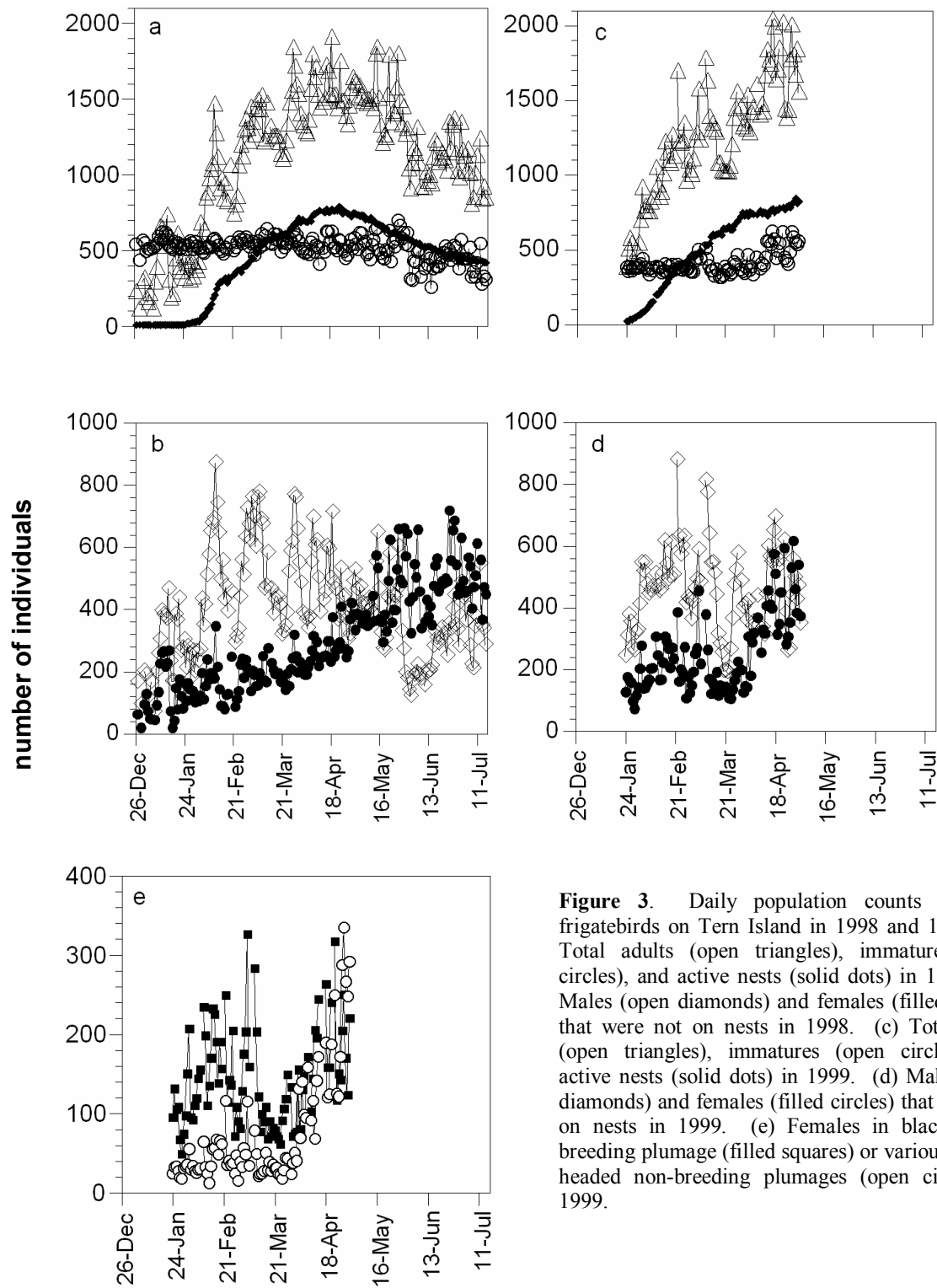
**Figure 3**. Daily population counts of great frigatebirds on Tern Island in 1998 and 1999. (a) Total adults (open triangles), immatures (open circles), and active nests (solid dots) in 1998. (b) Males (open diamonds) and females (filled circles) that were not on nests in 1998. (c) Total adults (open triangles), immatures (open circles), and active nests (solid dots) in 1999. (d) Males (open diamonds) and females (filled circles) that were not on nests in 1999. (e) Females in black-headed breeding plumage (filled squares) or various brown-headed non-breeding plumages (open circles) in 1999.

of females on the Island increased in April, a decreasing proportion of females were black-headed, meaning that most of the "new" females on the Island were non-breeders (Fig. 3e).

In an Island-wide census in late August 1999 (USFWS, unpublished data), we found 378 nestlings. Because there was no mortality at individually marked nests between late July and the fledging of the last chick in December, and because no nestlings at marked nests fledged before late September, it can be assumed that 378 is a good estimate of the number of frigatebird nestlings that fledged on Tern Island in 1999. Applying our estimate of reproductive success at marked nests during that year (18.0%), there were approximately 2,099 nests initiated during the 1999 breeding season. Among those birds that were marked at the start of the 2000 season (the only year for which we have such data from early-marked females) and then initiated nests (i.e., laid an egg) that year, the mean number of nests initiated per female was 1.30; for males, the mean number of nest attempts was 1.00. If these numbers are relatively constant across years, the population of frigatebirds actually nesting on Tern Island in 1999 likely consisted of approximately 1,615 females (2,099 nests with eggs / 1.30 eggs per female) and 2,099 males. This estimate can be combined with our measure of pairing success for females (89.3%) and males (18.75%) to estimate the number of adults that attempted to breed (i.e., including those that did and did not reach the stage of nest building). By this approach, the pool of birds attempting to breed in 1999 consisted of approximately 1,809 females (1,615 / 0.893) and 11,195 males (2,099 / 0.1875). Including those adults not breeding in 1999 (whether at sea, on other islands, or on Tern Island but not currently breeding), the total number of sexually mature adults in the Tern Island population is likely even larger, given that plumage evidence (see above) suggests that individuals whose nests succeed are likely to skip breeding for at least the following year.

Spatial analysis of AFLP data revealed no significant change in pairwise genetic dissimilarity between breeders across the categories of distance between nest sites, as the confidence interval for the Tanimoto dissimilarity index within each distance category spanned the overall mean of 0.3447. Thus, AFLP data suggest no spatial genetic structure within the Tern Island breeding colony, consistent with the finding of very little structure based on the multilocus minisatellite fingerprinting data (Cohen and Dearborn, 2004).

## DISCUSSION

This study sheds light on basic demographic processes in this population. We found that in a given year males were much more likely than females to try to obtain a mate but were much less likely to succeed at pairing. This difference in pairing success between the two sexes is consistent with behavioral descriptions of mate acquisition (which seems to consist entirely of female choice; Nelson, 1975) and with a male-biased operational sex ratio (Dearborn et al., 2001a). Females, but not males, occasionally nest multiple times in a season if the first nest fails; this difference between sexes is due to the difficulty that males have in attracting a mate, rather than to lack of interest in re-nesting by males. Overall, the coefficient of variation in pairing success was much greater for

males than females; this provides evidence that sexual selection is stronger on males in this population and supports the notion that the male-biased operational sex ratio is linked to sexual selection via variation in pairing success.

Following pair formation and egg laying, nesting attempts had a very low probability of success.  Although fledging success was high, hatching success was below 30% in all three years of this study.  Frigatebird reproductive output is affected by El Niño conditions at colonies further south in the Pacific (Schreiber and Schreiber, 1989), but our three years with low success included an El Niño year (1998), a La Niña year (1999), and a year of moderate Southern Oscillation Index.  Overall reproductive success was towards the low end of the range reported from other populations (Metz and Schreiber, 2002), though hatching success on Tern Island was somewhat higher in 2003 than in previous years (Juola and Dearborn, in press).  Nests failed during incubation for a variety of reasons, but three main causes seem to be aggressive interactions with other frigatebirds, severe weather events, and prolonged foraging trips by the mate that is currently off the nest (Dearborn, 2001).  Aggressive interactions could reduce nest success of frigatebirds in a density-dependent manner (Reville, 1988; 1991), though we do not yet have such data for Tern Island.  Prolonged foraging trips by a breeding bird are important because the body condition of the frigatebird currently incubating becomes a limiting factor in its ability to stay on the nest and continue fasting (Dearborn, 2001).  This, coupled with analyses of other seabird populations on Tern Island (Dearborn et al., 2001b), suggests that resource availability is a key component of individual- and population-level reproductive success for these birds.

Plumage data indicate that females do not breed in years following a successful breeding attempt; the plumage of those females feeding 1-year-old offspring was categorically different from that of females incubating eggs or new nestlings.  For males, the findings are more complex.  Males feeding 1-year-olds were much more likely to have brown breast plumage than males with eggs or new nestlings, but there was substantial overlap between the two groups of males.  Either plumage is a less discriminatory indicator of breeding status in males than in females or some males are simultaneously feeding 1-year-olds and tending new nests.  For both sexes, feather wear in the absence of molt is the likely mechanism by which birds feeding 1-year-olds are browner than birds involved in new breeding attempts, as brown is the basal coloration of black-tipped head and breast feathers in great frigatebirds (Metz and Schreiber, 2002).  Overall, these observations are consistent with the long-standing hypothesis that male frigatebirds try to breed annually and females  biennially (Stonehouse and Stonehouse, 1963; Diamond, 1973; Nelson, 1975; Trivelpiece and Ferraris, 1987; Carmona et al., 1995), but the evidence presented here is indirect.  Note also that this hypothesis of unequal breeding frequencies of males and females was driven by observations of magnificent frigatebirds (*Fregata magnificens*), in which males abandon the care of nestlings after just a few months (Osorno, 1999).  We have shown in this study that males in our population do taper off their parental care of fledglings sooner than do females, but male care extends well into the pair-formation part of the next breeding season.

Colony-wide counts detected as many as 1,171 males, 1,053 females, and 691 juveniles on the Island at a single time.  However, the frequent turnover of birds,

revealed by mark-resight data, indicates that the true number of adults using the Island is many times larger than this. Individuals vary extensively in their pattern of Island use (unpublished data), such that some individuals visit only briefly, others stay for weeks, and yet others come and go regularly over the course of many months. Similar complexities were seen in patterns of visits to other islands (e.g. Johnston Atoll) by frigatebirds that were wing-tagged on Tern Island (Dearborn et al., 2003). In light of these complexities in space use, the best way to define a population may be based on breeding individuals. Using a combination of nest counts and reproductive metrics, we estimated that 1,615 females and 2,099 males nested on Tern Island in 1999; this relatively small difference in number of breeders of the two sexes reduces the effective population size only slightly (from 3,714 to 3,651 in a given year; Kimura and Crow, 1963). Many additional birds attempted to breed but did not progress beyond the pair-formation stage. Based on the pairing success of marked individuals, we estimated that the pool of birds attempting to breed on Tern Island in 1999 was larger, particularly for males: 1,809 females and 11,195 males. Because plumage evidence suggests that birds are unlikely to breed in successive years, at least in years following the fledging of a chick, the actual size of the breeding population may be even larger. Our estimate of the number of birds breeding on Tern Island is substantially higher than the previous estimate for this population (300 – 375 pairs; Metz and Schreiber, 2002), and may reflect more exact information or an increasing population, or both; population increase in French Frigate Shoals is suggested by nest counts over the past 40 years (summarized in Cohen and Dearborn, 2004). Given that the global population of great frigatebirds has been estimated as only 54,000 – 68,000 breeding pairs (Metz and Schreiber, 2002), the Tern Island population may be a demographically significant one.

Using AFLP genetic markers, we found no evidence of spatial genetic structure within the Tern Island colony. This is consistent with our understanding of the history of this population and with our previous findings with multilocus minisatellite fingerprinting (Cohen and Dearborn, 2004). The lack of small-scale spatial structure alleviates the need to account for this in localized management decisions, although our earlier finding of substantial genetic differentiation among Tern Island, Johnston Atoll, and Christmas Island (Dearborn et al., 2003) is important.

A crucial gap in our knowledge of frigatebird ecology in the Northwestern Hawaiian Islands is foraging movements and destinations, particularly given the connection between reproductive success and adult body condition (Dearborn, 2001). Diet samples of frigatebirds in Hawaii show a preponderance of flying fish (Exocoetidae) and squid (Ommastrephidae; Harrison et al., 1983), but not knowing where the birds are foraging makes it difficult to assess potential threats to food availability. One plausible threat is the commercial fishery for large predatory fish, because a reduction in the number of such fish could reduce the frequency with which frigatebirds' prey are driven to the surface (Safina and Burger, 1985). Stocks of large piscivorous fish have declined markedly, both globally (Myers and Worm, 2003) and in the central Pacific (Cox et al., 2002). The ecological interaction between predatory fish and frigatebirds is a critical one because frigatebirds neither dive nor swim after their own prey. Furthermore, because frigatebirds soar in thermals extensively when traveling (Weimerskirch et al., 2003), they

may spend little time close enough to the surface to readily detect patchily distributed prey, which could heighten their dependence on the activity of predatory fishes. Mark-resight data (Dearborn et al., 2003) have reinforced the hypothesis that these birds routinely travel widely, but satellite telemetry studies such as those now being conducted in Madagascar (Weimerskirch et al., 2004) are needed to better delineate the flight patterns and foraging habitats of Hawaiian frigatebirds.

Overall, great frigatebirds are thought to be experiencing population declines, though this trend is geographically variable (Metz and Schreiber, 2002). Threats to frigatebirds in other parts of their range include habitat loss, nest site destruction by exotic herbivores, nest predation by exotic mammals, and human disturbance or predation (summarized in Metz and Schreiber, 2002), factors that are not currently threats in the Northwestern Hawaiian Islands. Frigatebirds are long-lived, they are slow to mature, and they are very limited in their reproductive output. Consequently, population declines resulting from increased adult mortality or decreased productivity would take many years to recover, such that we need to guard against them carefully. Because of the large and relatively well-protected populations of great frigatebirds and other seabird species in the Northwestern Hawaiian Islands, continued protection of these islands is crucial for seabird conservation.

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# DEVELOPMENT OF A BANDING DATABASE FOR NORTH PACIFIC ALBATROSS: IMPLICATIONS FOR FUTURE DATA COLLECTION

BY

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## ABSTRACT

The effects of fishery practices on black-footed (*Phoebastria nigripes*) and Laysan albatross (*Phoebastria immutabilis*) continue to be a source of contention and uncertainty. Some of this uncertainty is a result of a lack of estimates of albatross demographic parameters such as survival. To begin to address these informational needs, a database of albatross banding and encounter records was constructed. Due to uncertainty concerning data collection and validity of assumptions required for mark-recapture analyses, these data should be used with caution. Although demographic parameter estimates are of interest to many, band loss rates, temporary emigration rates, and discontinuous banding effort can confound these estimates. We suggest a number of improvements in data collection that can help ameliorate problems, including the use of double banding and collecting data using a 'robust' design. Additionally, sustained banding and encounter efforts are needed to maximize the value of these data. With these modifications, the usefulness of the banding data could be improved markedly.

## INTRODUCTION

Although there is much recent concern over the status and trends of north Pacific albatross species (American Bird Conservancy, 2002; Lewison and Crowder, 2003; EarthJustice, 2004), there are few demographic data to address these concerns, or to assess the effectiveness of possible mitigation measures. Generally, for long-lived species such as albatross, the demographic rate to which population change is most sensitive is adult survival (Cairns, 1992; Pfister, 1998; Doherty et al., 2004), and survival is arguably the demographic parameter of most current interest. Although other demographic parameters are of significance and needed for population models (e.g., Caswell, 2001) the interest in survival stems from the possible effects of historic and current fishery practices on albatross species (e.g., Lewison and Crowder, 2003). Although there is concern for all north Pacific albatross species, focus has been on the

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black-footed (*Phoebastria nigripes*) and Laysan (*Phoebastria immutabilis*) albatross, since short-tailed (*Phoebastria albatru*) and waved (*Phoebastria irrorata*) albatross populations have not been suggested as declining steeply.

Data to estimate survival can come from banding and subsequent encounter data. Fortunately, over the last ~70 years much albatross banding activity has taken place. Unfortunately, many of these albatross records have not been readily accessible. Even when accessible, there are many possible problems associated with using these data, including problems with identifying specific areas where banding took place, accounting for band loss, identifying birds with double and replaced bands, and tracking such bands over time.

Our overall goals were to: (1) gather and vet albatross banding and encounter data to construct a database, (2) assess the usefulness of the database for providing estimates of vital demographic rates, and (3) provide recommendations for future study design and data collection.

## METHODS AND MATERIALS

To address data needs for a demographic analysis of black-footed (BFAL) and Laysan (LAAL) albatross, with a focus on estimating survival, a database consisting of banding (first capture) and subsequent encounter (dead or alive) records was needed. A previous effort was made at constructing such a database, however this effort had shortcomings. The previous effort focused on BFAL and ostensibly included 114,884 banding and 24,324 encounter records. When these records were examined more closely, problems due to tracking replaced bands (i.e., albatross can outlive a band, and often more than one band is associated with a particular bird), errors in data entry (e.g., band numbers that did not correspond to albatross), and unfamiliarity with banding data, led to this database being unusable. We undertook a data entry and vetting initiative to construct a usable database for both BFAL and LAAL using this previous database as a starting point. Since the U.S. Geological Survey (USGS) Bird Banding Laboratory (BBL), in cooperation with the Canadian Wildlife Service, governs all U.S. and Canadian banding activities, and maintains a large database of banding data, we worked within the BBL with a goal of conforming to BBL database structure and data standards.

We first located as many of the albatross banding records as possible. Only banding data collected since 1960 were available in an electronic format at the BBL. Data previous to ~1950 were on microfiche, and data from the period ~1950 to 1960 were on paper. Finding all the older (pre-1960) albatross banding data was particularly challenging. We entered or re-entered all banding data previous to ~1970, with the earliest recorded bandings dating to 1936. Until recently, only locations to the nearest 10-minute block were stored by the BBL. When we re-entered data, we also entered exact location information if such information was available.

We then identified band associations (i.e., replaced bands and double bandings that would artificially increase the number of bandings if not recognized as a single bird). All such band associations were electronically available from ~1988. Records previous to this date were available on paper only, unless such associations had been noted upon

an encounter event. We searched for all band associations and re-entered these along with exact location data if it were available.

We then located and entered encounter data. Local encounter data (i.e., within the same 10-minute block of banding) has not been stored traditionally by the BBL, and few local encounter records were available directly from the BBL. The BBL is currently in the process of re-evaluating this policy and will most likely routinely store such information in the future. We obtained encounter data from many sources including the first albatross database, the BBL databases, paper records at the BBL, U.S. Fish and Wildlife Service (USFWS) personnel in Hawaii (including the banding records from a number of banders working on French Frigate Shoals), and directly from banders' personal records.

In constructing the database, data were entered once, as resources were not available to enter data more than once. However, many records were entered multiple times due to duplicate records from different data sources. Whenever an error or inconsistency was discovered, we went back to the primary source (i.e., paper records) and verified the data. In vetting these records, we made sure that every banding was indeed an albatross and that every encounter record had a matching banding record. We also checked for internal inconsistencies between bandings and encounters (e.g., species, sex, age, dates of encounters being later than banding date).

Our database was formatted to conform to BBL procedures and codes. These formats/codes are available online (http://www.pwrc.usgs.gov/). The BBL is currently in the process of updating its databases (from a mainframe system to an Oracle-based client-server system). When this process is complete, our albatross database will be imported into the BBL databases, with additional vetting related to importing procedures happening at that time, and access will be the same as for any other BBL banding data.

## RESULTS

Database Records

We identified 109,372 BFAL, 252,540 LAAL, 16 hybrid, and 1 unidentified albatross bandings (total = 361,929). With long-lived species such as albatross, double banding and replaced bands are common. Tracking such band associations is crucial for data to be usable, or biased estimates will result. Previously to our efforts we were aware of ~9,600 band associations (both species inclusive). We now recognize 25,404 band associations (5,305 BFAL; 20,097 LAAL; 2 hybrids).

We recognize a total of 163,455 encounters (39,762 BFAL, 123,583 LAAL, 6 hybrids, and 104 unknown albatross species). Many banders replaced bands through the years, and there were multiple duplicate records that have now been rectified. One important exception that should be noted is that there were a number of banding schedules that were never submitted to the BBL (and cannot be located by the permit holder) for which there were numerous (110) encounters, but no banding data. These 110 records currently are left in the database.

Potential Analyses

We suggest the database is of limited use. The data are too limited to generate annual survival estimates for both albatross species for the last half century. In preliminary analyses we were able to generate survival estimates for groups of years (i.e., years grouped together in which survival is assumed constant) from dead-encounter data and annual estimates for short series of years from live-encounter data.

Goodness-of-fit is likely to be a problem in using these data, and variance inflation factors will be needed to help adjust for these lack-of-fit problems.


## DISCUSSION

With the hundreds of thousands of banding and encounter records known to exist from 1936 (and now available), there are high hopes that much of the informational needs relating to north Pacific albatross species will be met. Unfortunately, due to inadequate record keeping and inconsistency in data collection, these hopes will not be entirely met. However, there is information to be garnered from these data, and these data point to needed improvements in study design and record keeping. We first will discuss the database, and close with comments on the results and study design considerations.

The database was formed to conform to BBL standards and to eventually be imported into the BBL's new database. Thus users of the database should be familiar with the BBL operations. Fortunately, access to BBL data is free and details about BBL operations are available on-line.

Although we identified many errors, there are surely many more that will continue to be detected as the data are used and future records are added. Significant possible sources of errors and/or missing data are:

1) Not all of the old banding data (e.g., microfiche and paper) were located and entered. We are confident we located and entered most of the major banding efforts, but there may be small numbers of very old bands that we did not find.

2) Not all encounter records were located and entered. There are certainly recapture data available that we did not locate. We think we located much of the available data, with an exception of data from individual banders operating during the late 1970s and early 1990s. We had many replaced band records (mandatory submission to the BBL) from these time periods, and we think there may be additional recapture records that were not submitted to the BBL. Additionally, file cabinets on Midway probably contain encounter data that were not entered by staff (volunteer and contractor) before the accessibility to Midway was reduced in the early 2000s.

3) Not all band associations were identified. We scoured the BBL records for band associations and almost tripled the number of known band associations. There are likely others, although few in number, which we did not detect. These few birds would be considered as new bandings and artificially increase the number of birds banded. Most likely, this would negatively bias estimates of survival.

4) Specific banding location data are error-prone or not available. We re-entered banding data previous to ~1970 and captured any specific location (more precise than

a 10-min block) data that were available.  Although banding data post- ~1960 were available electronically, these data would not have specific location data associated with the electronic record.  It may be useful to go through additional banding records (post- ~1970) and enter any specific banding information that may be available on paper.

We think the data fields associated with specific location information are especially prone to error as there was no way to verify or check these fields.  For example, data collected at Sand and Eastern islands (Midway Atoll) were sometimes given the same latitude-longitude coordinates and sometimes different coordinates.  Extreme care must be taken with the use and interpretation of these data.

5) Any inconsistencies that could not be resolved by examining the original sources were left for the user to decide how to handle.  These include species or sex that differs on banding and encounter, as well as an encounter that happens after a dead recovery.  There are few of these instances (<1000), but the user must be careful.

This database is viewed as temporary storage until the records can be imported into BBL databases and final vetting is conducted.

Analysis and Implications for Future Study Design

Although we are able to generate estimates of survival from the database, lack of fit for capture data will be a concern, and some estimates will be difficult to judge and interpret.  Much care must be taken and many caveats must be recognized when using and interpreting these data.  These caveats include:

1) Estimates could be biased due to inadequate design and/or sparse data leading to lack of fit.

2) Little data exists to associate breeding populations with stressors (i.e., fishery activity).

3) There are too many years with inadequate (or no) capture effort.

From our experience in the construction of the database and from preliminary analyses we have many suggestions for future data collection and storage.  We are working with the USFWS to construct exact protocols for their surveys on Tern Island and Midway Atoll.  Below are some of the suggestions we think could be of value:

1) The BBL is the most logical repository for databases such as this albatross database (Kendall et al., 1998).  With the new database developments, as well as developments of band management software (i.e., Band Manager), such storage should be within reason.

2) If annual estimates of survival and other demographic parameters are deemed warranted, then a consistent effort needs to be maintained on the nesting islands.  Study plots should be chosen to be representative of the islands and to be able to make inference to the island as a whole.  By a consistent effort we mean annual effort in which greater than 2,000 adult albatross are captured per year.  Efforts should be made to identify breeding from nonbreeding birds, and if a choice needs to be made, effort should focus on breeding birds.  Relying solely on volunteers and opportunistic banding efforts will not provide the information needed.

3) Band loss negatively biases survival estimates from banded birds (in direct proportion to the loss rate).  Double-banding a subset of the birds that are banded will

permit estimation of band loss and adjusting of survival estimates for this loss. In this particular situation, we suggest trying for a goal of double banding at least 10% of the birds. This also obviates the need to always record all bands that are on recaptured or resighted birds.

4) By splitting annual capture or resighting effort into at least two full sampling sessions within each breeding season the probability of a breeder skipping a year of breeding can be estimated with some degree of certainty. This would also remove potential bias in estimates of survival rates caused by skipping. We suggest, as a starting point, splitting capture effort into two equally sized sampling intervals. In the first interval, you would capture as many individuals as possible, avoiding recaptures if possible. In the second sampling interval, you would sample individuals randomly, regardless of whether an individual was captured in the first sampling interval. Therefore, a capture history is constructed for an individual within as well as between breeding seasons. For a three-year study, an example capture history would be:

11 00 01,

where a '1' indicates capture in that sampling interval. So this individual was first captured in sampling interval 1 of year 1. It was then recaptured (or the band resighted) in sampling interval 2 of that same year. In year 2, it was not captured/resighted at all, indicating it skipped breeding that year, bred but not in the study plot, or was present and was simply missed. In year 3, it was missed in sampling interval 1 but was captured/ resighted in interval 2. This is Pollock's robust design (Pollock, 1982), which permits the estimation of many parameters including temporary emigration (Kendall et al., 1997). Accounting for skipped breeders can be further aided by recording whether the breeding attempt by an albatross in a given year is successful.

5) For study areas defined by plots amid other nesting habitat, the movement of a breeder outside the plot in the following year could be confused with a decision to skip breeding (because in either event the bird is invisible to capture effort within the plot). By establishing a boundary strip around the plot, this edge effect can be neutralized. To accomplish this, the width of the boundary strip should be wide enough to encompass individual breeding pairs that might have been captured and marked in the study plot in the past. A reasonable boundary strip width may be 10 m for these albatross species. Each time field crews capture/resight birds within the plot, they also search the boundary strip. They should not capture unmarked birds, but should search for and record band numbers of previously marked birds.

6) Telemetry and/or data loggers could also be used as direct information on survival and the decision about whether to breed in a given year, as well as the spatial-temporal juxtaposition of the bird's location with longline fishing fleets.

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# DIET COMPOSITION AND TERRESTRIAL PREY SELECTION OF THE LAYSAN TEAL ON LAYSAN ISLAND

BY

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## ABSTRACT

The Laysan teal (*Anas laysanensis*) is an endangered dabbling duck endemic to the Hawaiian Archipelago but currently restricted to a single breeding population on Laysan Island. We studied its diet using fecal analysis and behavioral observations. Laysan teal fecal samples (N=118) contained prey items in 15 primary prey categories with a mean of 2.9 (range 0-7) taxa per sample. Sixty-two of these fecal samples were quantified with 2,270 prey items identified (mean items per sample 37; range 0-205). Based on fecal analysis and behavioral observations, we learned that the Laysan teal is not strictly a macroinsectivore as previously reported, but consumed seeds, succulent leaves, and algae, in addition to adult and larval diptera, ants, lepidoptera, coleoptera, and *Artemia*. We compared abundance of invertebrates from two terrestrial foraging substrates, soil and standing vegetation, to the abundance of invertebrate prey items counted in fecal samples collected from these habitats for the same period. In the soil substrate, Laysan teal selected two of the most abundant invertebrates, lepidoptera larvae and coleoptera. In the standing vegetation, Laysan teal selected the most abundant taxa: coleoptera. Amphipods were consumed in proportion to their abundance, and small gastropods (*Tornatellides sp.*), isopods, and arachnids were avoided or were identified in fecal matter in disproportion to their abundance in the foraging habitat. We compared fecal composition of samples collected in aquatic and terrestrial habitats and detected significant differences in samples' species compositions. The conservation implications of the adult Laysan teal's diet are positive, since results indicate that the Laysan teal are opportunistic insectivores, and exhibit dietary flexibility that includes seeds and other food. Dietary flexibility improves the possibility of successfully reestablishing populations on other predator-free islands.

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## INTRODUCTION

The Laysan teal, an endangered species, is restricted to a single breeding population (approximately 500 birds) on Laysan Island and a small, recently translocated population on Midway Atoll (42 birds). The species was previously widespread across the Hawaiian Archipelago, but was extirpated from the main islands during Polynesian colonization and associated mammalian predator introductions (1,400-1,600 ybp) (Cooper et al., 1996; Burney et al., 2001). Due to the remoteness of Laysan Is., only three other studies have preceded the current work (Warner, 1963; Moulton and Weller, 1984; Marshall, 1989).

Little is known about the food habits of Laysan teal, and what information exists is conflicting. Observations in the late 1950s indicated that the birds fed primarily on moth (*Agrotis dislocata*) larvae (Warner, 1963). More recent work suggests that brine flies are the most important dietary component (Caspers, 1981; Moulton and Weller, 1984). Whether this shift in diet was due to environmental conditions on Laysan during the early observations (which were conducted during dry years) or the effect of introduced insects, such as predatory ants, depleting *Agrotis* larvae is unknown.

To learn more about the ecology and conservation potential of this endangered species, we studied the diet of Laysan teal and the relationship between terrestrial invertebrate prey abundance and food habits by sampling invertebrates, analyzing teal feces, and observing teal foraging behavior.

## METHODS

Study Site

Laysan Is. is an important nesting colony for several million seabirds. Although plumage collectors, seal and turtle hunters, and other mariners visited the island, there is no evidence of human habitation on Laysan before guano miners who occupied the Island from 1893-1909 (Ely and Clapp, 1973). U.S. President Theodore Roosevelt declared the Island a bird reserve in 1909, subsequent to which exploitation of Laysan's wildlife was much reduced. A small U.S. Fish and Wildlife Service (USFWS) field camp exists on Laysan today, and the Island is part of the Hawaii Islands National Wildlife Refuge (NWR).

Laysan Is. has the largest continuous land area of the Hawaiian atoll islands. It is roughly rectangular, approximately 3 km long from north to south and 1.5 km east to west. Laysan lies 1,506 km northwest of Honolulu (25º46' N latitude, 171º44' W longitude) and is accessible only by boat (Fig. 1). The island consists of 187 ha of mostly low herbaceous vegetation, a 105-ha interior lake and associated mudflats, and approximately 123 ha of unvegetated blowout areas, coastal dune, and beach (Moulton and Marshall, 1996). The highest point of the Island is 12 m above sea level, and coastal reef flats and tide pools surround its perimeter.

Laysan's lake is characterized by hypersalinity, high nutrients, and low species diversity.  Evaporation frequently exceeds precipitation, and salinity is two to four times oceanic salinity (5.8-13.0 g/100g; USFWS data).  The lake supports algal and cyanobacterial growth (*Dunaliella spp.*, *Schizothrix sp.*), and dense populations of brine shrimp (Anostraca: *Artemia franciscana*) and brine flies (Ephidridae: *Scatella sexnotata*; Caspers, 1981; Lenz, 1987).  *Artemia* feed on phytoplankton and occur throughout the lake's water column.  Larvae of *S. sexnotata* are salt-tolerant and aquatic and feed on microorganisms and detritus. Pupae adhere to the algal substrate on the lake bottom, and the adult flies feed on organic matter occurring in the wetlands surrounding the lake.  A subterranean freshwater lens occurs on Laysan, and fresh-to-brackish (0.0 - 3.0 g/100g) water seeps occur in the interior of the Island surrounding and within the lake, and at several locations on the coast (Reynolds, 2002; Warner, 1963).  The lake's maximum depth was 6.5 m. in 1984 (USFWS data), but size and depth vary seasonally.  Rainfall on Laysan is moderate, averaging 79 cm per year from 1992 to 2000 (range 38-120 cm per yr; USFWS data).

Vegetation associations form concentric bands between the coast and the lake. Scattered ground cover dominated by *Nama sandvicensis* is found closest to the coast. Moving inland, vegetation consists of 1) coastal shrubs, 2) interior bunch grasses, 3) vines 4) interior shrubs, and 5) wetland vegetation.  The dominant species of these vegetation associations are 1) *Scaevola sericea,* 2) *Eragrostis variabilis,* 3) *Ipomoea pes-caprae* or *Sicyos maximowiczii, S. pachycarpus,* or *S. semitonsus, 4) Pluchea indica,* and 5) *Sesuvium portulacastrum, Heliotropium curassavicum,* and *Cyperus laevigatus* (Newman, 1988).  The bunch grass association and the viney association comprise 112.6 ha and 50.8 ha, respectively (Morin, 1992).  Laysan Island has four general habitat zones used by the Laysan teal. The coastal zone includes area below the high surf zone and coastal or dune areas on the outer perimeter of the interior bunch-grass associations. The "camp" zone includes all areas within 60 m of human structures and storage areas associated with the camp.  The terrestrial zone is comprised of vegetation bands 1-4. The "lake zone" consists of all wetland plant associations, mudflats, ephemeral wetlands, and the hypersaline lake.

Diet

Fecal analysis is a nonintrusive prey sampling method, appropriate for endangered species (Rosenberg and Cooper, 1990).  We collected fecal samples from birds within each of the four habitat zones, assuming this represented what birds typically ate. Scleritized arthropod body parts are identifiable after passing through the bird's digestive system.  Fecal samples were collected within 5 minutes of deposition, during banding, radio telemetry, and behavioral observations from the four habitat zones from March 1998 – July 2000, and preserved in 70% ethanol.

For identification, samples were placed in Petri dishes and separated using forceps and fine probes.  Prey items were viewed at 160-400x with a binocular scope (Leica MZ6) and identified using reference specimens and taxonomic keys. (Zimmerman, 1948; Gepsink, 1969; Hardy and Delfinado, 1980; McAlpine, 1987).  Reference specimens

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were collected and crushed to better resemble the parts found in fecal samples.  For all samples, the frequency of occurrence (presence or absence) of prey items in an individual fecal sample was determined.  A subsample was analyzed further, and identified taxa were counted.  Taxa were classified by order and, when possible, by species and life stage.
Foraging Behavior

We studied the Laysan teal's foraging by observational sampling of behavior in 1998-2000.  Continuous focal sampling was conducted on radio-tagged birds located as part of home range studies (Reynolds, 2004). To supplement this sample, focal animals lacking radio tags were selected by traversing a particular habitat zone in a random direction until an individual was encountered.  All focal samples were 20 minutes in duration (Altmann, 1972; Reynolds, 2002).

Behavioral observations were collected from each habitat zone during the same four time periods: morning (2 hrs before and after sunrise: approx. 0400– 0830 hrs), day (approx. 0900-1530 hrs), evening (2 hrs before and after sunset: approx. 1600-2030 hrs), and night (2100-0300 hrs).

Terrestrial Prey Abundance

We collected data on prey abundance to relate habitat use and diet to the resource base (see also Reynolds, 2004).  We sampled prey abundance, the total amount of prey in the environment, by sampling terrestrial substrates (soil and vegetation) for taxa previously identified in the diet of Laysan teal (Warner, 1963; Caspers, 1981; Lenz and Gagne, 1986).  We acknowledge that prey availability, the amount of prey actually available to the individual bird, may differ from abundance, because we cannot sample the environment as the birds themselves do (Hutto, 1990).

Macroinvertebrates were sampled from soil and vegetation during active feeding hrs of the Laysan teal between 2100 and 0100 hrs, at randomly chosen locations along a trail used by Laysan teal for foraging, nesting, and cover.  The trail, which meanders from the coast to the interior wetlands, was used to prevent disturbance to nesting birds and damage to the seabird burrows that honeycomb the island.  Prior to each sampling session, a random point was selected as the starting location for collecting samples every 5 m at the nearest vegetation clump, alternating to the left and the right of the trail.  If a nesting or resting seabird prevented our collecting a sample at a designated vegetation clump, the next nearest vegetation clump was sampled.  Each type of vegetation sampled was classified to genus and later grouped into the following categories:  grassy (bunch grass), viney, shrubby, or mixed (Table 1).  Ten samples were collected twice monthly between May 1998 – Oct 1999 from the soil, and from November 1998 – October 1999 from the vegetation.  We intensified sampling and collected invertebrates weekly from both the soil and vegetation from April – July 2000.

Soil samples (excavations of 360.7 cm$^3$ each) were sieved for macroinvertebrates (> 1 mm) using three screen sieves (mesh sizes 10, 60, and 230 openings per linear inch; Hubbard Scientific soil profile kit 3196).  Invertebrates from sieved soil samples were counted, categorized by order, and released the next day.  Unknown taxa were collected and preserved in 70% ethanol for later identification.  Ants (Formicidae) were too numerous to quantify, and we determined only their presence or absence.

Vegetation was sampled by expulsion of invertebrates using a stick and "beating sheet" (0.5 m² per sample; Southwood, 1978). Dislodged macroinvertebrates were counted, categorized, and released at the sampling site. Unknown and some commonly occurring taxa were aspirated into vials for later identification and used as reference specimens for fecal analysis. Again, ants were not counted but categorized as present or absent. Additional data collected during each sampling period included time, weather, index of soil moisture, wind speed, and direction.

Data Analysis

We used nonparametric tests (Kruskal Wallis) for statistical comparisons of fecal data that lacked a Gaussian distribution (SYSTAT version 9; Zar, 1999). Prey selection indices are based on ratios of used and available resources (Manly et al., 1993):

$$w_i = \frac{o_i}{p_i},$$

where $w_i$ = the selection index for invertebrate taxon $i$,
$o_i$ = the proportion invertebrate taxon ($i$) used by Laysan teal, and
$p_i$ = the proportion of invertebrate taxon ($i$) available in the environment (estimated).

Resource ratio indices, $w_i$ of 1.0 indicate resources are used in proportion to availability; indices above 1.0 provide evidence of "selection," and values less than 1.0 suggest "avoidance" or use disproportionately less than availability. Resource indices are statistically significant if the confidence intervals for $w_i$ do not contain the value 1.0 (Manley et al., 1993). Standardized selection indices also are given by Manley et al. (1993):

$$B_i = \frac{w_i}{\sum\limits_{i=1}^{n} w_i},$$

where $B_i$ = standardized selection index, and $n$ is the number of resource categories (i.e., invertebrate taxa). Values of $B_i < 1$ indicate no preference, and values above or below 1 provide evidence of preference and avoidance, respectively. To test the null hypothesis that the Laysan teal are selecting resources at random, G-tests were used, assuming a chi-square distribution (Manly et al., 1993; Krebs, 1999):

$$\chi^2 = 2\sum_{i=1}^{n}\left[u_i \ln\left(\frac{u_i}{Up_i}\right) + m_i \ln\left(\frac{m_i}{(m_i + u_iM/(U+M))}\right)\right],$$

where $\chi^2$ is the chi-square value (df = n-1), $u_i$ = the number of observations of each invertebrate taxon ($i$), $m_i$ is the number of observations of available invertebrate taxon ($i$), $U$ is the total of observations of use, and $M$ is the total observations of availability. Standard errors and confidence limits for multiple tests of selection ratios are given by

Manly et al. (1993). Assumptions of these analyses are that 1) resource availability and use have been correctly identified, 2) resource availability and use do not change during the study, 3) birds have free access to all resource units, and 4) resource units were sampled randomly and independently.

## RESULTS

Fecal Analysis

Laysan teal fecal samples (N=118; 59 females, 53 males, 4 fledged juveniles, and 2 adults of unknown sex) contained prey items in 15 primary prey categories with a mean of 2.9 taxa per sample (range 0-7 taxa). Many samples contained sand and prey parts too finely ground for identification or quantification. Dipteran adults were most abundant, occurring in 47% of the samples, followed by dipteran larvae and pupae (39%), ants (36%), seeds (31%), lepidopteran larvae (25%), and coleopteran adults (23%) (Table 2).

Sixty-two fecal samples were analyzed by counting diet items in the samples. The number of prey items averaged 36.7 per sample (range 0-205). Dipteran adults made up 32% of the total identified prey items counted, followed by *Artemia* (21%), dipteran larvae or pupae (16%), lepidopteran larvae (8%), seeds (8%), and plant fibers (7%; Table 3). Ants made up only 2% of the total items counted despite their high frequency of occurrence in the samples. Nearly half (47.4%) of the seeds counted were from succulent plants, *Portulaca spp.*, found in the terrestrial zone. Other intact seeds identified in fecal samples included *Cyperus laevigatus, Fimbristylis cymosa,* and *Mariscus pennatiformis* ssp. *bryanni.* An unpublished analysis of fecal samples (N=28) collected from birds at the lake during the summer of 1985 showed higher occurrence of *Artemia* and *Blattaria*, fewer ants, and no seeds (Lenz and Gagne, unpublished data; Table 2)

We tested for differences in the frequency of occurrence between the composition of prey items collected from two habitat zones where the ducks spent most of their time: the lake zone (N= 45 fecals) and the terrestrial zone (N=30 samples; Fig. 2). We lacked data on an individual bird's time spent in the zone prior to the collection of fecal samples and the food passage rates for these prey species, therefore variation due to birds recently foraging in other areas was expected. Significant differences in the occurrence of taxa were found for ants, lepidopteran larvae, and seeds, which occurred more frequently in samples collected from the terrestrial zone, and adult dipterans, which occurred with greater frequency in the samples from the lake zone (Table 4). *Artemia* occurred in only 14 samples from the lake and terrestrial zones, and its frequency of occurrence did not significantly differ between them. However, the number of *Artemia* counted was significantly higher in the lake-zone samples than the terrestrial samples (Kruskal Wallis H=4.72, p=0.030). *Artemia* are found exclusively in the lake, and lepidopteran larvae typically are absent from the lake zone.

Behavoral Observations

Because of the difficulty in observing the consumption of small dietary items in dabbling ducks, diet from focal observations could not be reliably quantified from focal observations. Nevertheless, visually biased diet observations are valuable since we suspect that succulent leaves, algae, and adult lepidopteran, which were well represented in foraging observations (Table 6), may have been underrepresented or not identified in the fecal samples.

We analyzed 402 focal observations from 123 males, 251 females, and 28 unknown birds totaling 8,511 minutes from 1998-2000. Focal observations are summarized in Table 5 and 6. Adult and larval lepidopteran, terrestrial dipteran adults and larvae including maggots from seabird carcasses, *Blattaria* (cockroaches), grass seeds (*Sporobulus* spp.), sedge achenes, *Fimbristylis cymosa*, and succulent leaves from *Portulaca sp.* were taken while foraging in the terrestrial habitat. Laysan teal in the lake zone ate mostly wetland invertebrates and algae.

Prey Abundance and Selection

The most abundant soil invertebrates captured during sieve sampling were lepidoteran larvae (24%), gastropods (19%), coleopteran (14%), and amphipods (10%) (N=487 sieve samples; Fig. 3). Note that in the field we could not easily distinguish from live, dead, and estivating snails, thus the abundance of gastropods in the sieve samples is an overestimate of available live prey. Dominant taxa counted from the standing vegetation (N=367 samples; Fig. 4) included coleoptera (37%), arachinida (19%), lepidopteran adults (15%), and diptera adults (12%).

Invertebrate abundance for the two terrestrial substrates sampled, soil (N = 487) and standing vegetation (N=367), was analyzed separately to explore differences in composition and abundance of invertebrates among grassy, viney, and mixed substrates using Kruskal Wallis tests. Soil samples within the grassy (N=302), viney (N=101), and mixed vegetation (N=84) were tested for differences in the abundance of taxa captured between vegetation types. Significant differences were identified for lepidopteran larvae (H=26.712; df = 2; p<0.0001), gastropods (H=6.597; df=2; p=0.037), "other" combined taxa (H=7.279; df=2; p=0.026), and coleoptera (H=7.562; df=2; p=0.023). Lepidopteran larvae were more abundant in soil of the mixed and viney vegetation than the grassy vegetation. Gastropods were more abundant in the grassy vegetation's soil, "other" invertebrates were more abundant in the mixed vegetation soil, and coleoptera in the viney vegetation soil.

Invertebrates sampled in the standing vegetation (grassy N=231, viney N=67, and mixed vegetation N=69) showed significant differences for coleoptera (H=68.47, df=2, p<0.0001), arachnida (H=51.91, df=2, p<0.0001), diptera (H=53.86; df=2; p<0.0001) and adult lepidoptera (H=13.09; df=2; p=0.001). Pair-wise comparisons indicated coleoptera were more abundant in the viney standing vegetation, arachnida in the grassy vegetation, diptera in the viney vegetation, and adult lepidoptera in the mixed and viney vegetation.

We compared abundance of invertebrates from two terrestrial foraging substrates,

soil and standing vegetation, to the abundance of invertebrate prey items counted in fecal samples collected from these habitats for the same period. An assumption of the analysis, that available food resources are constant during the study period, is difficult to satisfy for most studies (Manly et. al., 1993), and was not met for this study because some taxa, such as adult diptera, showed seasonal variability (Reynolds, 2002). In this case, prey selection inferences are made with respect to "typical" conditions during the study period (Manly et. al., 1993). We excluded aquatic prey (*Artemia*) and diptera that could be from either wetland or terrestrial habitats, but included diptera identified as terrestrial. We tested the hypothesis of equal use with a chi-squared log likelihood statistic. Results provide evidence of nonrandom prey use in both the soil substrate ($X^2$ =341.517, df =7, P<0.0001), and standing vegetation ($X^2$ =77.54, df =4, p<0.0001; Table 7). Laysan teal selected the most abundant invertebrates in some cases but did not use other abundant taxa. In the soil substrate, Laysan teal preferred two of the most abundant invertebrates, lepidoptera larvae and coleoptera. Amphipods were selected in proportion to their abundance, and small gastropods (*Tornatellides sp*.), isopods, and arachnids were not consumed or were used in disproportion to their abundance. We did not distinguish between live, dead, or estivating snails and suspect many were dead, and unlikely prey. In the standing vegetation, Laysan teal preferred the most abundant taxon: coleoptera. Laysan teal avoided arachnids, however sample sizes of resource use (fecals containing identifiable arachnid parts) were too low to be reliable (Table 7).

## DISCUSSION

Previous researchers described the Laysan teal as a 100% macroinsectivore (Moulton and Weller, 1984; Moulton and Marshall, 1996); however, fecal analysis and behavioral observations reveal that seeds and other plant parts are important components of their diet. We observed significant differences in prey compositions from samples collected in the lake and wetlands compared to terrestrial habitats indicating the potential importance of habitat bias from fecal diet studies. The discrepancy between our research and earlier studies may be because most of the granivory and herbivory occurred in the terrestrial zone and therefore was more difficult to observe than foraging at the lake where naturalists made most of their observations.

The prevalence of terrestrial foraging and the importance of lepidopteran larvae in the diet were first described by Warner (1963). He also described cutworm larvae climbing the vegetation at night. We did not observe this phenomenon, but found that lepidopteran larvae were common in the soil substrate, particularly in the viney *Ipomoea-Sicyos* and mixed vegetation complexes. Indeed, radio-tracking studies indicated these habitats and substrates were used more for nocturnal foraging than would be expected by chance (Reynolds, 2002).

The Laysan teal consumes a wide variety of prey using a broad foraging strategy. Comparisons between fecal and invertebrate samples indicate that the most abundant prey was often the most frequently consumed. However, some abundant invertebrates were not consumed in relation to their abundance. These abundant invertebrates may lack

required nutrients or be energetically expensive to process due to high sodium content, for example *Artemia* (Reynolds, 2002). Other prey not selected may be unpalatable (e.g., ants due to formic acid), difficult to capture, or have defenses against predators (e.g., some spider and cockroach species) rendering them less available as prey. Collection of fecal samples and behavioral observation from all habitats used by the Laysan ducks (see also Reynolds, 2004) was essential to identify the variety of food consumed.

The Laysan teal appear to be opportunistic in that they consume the most abundant "profitable" prey. Although we have limited long-term historical data on food resources on Laysan, it is possible that this "opportunistic" foraging strategy likely helped it survive during prey and food scarcity from the past rabbit invasion (Dill and Bryan, 1912). The high risks of extinction for this isolated population, together with the evidence of the species' previously wide distribution in Hawaii (Cooper et al., 1996), provide justification for translocation to promote the species' conservation. The diet plasticity exhibited by the adults of this species improves the chance for successful re-establishment in mammalian-predator-free habitats on additional islands where terrestrial and aquatic prey are abundant. Most islands of the Hawaiian Archipelago are dissimilar to Laysan and lack hypersaline ecosystems, including important wetland and aquatic prey brine flies and *Artemia*. However, we anticipate that the Laysan teal's foraging flexibility and opportunism will allow them to adapt to novel environments with suitable habitat. The importance of a varied and abundant prey base, dense vegetative cover, a source of fresh water during brood rearing, and the absence of mammalian predators should be emphasized when choosing suitable habitat for new populations.

## ACKNOWLEDGEMENTS

Table 1. Vegetation categories and habitat zones of plant species sampled for terrestrial invertebrates.

| Category | Habitat Zone | Plant species |
| --- | --- | --- |
| Grassy | Terrestrial | *Eragrostis variabilis, Fimbristylis cymosa, Boerhavia repens* |
| Viney | Terrestrial | *Ipomoea pes-caprae, Sicyos* spp., *Tribulus cistoides* |
| Shrubby | Terrestrial | *Scaevola sericea, Tournefortia argentea* |
| Mixed | Terrestrial or lake transition | *Portulaca lutea, Conyza bonariensis* |

Table 2.  Frequency of occurrence (percent of samples with prey types) of taxa in Laysan teal fecal samples collected on Laysan Island during 1985 and 1998-2000.

| Prey type | 1998-2000[1] (N=118) | 1985[2] (N=28) |
| --- | --- | --- |
| Diptera adult | 47 | 39 |
| Dipteran larvae/pupae | 39 | 21 |
| Formicidae | 36 | 4 |
| Seeds | 31 | 0 |
| Lepidopteran larvae | 25 | 32 |
| Coleoptera | 23 | 0 |
| Plant fibers | 17 | 0 |
| Artemia | 15 | 32 |
| Acari | 11 | 7 |
| Amphipoda | 8 | 14 |
| Unknown arthropod | 7 | 0 |
| Blattaria | 3 | 21 |
| Diptera terrestrial | 3 | 11 |
| Lepidopteran adult | 3 | 0 |
| Araneida | 2 | 7 |
| Dermoptera | 0 | 4 |

[1] MHR data from samples collected from all habitats and seasons.
[2] Lenz & Gagne (1986) unpublished data from samples collected from the lake zone in 1985.

Table 3.  Total number of prey items and percent of total items identified in Laysan teal fecal samples collected on Laysan Island 1998-2000 (N=62 samples).

| Prey type | Number | Percent of total items identified |
|---|---|---|
| Dipteran adult | 725 | 31.9 |
| Artemia | 472 | 20.7 |
| Dipteran larvae or pupae | 355 | 15.6 |
| Lepidopteran larvae | 188 | 8.3 |
| Total Seeds | 179 | 7.9 |
|    Portulaca seeds | 85 | (47.4 % of seeds; 3.7 % of total items) |
| Plant fiber | 149 | 6.6 |
| Coleoptera | 81 | 3.6 |
| Formicidae | 47 | 2.0 |
| Amphipoda | 37 | 1.6 |
| Lepidopteran adult | 13 | 0.5 |
| Acari | 12 | 0.5 |
| Dipteran terrestrial | 9 | 0.3 |
| Blattaria | 3 | 0.1 |

Table 4.  Results of Kruskal Wallis tests comparing taxa counted in fecal samples from lake and terrestrial zones.

| Taxa counted | H | P-value |
|---|---|---|
| Amphipods | 0.77 | 0.38 |
| Ants | 6.43 | *0.01 |
| Artemia | 2.44 | 0.12 |
| Coleoptera | 1.84 | 0.18 |
| Diptera adult | 4.25 | *0.04 |
| Diptera larvae or pupae | 1.08 | 0.3 |
| Lepidoptera larvae | 7.61 | >*0.001 |
| Plant fiber | | |
| Seeds | 5.52 | *0.02 |

*Significant at 95% level

Table 5. Total number of food items and water consumed (events) by Lasyan teal during behavioral observations in four habitat zones on Laysan Island.

| Consumption observed | Camp | Coast | Lake | Terrestrial | Total |
|---|---|---|---|---|---|
| Algae | | | 11 | | 11 |
| Amphipod | | | 1 | | 1 |
| Artemia | | | 2 | | 2 |
| Brine fly | | | 1274 | | 1274 |
| Blattaria | | | | 5 | 5 |
| Terrestrial Diptera (adult) | 49 | | 155 | 481 | 685 |
| Maggot | | | 6 | 99 | 105 |
| Moth | 37 | | | | 37 |
| Portulaca | 4 | | | 2 | 6 |
| Seeds | | | | 36 | 36 |
| Spider | 1 | | | | 1 |
| Unk. soil inverts. | | | | 20 | 20 |
| Unknown | 11 | 1 | 15 | 33 | 60 |
| Water | 181 | 27 | 220 | 31 | 459 |

Table 6. Indices of preference (w) for select prey types from the terrestrial zone based on abundance (all dates combined) from soil and standing vegetation sampling and the number of prey items counted in fecal samples (n=62).

| Prey type | Amt. prey[1] | Proportion Prey | Prey counted in fecal samples | Proportion prey in fecal samples | 95% CI | $(w)^2$ | Bonferroni 95% CL | Standardized selection index $B^3$ |
|---|---|---|---|---|---|---|---|---|
| **Soil samples N=487** | | | | | | | | |
| Larval Lepidoptera | 366 | 0.26 | 188 | 0.63 | 0.55-0.70 | 2.42* | 2.00-2.83 | 0.45 |
| Gastropoda | 301 | 0.21 | 0 | 0.0 | 0-0 | 0 | 0 | 0 |
| Coleoptera | 225 | 0.16 | 76 | 0.25 | 0.18-0.32 | 1.59* | 1.08-2.05 | 0.29 |
| Amphipoda | 150 | 0.11 | 34 | 0.11 | 0.06-0.16 | 1.07 | 0.54-1.59 | 0.20 |
| Other | 136 | 0.10 | 0 | 0.0 | 0.0 | 0 | 0.0 | 0 |
| Isopods | 134 | 0.10 | 0 | 0.0 | 0.0 | 0 | 0.0 | 0 |
| Arachida | 67 | 0.05 | 1 | 0.003 | 0-0.01 | 0.07 | 0-0.26 | 0.01 |
| **Standing Veg. N=367** | | | | | | | | |
| Coleoptera | 2132 | 0.40 | 76 | 0.77 | 0.66 | 1.91* | 1.62-2.19* | 0.56 |
| Arachnida | 1158 | 0.22 | 1 | 0.01 | 0-0.04 | 0.05 | 0-0.17 | 0.01 |
| Adult Lepidoptera | 880 | 0.17 | 13 | 0.13 | 0.04-0.22 | 0.79 | 0.26-1.32 | 0.23 |
| TZ Diptera[4] | 721 | 0.14 | 9 | 0.09 | 0.02-0.01 | 0.67 | 0.12-1.22 | 0.20 |
| Gastropoda[5] | 407 | 0.08 | 0 | 0.00 | 0-0 | 0 | 0 | 0 |

[1] Amount prey =invertebrate abundance is the pooled total of abundant taxa identified during sampling from 1998-2000.

[2] $w$= proportion of prey used by Laysan teal/proportion of prey available in the environment (estimated).

[3] B = standardized selection index. Values less than 1 divided by the number of resources indicate no preference and values above or below provide evidence of "preference and avoidance", respectively.

[4] The taxa category "Diptera" from the fecal samples was excluded from the analysis because it included mixed species, some from the wetland habitat. Taxa in fecal samples identified as terrestrial diptera were likely underestimated due to the difficulty in separating and identifying members of this order.

[5] Both live and dead gastropods were included in the total abundance; therefore live prey is likely to be overestimated.

* Indicates strong evidence of selection.
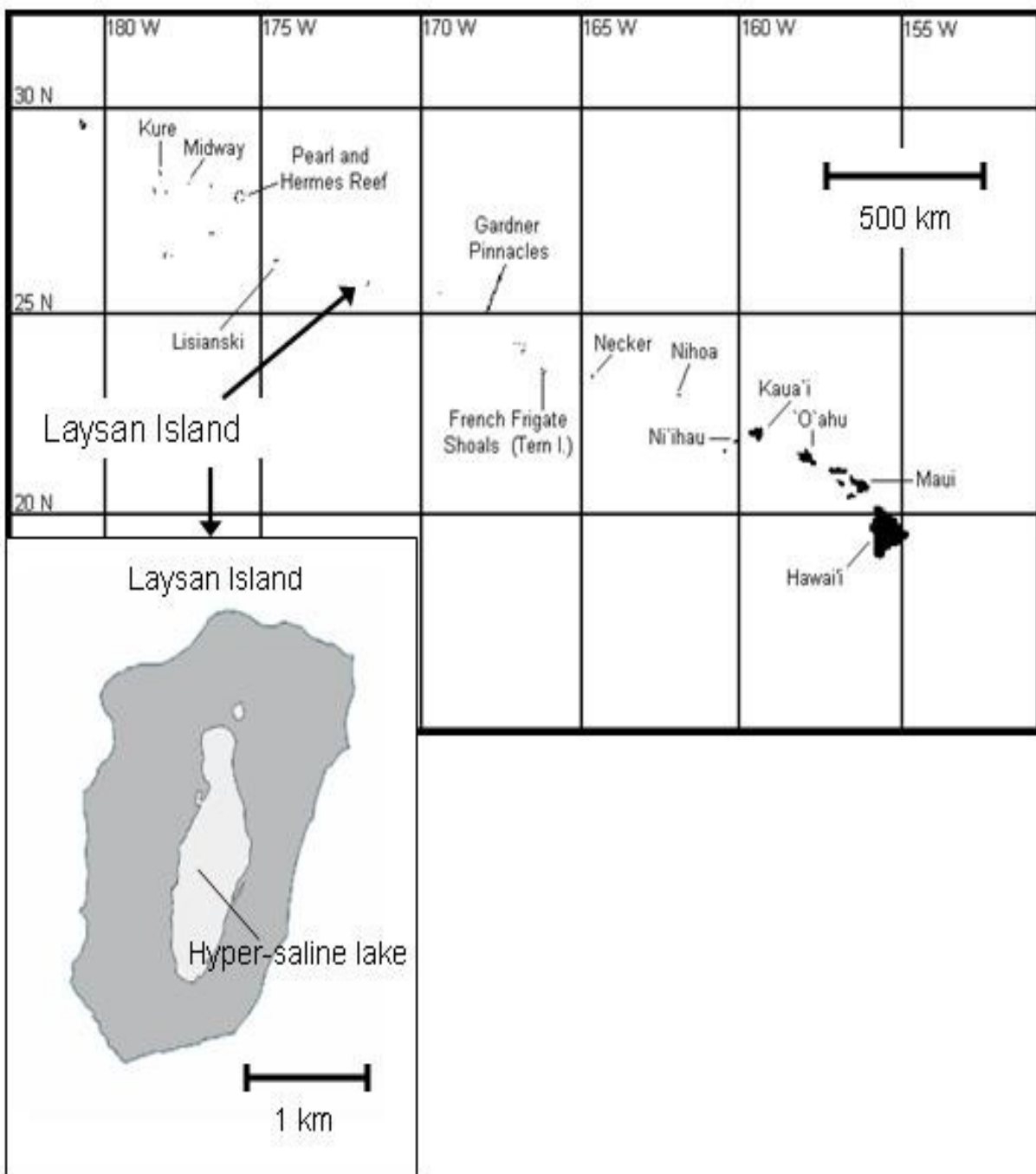
**Figure 1**. Map of NWHI with Laysan Island enlarged in inset.
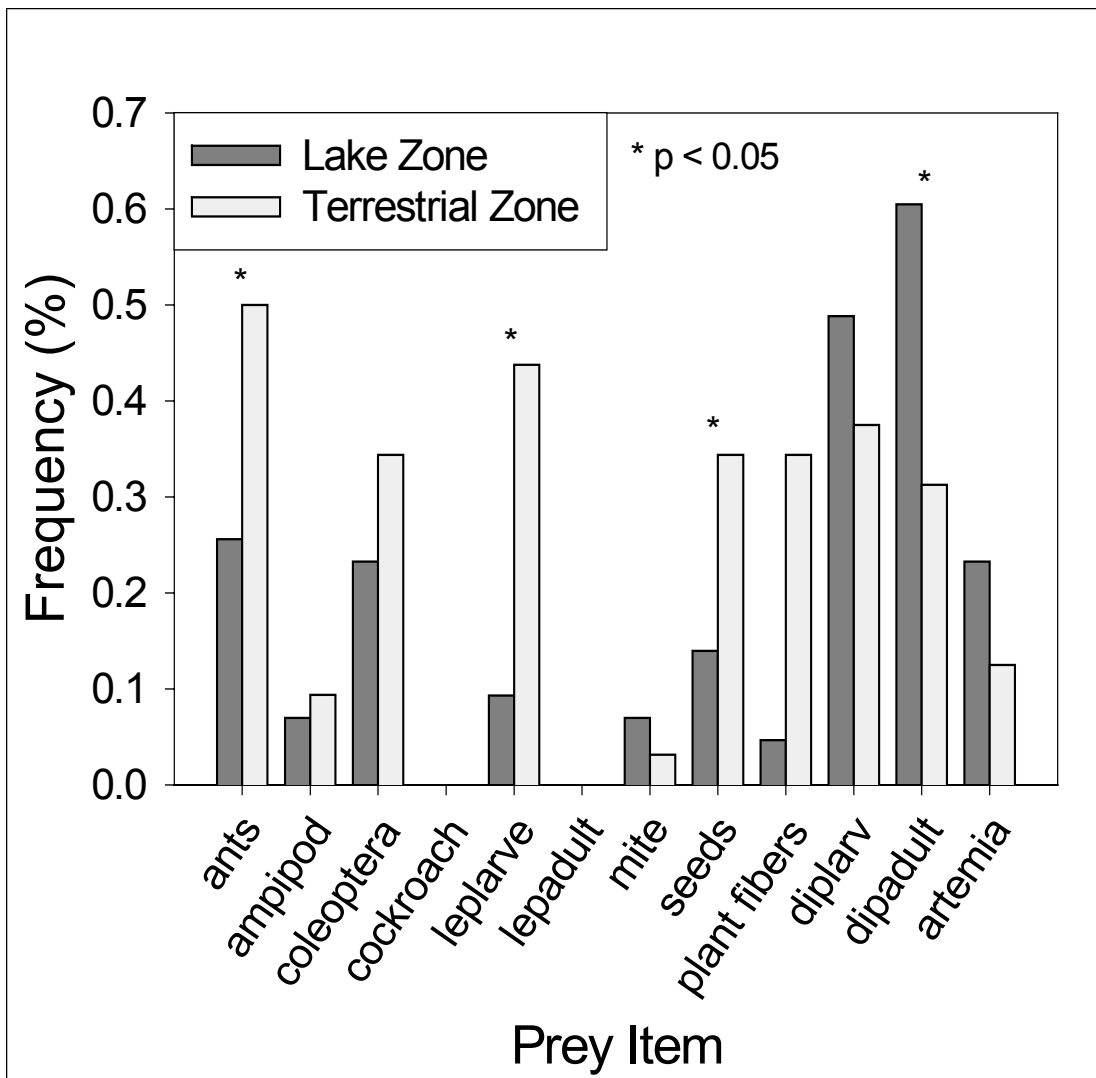
**Figure 2.** Frequency of prey items in fecal samples collected from lake zone (N=45) and terrestrial zone (N=30). Differences between zones revealed by Kruskal Wallis tests are indicated by *. Lep=Lepidoptera, dip=diptera. .
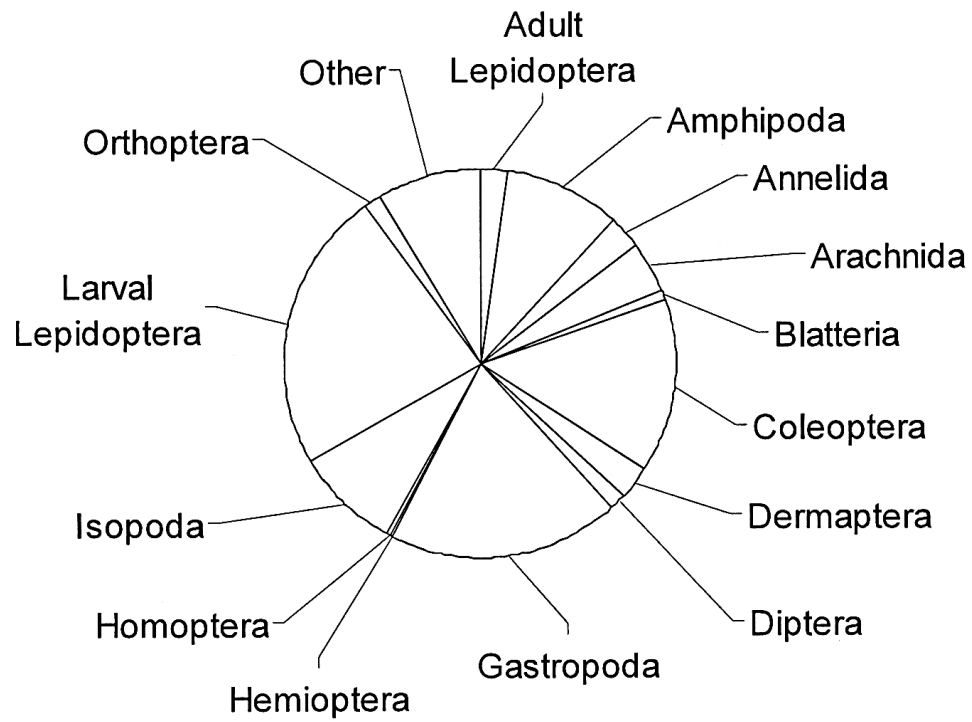
**Figure 3.** Macroinvertebrate composition of N=487 soil sample sieves collected in terrestrial habitats of Laysan Island, 1998-2000.
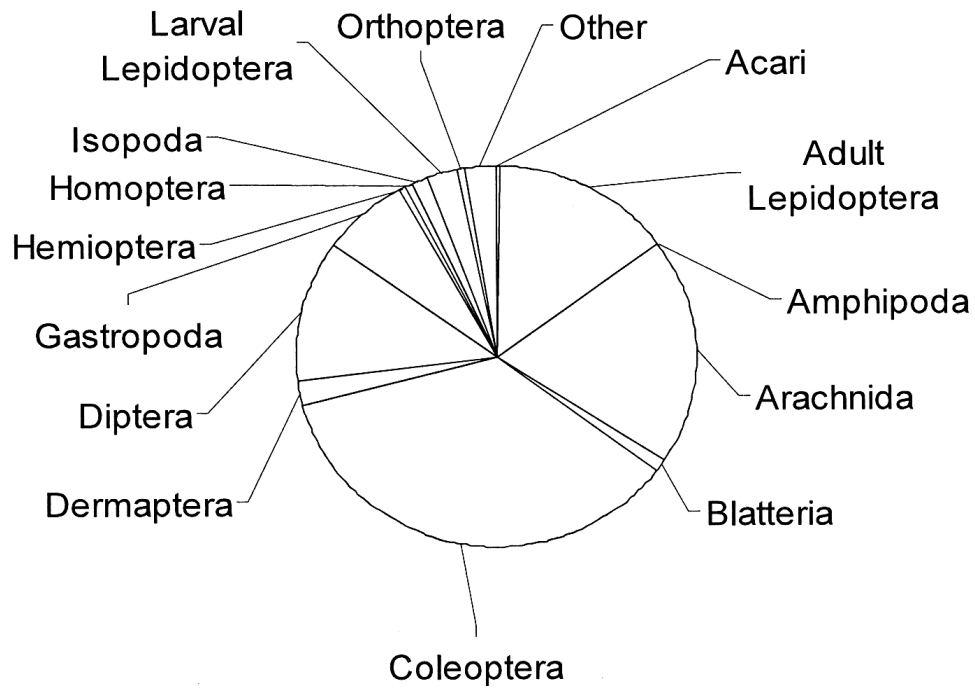
**Figure 4**. Macroinvertebrate composition of N=367 standing vegetation samples collected in terrestrial habitats of Laysan Island, 1998-2000.

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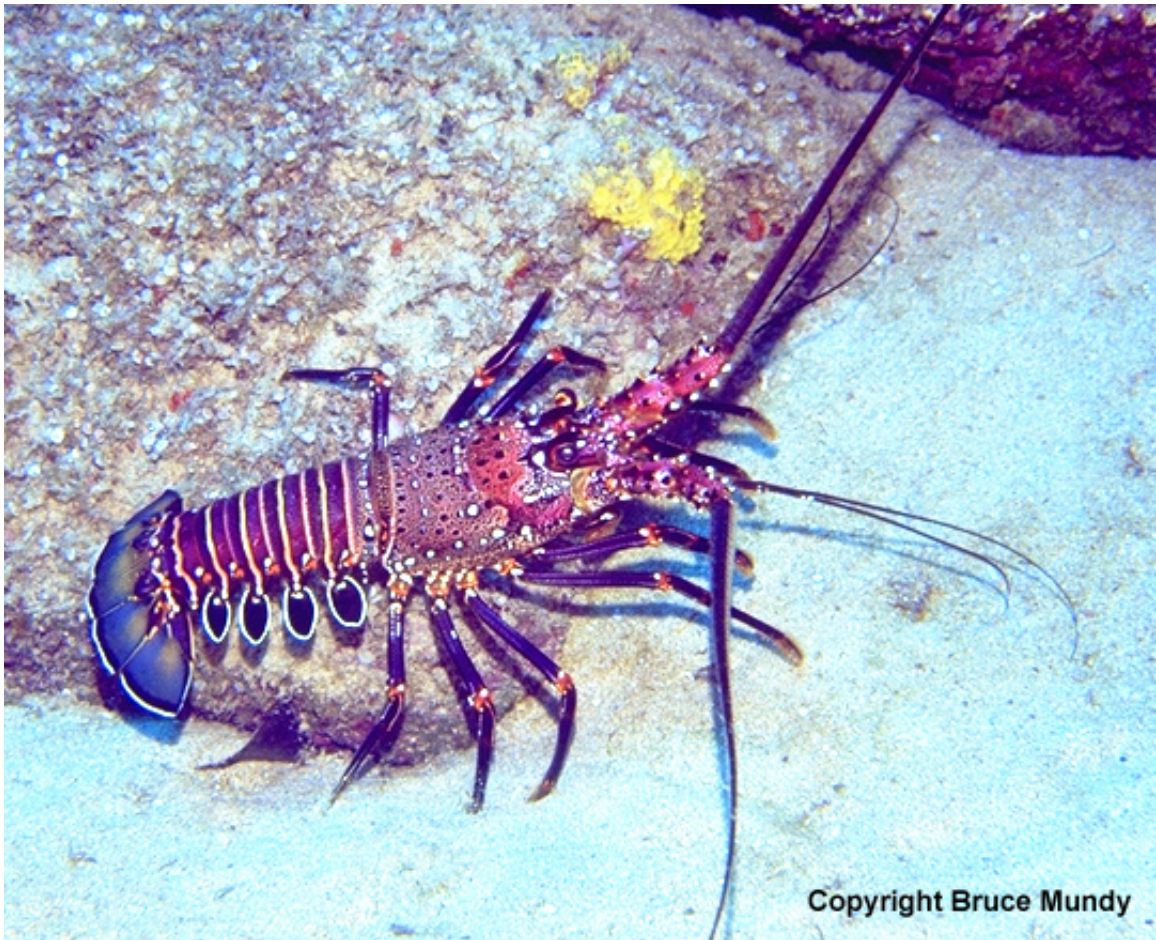
# COMPENSATORY REPRODUCTION IN NORTHWESTERN HAWAIIAN ISLANDS LOBSTERS

BY

EDWARD E. DeMARTINI[1]

## ABSTRACT

Several related life-history attributes (size-specific fecundity, egg size, and body size at sexual maturity) were examined for Hawaiian spiny (*Panulirus marginatus*) and slipper (*Scyllarides squammosus*) lobsters sampled during the 1990s through 2001. Slippers were studied at Maro Reef, and spinys primarily at Necker Island bank. Size-specific fecundities of spinys were estimated at both reefs in 1991 and compared with respective estimates using lobsters collected a decade prior in 1979-81. Fecundities increased 16% on average (per female) between the two periods at Necker, where most commercial extraction had occurred, but did not change at Maro. An extended comparison was made using spinys collected from Necker in 1999; this documented a further 18% increase in fecundity and confirmed the prior suggestion that egg size is not a temporally labile trait in this species, at least at this bank. The cumulative one-third increase in observed fecundity was concurrent with a fivefold decrease in density based on lobster catch per trap-haul for the commercial fishery and research surveys. A companion study estimated size-specific fecundity and egg size for slippers at Maro. Other research demonstrated a decline in median body size at sexual maturity for spinys at Necker around the peak of the commercial trap fishery in the early 1990s that persisted at least through the 2001 research survey. Yet another study described a morphological metric (allometric pleopod-to-tail width relation) suitable for identifying body size at functional maturity of both species, which provides a previously lacking capability for slippers. These papers, whether directly or indirectly describing compensatory responses important to lobster management, together provide the reproductive parameter estimates that are necessary, but in themselves not sufficient, for the spatially structured assessments of lobster stocks in the Northwestern Hawaiian Islands (NWHI) that have recently been initiated.

## INTRODUCTION

A NWHI lobster trap fishery developed in the late 1970s; by 1983 the fishery was well developed, generating annual catches of about 100,000-600,000 lobsters during the period from 1983-92 (DeMartini et al., 2003). Starting in 1998, the fishery, which prior to this had targeted the endemic Hawaiian spiny lobster almost exclusively, additionally

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targeted a species of non-endemic slipper lobster because of its increasing proportion in the lobster catch and declines in catch rates of spiny lobster. The fishery was closed in 2000 because of growing uncertainty regarding the population models used to assess stocks (DeMartini et al., 2003).

Evaluation of the status of lobster resources to date has been based on delay-difference models that rely on catch and effort data, adjusted by grossly estimated or assumed values of growth, recruitment, and mortality. Quantitative estimates of vital (birth-immigration, growth, mortality-emigration) rates, required as inputs to stage- (size- or age-) structured stock assessments, are outdated or lacking. Modern assessments of lobster stocks must incorporate density-dependent growth and reproduction; compensatory somatic growth, for example, has been described for many lobster stocks (Pollock, 1995a,b). The present depressed status of NWHI lobster stocks calls for a broad biological underpinning of management decisions and for a species-specific, spatially structured approach to future assessments of lobster stocks in the NWHI.

My objectives are to briefly review recent research on the reproductive life history of spiny and slipper lobsters in the NWHI, with emphasis on possible compensatory reproduction. I also note the types of information that are still lacking and needed before - spatially structured stock assessments can be made, and offer some suggestions for future research.

## REPRODUCTIVE BIOLOGY OF NWHI  LOBSTERS

The first study of NWHI lobster reproductive biology, conducted subsequent to the 2nd NWHI Symposium in 1984, was that of Polovina (1989) on spinys, then the major target species of the fishery. Polovina (1989) provided the first evidence suggesting a density-dependent response in life history characteristics—i.e., a 9-10% decline in body size at sexual maturity for female spinys between the pre-exploitation period in 1977 (Necker bank: 67.8 cm, Maro Reef: 74.8 cm carapace length CL) and an early peak period of the fishery in 1987 (60.8 and 68.2 cm CL, respectively; Fig. 1). Based on these specimen measurements, purportedly representative of populations at their respective reefs of collection, the observed declines in size at maturity were  interpreted either as compensatory responses to per capita increases in resource availability (e.g., food, shelter, or their interaction: see Parrish and Polovina, 1994) at reduced population densities or as behavioral responses among females of different sizes. The response was observed at both Necker bank and Maro Reef, and both areas had been harvested heavily by the fishery prior to that time (Polovina, 1989).

Lobster research in the early 1990s continued to focus on spiny lobster. DeMartini et al. (1993) presented data suggesting that, between pre-exploitation (1978-81) and peak exploitation (1991) periods, size-specific fecundity increased 16% for spiny lobster at Necker bank, where most fishing effort and the majority of catches had occurred, but not at Maro Reef, another area where fishing effort and catch was high prior to 1991(Fig. 2). If real (and there was no reason either then or now to doubt that specimens were representative), this average 16% increase in the fecundity of individual females at Necker was biologically important as well as statistically significant. Increased
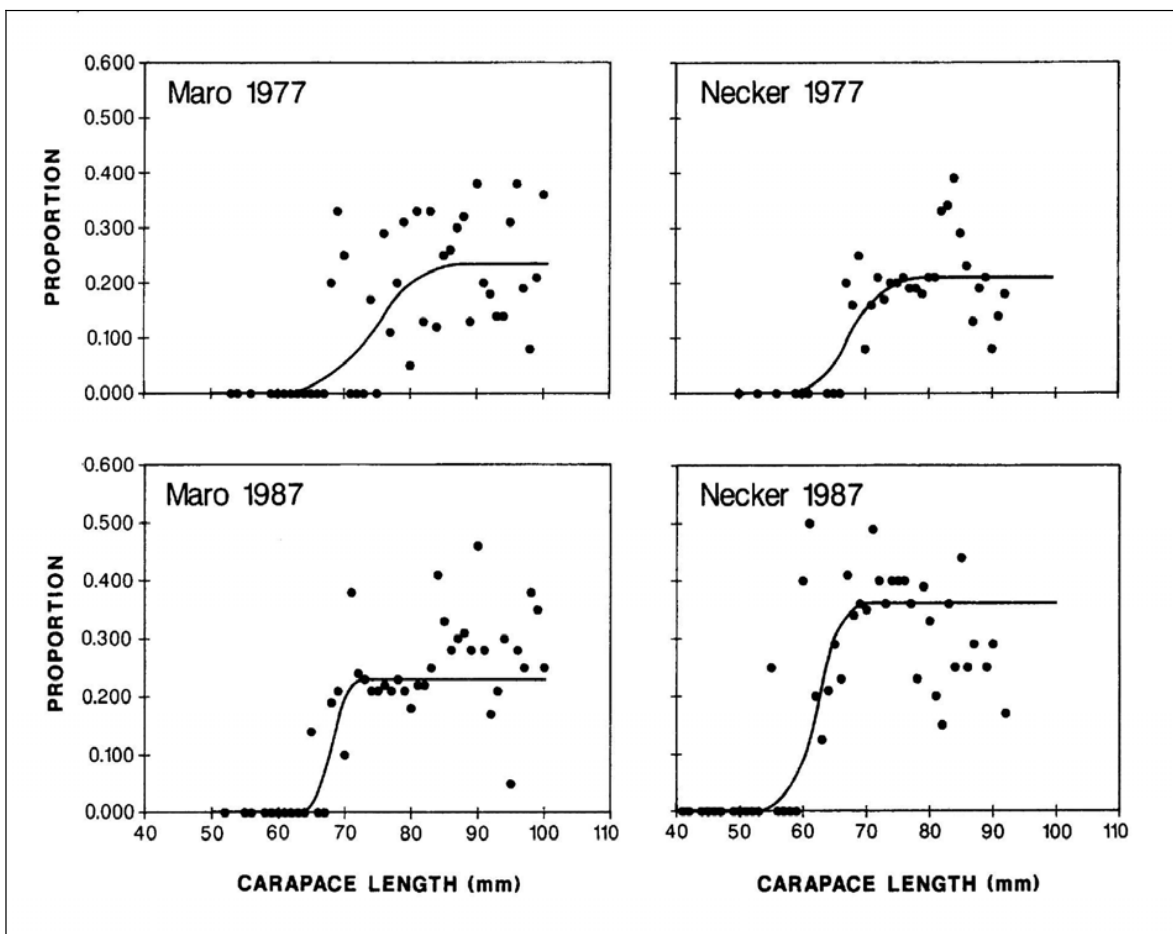
**Figure 1.** Proportion of female spiny lobsters at Necker bank and Maro Reef with eggs as a function of carapace length for 1977 and 1987. Source: Figure 4 of Polovina (1989).

egg production by individual females was interpreted as consistent with greater per capita resource availability at lower densities at Necker (DeMartini et al., 1993). It is intriguing that this compensatory increase in reproductive effort occurred despite sound evidence for a shift into a lower productivity regime between the two sampling periods (Polovina et al., 1994; Polovina 2005). A preliminary attempt to test the prediction that, at greater per capita food availability, the somatic condition of individual spiny lobster should have increased, produced equivocal results (Parrish and Martinelli-Liedtke, 1999).

Lobster density-fecundity relations were again revisited, adding size-specific fecundity data collected in 1999. An additional 18% increase in size-specific fecundity was observed, for a cumulative one-third increase between the pre-exploitation period and shortly before fishery closure (Fig. 3; DeMartini et al., 2003)—a striking augmentation of per capita egg production. As for the initial fecundity comparisons using 1991-collected specimens (DeMartini et al., 1993), the capture locations of specimens were cloaked to protect against unwitting bias when counting egg samples for fecundity comparisons, further ensuring that the observations were real. Fishery-dependent catch-
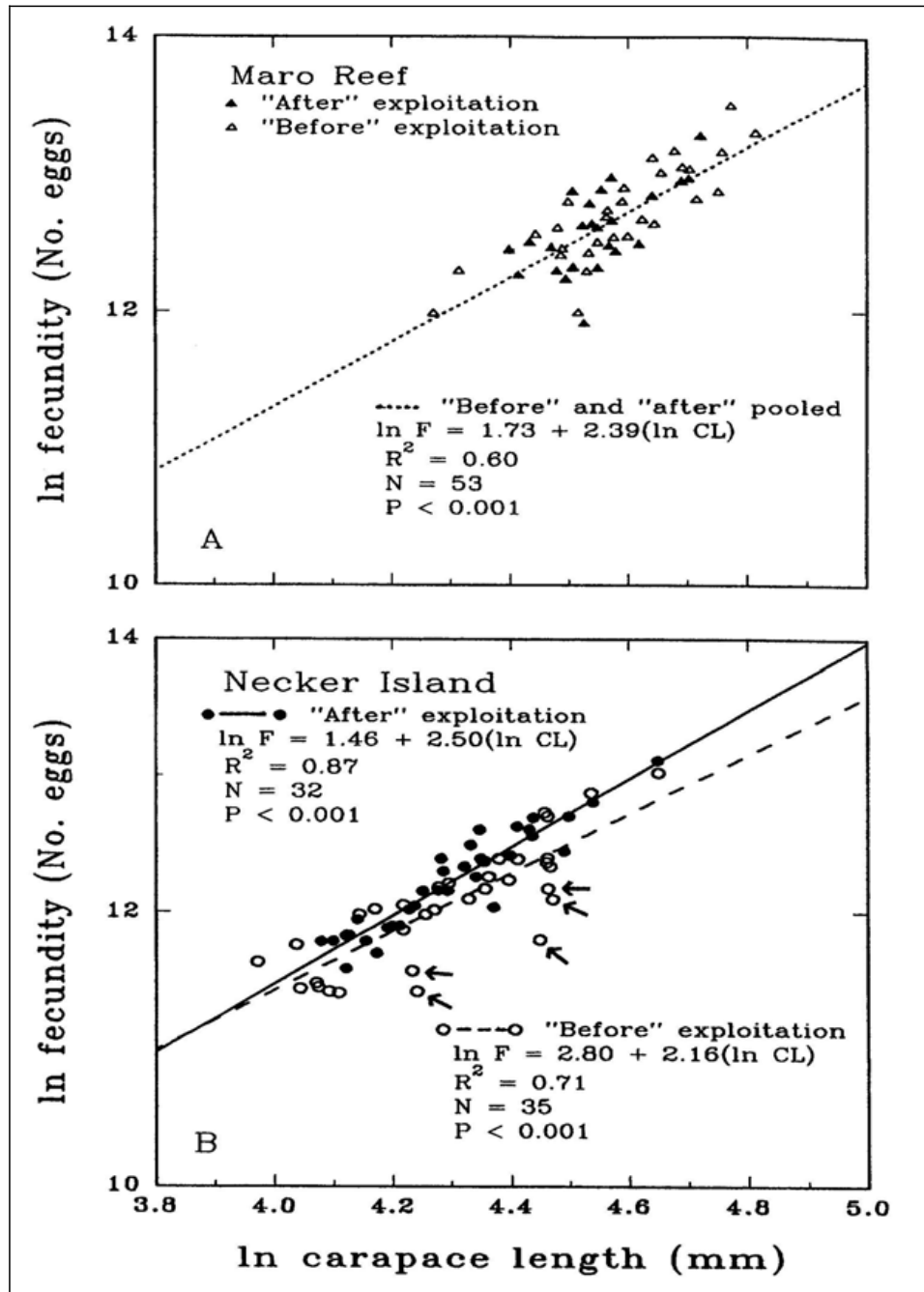
**Figure 2.** Scatterplots, least squares regressions, and regression statistics for fecundity (ln number of eggs) versus ln carapace length (in mm) for berried female spiny lobster trapped at two locations in the NWHI. Maro Reef (top): Data for the "before" (1978-81) and "after" (1991) periods are pooled for the regression analysis but plotted separately. Necker (bottom): Data for the "before" and "after" periods are plotted and analyzed separately. Arrows indicate the five most extreme "before" data that were deleted in a conservative re-analysis of the data. Source: Figure 1 of DeMartini et al. (1993).
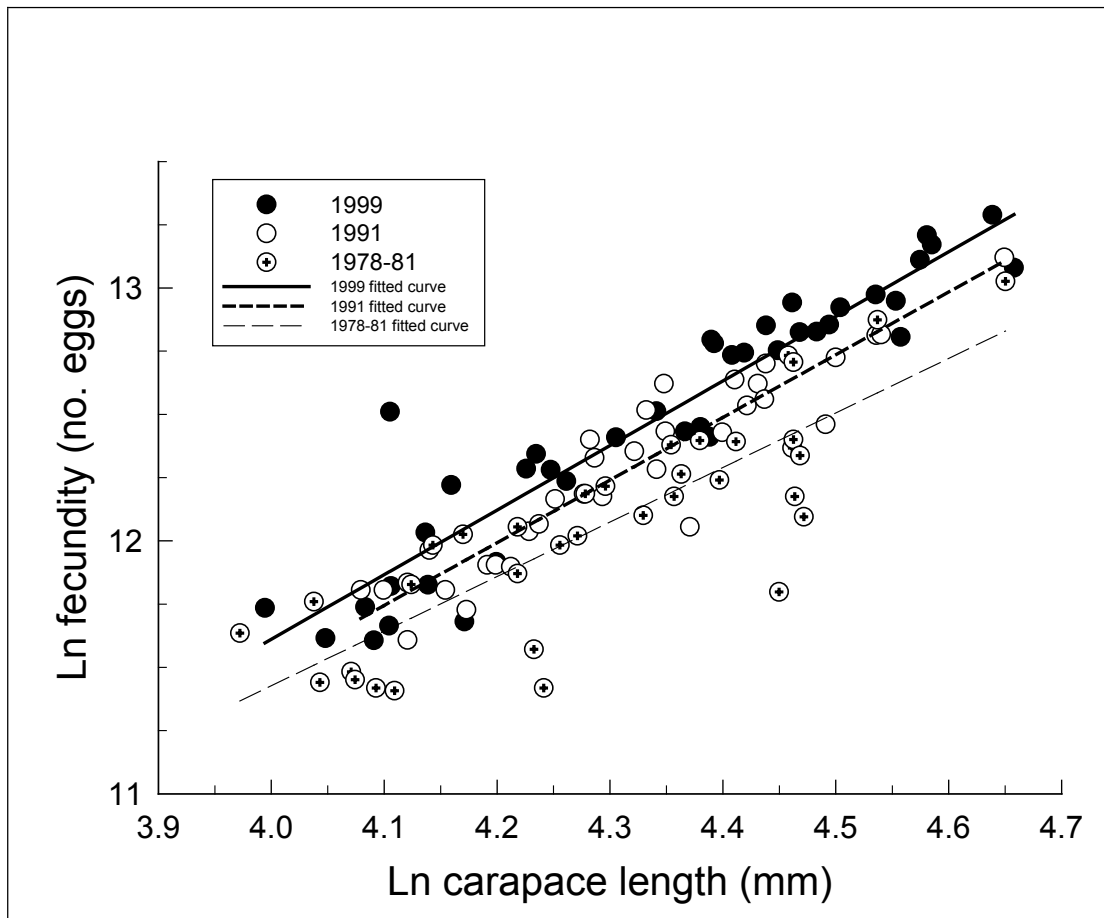
**Figure 3.** Log-linear scatterplot of fecundity (ln number of brooded eggs) versus carapace length (ln CL, in mm) for spiny lobster collected at Necker bank during three periods (1978-81, 1991, and 1999). Source: Figure 4 of DeMartini et al. (2003).
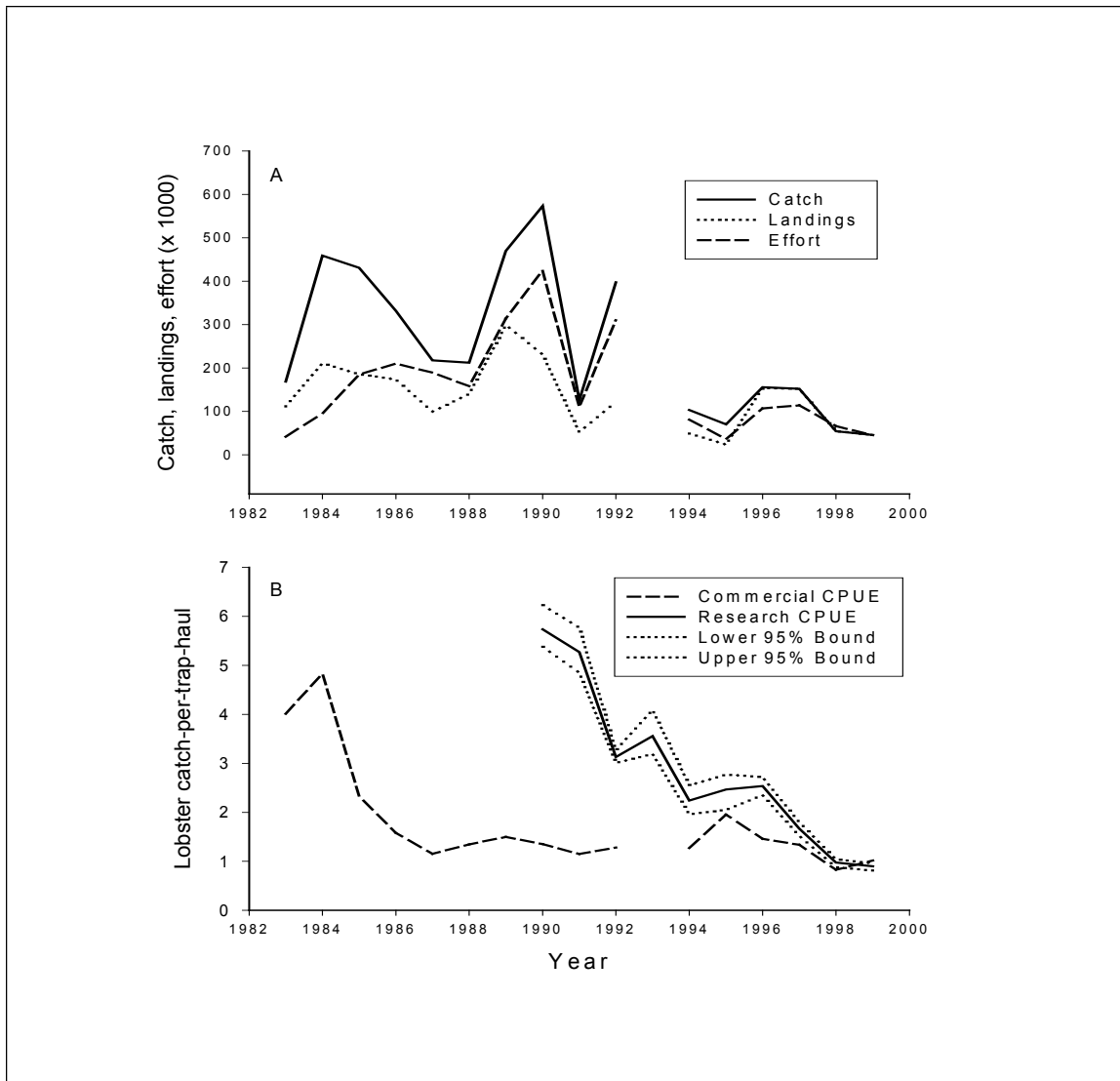
**Figure 4.** Time series plots of (A) the Necker bank, NWHI commercial trap catch and landings of Hawaiian spiny lobster (no. lobsters x 1000) and effort (no. trap-hauls x 1000); and (B) total spiny lobster catch per-trap-haul (CPUE) at Necker bank during the 1983-99 commercial fishing seasons and as assessed on 1988-99 lobster research cruises. Dashed lines framing the research curve in B represent bootstrapped 95% confidence intervals. Replotted from Figure 1 of DeMartini et al. (2003) to show year-specific estimates.

per-unit-effort (CPUE) data and analogous, fishery-independent data collected on annual lobster research surveys suggested successive half order of magnitude decreases in abundance between the early 1980s-early 1990s and between the early-to-late 1990s, respectively (Fig. 4; DeMartini et al., 2003). Detailed estimates of the mean and variance of fecundity estimates in 1999 further allowed for a characterization of size-specific egg production, which showed that, just before the fishery was closed, nearly one-half of all of spiny lobster eggs at Necker bank were being produced by small individuals of 50-57 mm tail (abdomen) width (DeMartini et al., 2003). The size (mass) of individual eggs, although independent of female body size, increased by an estimated 11% for spiny lobster at Necker bank between 1991 and 1999, a response further consistent with greater per capita food availability at lower densities (DeMartini et al., 2003).

At the same time, additional declines in size at maturity of female spinys were occurring during the early 1990s (Fig. 5A; DeMartini et al., 2002). This study also provided the first formal estimates of size at sexual maturity for female slipper lobster in the NWHI (Fig. 5B; DeMartini et al., 2002). The authors noted a problem of unacceptably poor precision when using conventional external characteristics (berried condition) to macroscopically score the maturity of individual slipper lobster. A companion paper (DeMartini and Williams, 2001) provided size-specific fecundity (Fig. 6) and egg size estimates for slipper lobster at Maro Reef, where this species was then targeted by the fishery.

In response to the precision problem encountered when evaluating maturity of slipper lobster, a morphological metric was developed for identifying body size at functional maturity; and this was verified by histology to closely approximate physiological maturity (DeMartini et al., 2005). This metric (an allometric pleopod-to-tail width relation) was derived for spinys, as well as slippers, although its primary application was for the latter (Fig. 7; DeMartini et al., 2005). Size at maturity of slipper lobster is now estimable from data collected on one or two annual research cruises—a capability previously lacking for this species. Prior to this, estimates based on berried condition (then the only gross characteristic available) were highly imprecise as well as inaccurate (biased), even if data were pooled over many years (Fig. 5B; DeMartini et al., 2005).

## DATA NEEDS, MANAGEMENT IMPLICATIONS, AND FUTURE RESEARCH

Current estimates of size-specific, annual egg production for lobster individuals and populations are limited by lack of information on the spawning frequency of individual females and how this might vary among females of different sizes (DeMartini et al., 2003). Long-term characterizations of size-specific spawning seasonality are necessary for both spinys and slippers. Much, perhaps all, of the data required on seasonal estimates of berried condition are being collected as part of an ongoing, large-scale tag-recapture program (see below).

More information is necessary on the scope of compensatory responses for which NWHI lobster are capable. Additional comparisons of size-specific fecundity and size at sexual maturity would require the sacrifice of relatively few (at most several hundred) specimens. Such an evaluation would provide much discriminatory power to test the
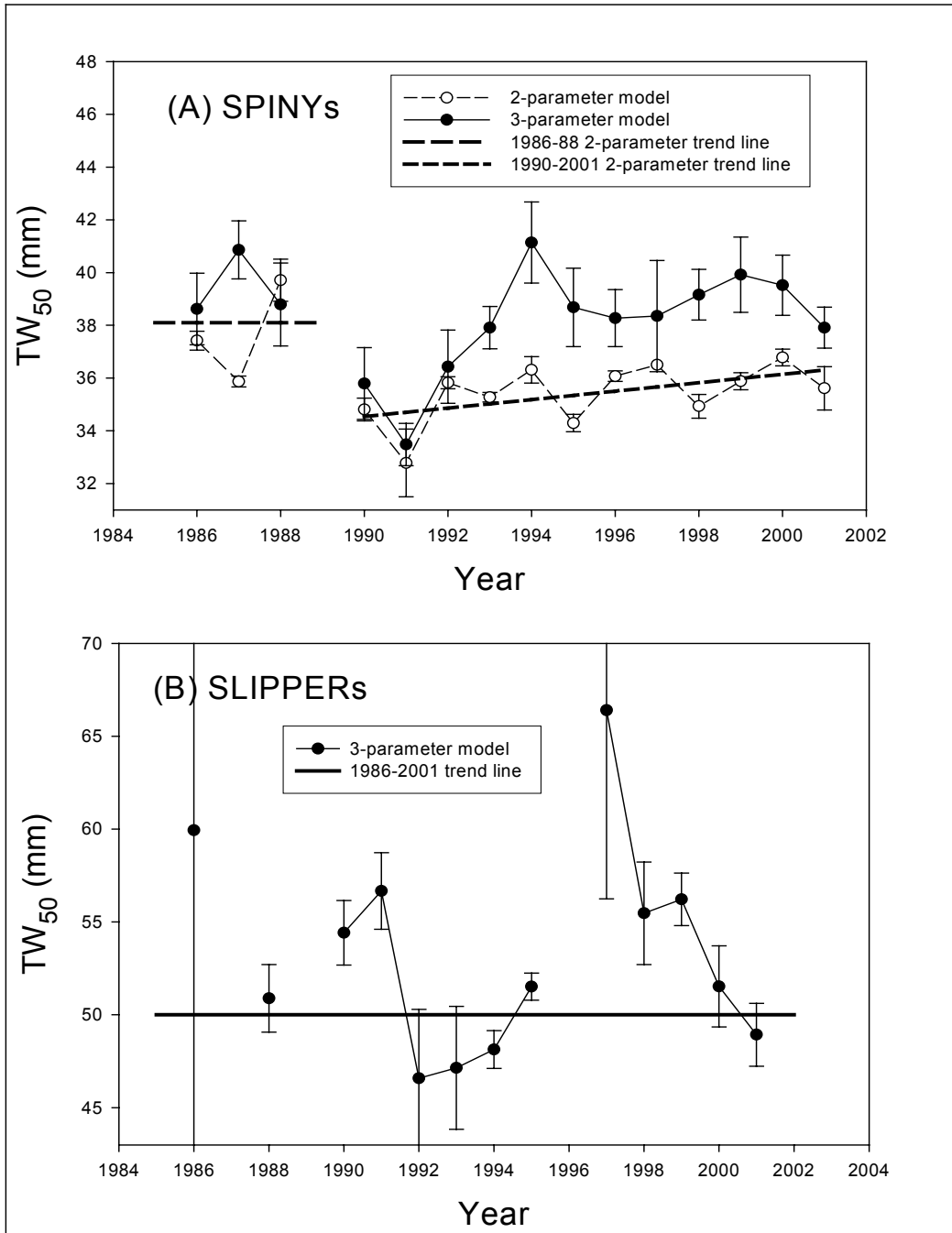
**Figure 5.** Scatterplot and fitted trend line for survey-year estimates of tail width at which 50% of all females were sexually mature ($TW_{50}$) during the period from 1986 to 2001, for (A) Hawaiian spiny lobster and (B) slipper lobster. Vertical lines indicate ±1 SE of the $TW_{50}$ estimate for the specific survey-year. Bold lines indicate means of (spiny, 1986-88; slipper, 1986-2001) or trends in (spiny, 1990-2001) $TW_{50}$ estimates. Source: Figure 2 of DeMartini et al. (2002).
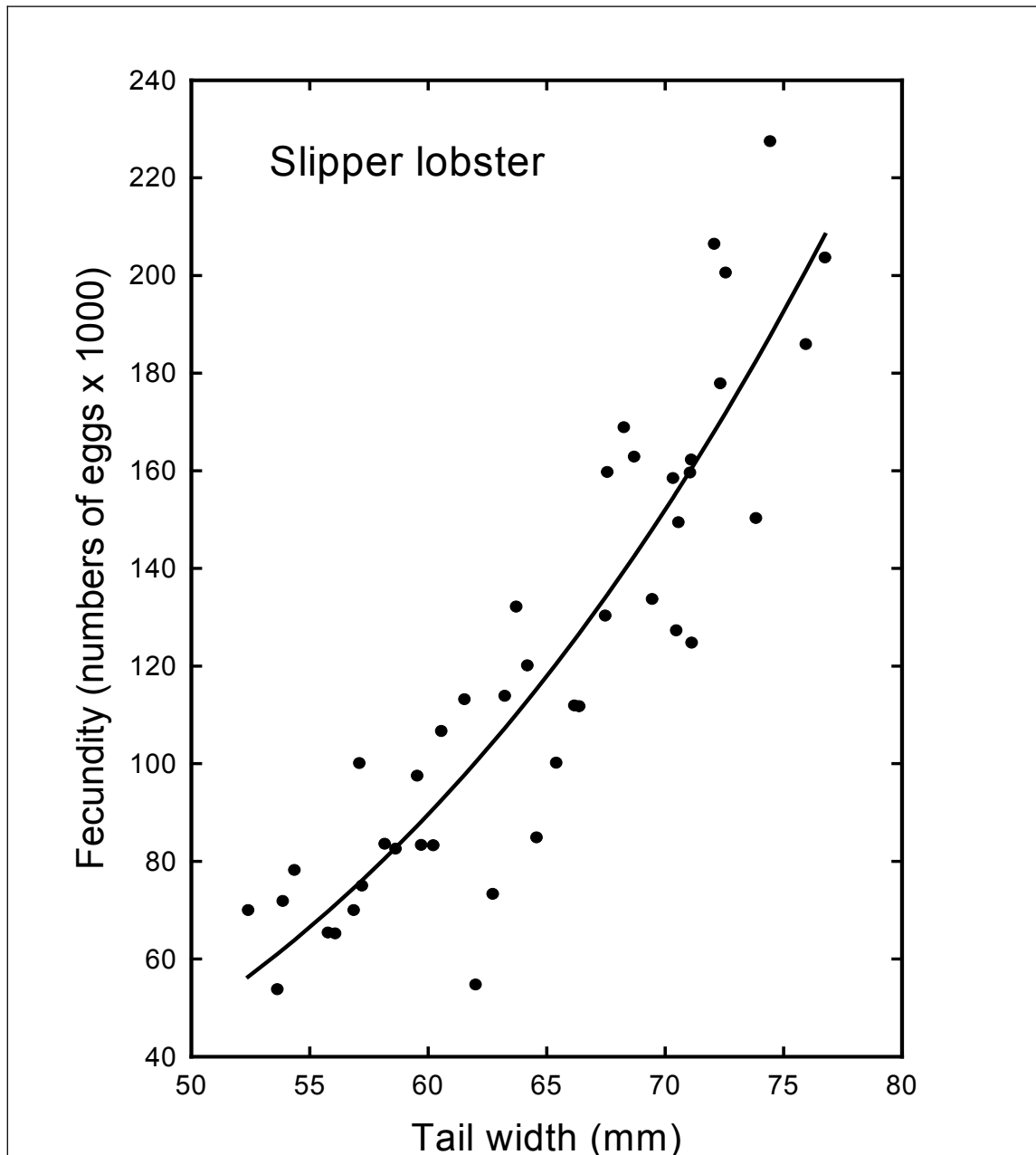
**Figure 6.** Scatterplots and best fit (nonlinear) relationship between fecundity (F, the number of eggs present on pleopods) and tail (abdomen) width (TW, mm) of slipper lobster from Maro Reef, NWHI, in June 1999. Source: Figure. 1 of DeMartini and Williams (2001).
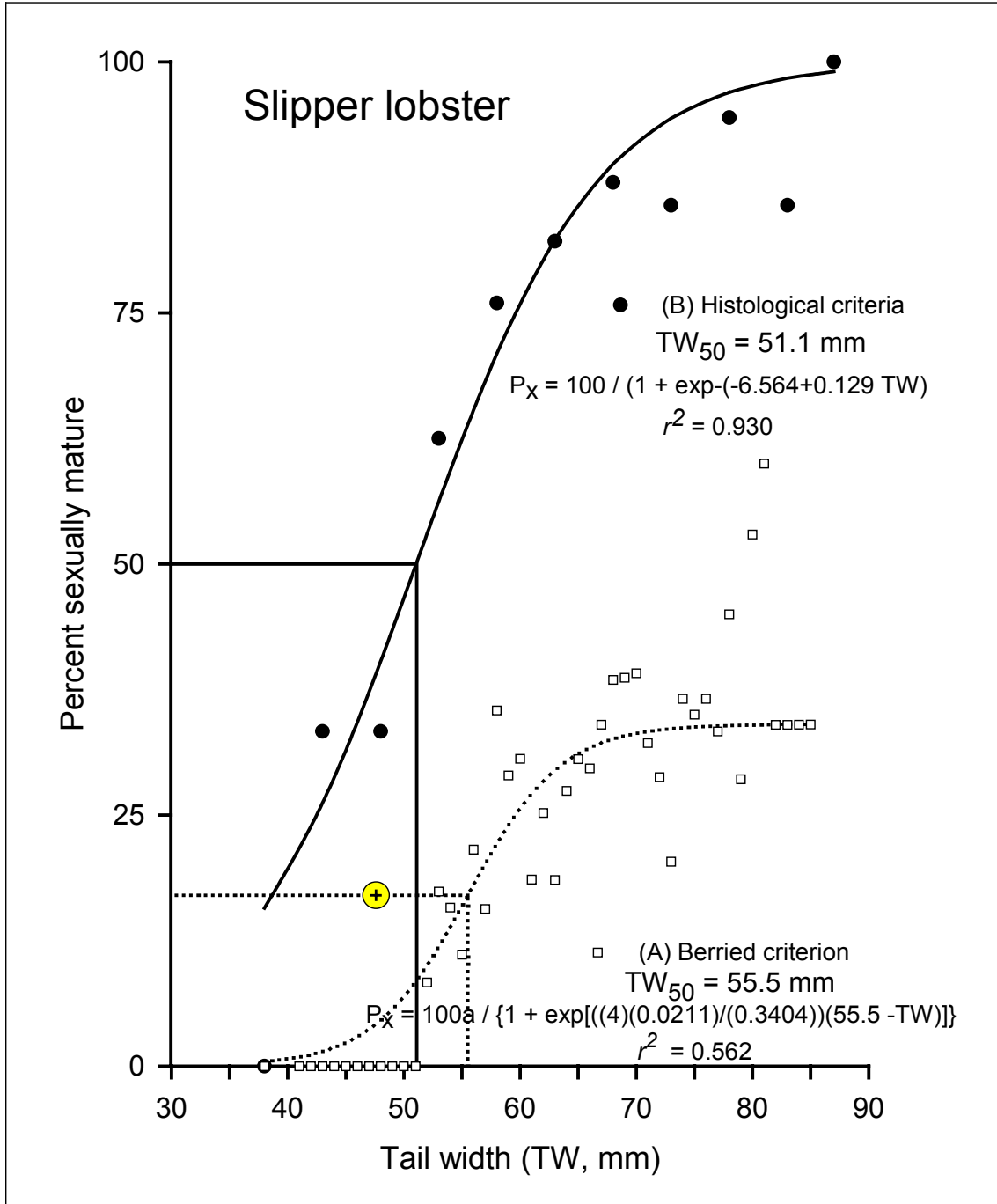
**Figure 7.** Scatterplots and fitted curves of the relations between body size (tail width, TW) and percent sexual maturity based on (A) functional maturity gauged by presence-absence of berried condition; overlaid on (B) gonadal maturation gauged by microscopic examination of ovaries, with the pleopod length-based morphometric maturation point estimate of size at functional maturity indicated by the large circle with cross-hairs, for slipper lobster. A 3-parameter logistic equation was necessary to fit curve A; a 2-parameter logistic was sufficient to fit curve B. Source: Figure 4 of DeMartini et al. (2005).

opposite predictions that size-specific fecundity should decrease while size at maturity increases at higher population densities. One necessary precaution is that a minimum one-year lag between a density rebound and collection would be required, and specimens would have to be collected before a fishery were to re-open and reduce densities.

It is further obvious that complementary research on growth, mortality, and movement is needed before a complete suite of vital rate estimates enable spatially-structured stock assessments for spiny and slipper lobsters in the NWHI. Obtaining estimates of individual growth rates is problematic because of the continuing dearth of information on age and growth of lobsters in the NWHI. A continuing, long-term tag-recapture study, utilizing both external and PIT tags is building the capacity to estimate movement patterns, rates of natural mortality and growth, and fishing mortality rates (if a fishery were to be re-opened: G. DiNardo, National Oceanic and Atmospheric Administration (NOAA) Fisheries, Pacific Islands Fisheries Science Center, Honolulu, pers. comm.).

Methods for aging lobsters are seriously complicated by the lack of an available age-marker that can be used to characterize the growth of individuals. Lobsters, like other crustaceans that molt, provide no evidence of sizes at previous ages such as growth checks recorded in a persistent hard part, so in most cases growth can be described only from observations of tag-recaptured individuals (longitudinal study). If the latter approach is taken, correction for possible growth retardation due to capture, handling, and the tag itself may need to be evaluated. Recent characterizations of the age and retrospective growth of individual crustaceans using chemical or morphological assays of the autofluorescent age-pigment lipofuscin have been encouraging (Ju et al., 2003; Sheehy et al., 1999), although some complications in distinguishing chronological from physiological age still persist.

One partial solution to the problem of aging lobsters and other crustaceans, regardless of whether the approach is longitudinal or retrospective using conventional methods, involves effectively decoupling the growth increment per molt from molting frequency for lobster spanning the range of sizes and ages in the population. One type of "biological tag" (a tissue implant that records molting history) has recently been shown capable of adequately estimating molt frequency for several spiny lobster species elsewhere (Melville-Smith et al., 1997), thereby providing the precise estimates of size-specific growth per molt needed for stage-structured stock assessment.

A preliminary series of tank experiments evaluating whether telson tissue implants could be used to characterize molting frequency were encouraging for slipper lobster but completely unsuccessful for spinys. These experiments, conducted by personnel at the Kewalo Research Facility, Honolulu Laboratory, NOAA Fisheries, in 2000, were compromised because spiny lobster experienced developmental problems during molting that were likely related to unnaturally high water temperatures or other aspects of water quality. Carefully executed experiments conducted in a temperature-controlled environment with improved water quality would be required; the precise estimates of size-specific molting frequency that might result from such an effort would have sufficient importance to warrant the expense.

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# SPATIOTEMPORAL ANALYSIS OF LOBSTER TRAP CATCHES: IMPACTS OF TRAP FISHING ON COMMUNITY STRUCTURE

BY

ROBERT B. MOFFITT[1], JAMI JOHNSON[2], and GERARD DINARDO[1]

## ABSTRACT

Commercial and research lobster trapping, targeting two species of lobster (*Panulirus marginatus* and *Scyllarides squammosus*), began in the Northwestern Hawaiian Islands in the mid 1970s. Commercial fishing effort peaked in 1986 at 1.3 million trap hauls. A corresponding site-specific, depth-stratified research-monitoring program began in 1986 with two sites, Necker Island and Maro Reef, visited annually. Two types of traps were used in the commercial and research fisheries, initially a 2x4-inch-mesh wire trap and later a 1x2-inch-mesh plastic trap. Research trapping was carried out in two depth strata: 18-37 m (shallow) and 38-91 m (deep). Both trap types are highly selective with target species comprising 90% and 73% of the research catch for wire and plastic traps, respectively. Changes in diversity and species abundance of the research trap catches from 1976-2003 are evaluated and discussed in terms of potential impacts due to fishing activity. The Simpson diversity index measured for the community, using plastic trap catch data, showed a significant increase over time for both depth strata at Necker Island, but a significant decline over time for the shallower depth stratum at Maro Reef. Significant increases in species richness for all sites as measured by Margalef's diversity index were strongly related to increases in trapping effort. Simpson's measure of evenness declined significantly over time for both depth strata at Maro Reef. Declines in abundance of both target species attributed to direct removal (harvest) occurred at Necker Island and for spiny lobster at Maro Reef. Declines in abundance for nontarget species were not observed. Increases in species abundance possibly attributed to competitive replacement were observed for slipper lobster at Maro Reef and for nontarget crab species at both study locations. Recent increases in whitetip reef shark abundance were observed for both Necker Island and Maro Reef, but they could not be explained in terms of fishery impacts.

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**INTRODUCTION**

Impacts of Fishing on the Ecosystem

High biodiversity is thought to provide stability to an ecosystem exposed to stress including anthropogenic disturbances such as pollution and fishing pressure (Jennings and Kaiser, 1998; McCann, 2000; Magurran, 2004; Kiessling, 2005), and the protection of ecosystems and their biodiversity is a goal of many resource management and conservation organizations. All fishing activities impact the ecosystem in some manner. The nature and extent of the impact varies with the fishery, gear used, and effort expended. Due to their extractive nature, fisheries, at the very least, directly reduce the available biomass of target species. Active gears such as trawls and dredges generally have larger impacts to the ecosystem than do passive gears such as traps or hooks (Alverson et al., 1994; Jennings and Kaiser, 1998). Trawls typically have low selectivity for target species with the discarded bycatch comprising as much as 90% of the total catch (Alverson et al., 1994). Active gear can also drastically alter the structure of the habitat, which can lead to changes in biodiversity, species composition, and productivity (Jennings and Kaiser, 1998). Passive gears, by contrast, generally have lower rates of bycatch and are less likely to directly alter the substratum (Alverson et al., 1994; Jennings and Kaiser, 1998). Not all fishing impacts are direct. With the complex interactions within any food web, direct alterations in abundance of any one species may indirectly cause changes in abundance of another dependent species by prey removal, prey release, competitive replacement, or scavenger enhancement.

Diversity measures are comprised of two components, richness and evenness, and various indices emphasize one or the other component differently. Fishing activities can impact either component. In some cases the impacts of fishing activities are restricted to changes in target species size and abundance, either with no observable change in community diversity or species richness (Watson et al., 1996), or with no change in richness but changes, including increases, in diversity due largely to changes in evenness (ICES, 1996; Rice, 2000; Bianchi et al., 2000). In other cases fishing activities have led to declines in richness and diversity through extirpation of target species (Randall and Heemstra, 1991; Jennings et al., 1995; Jennings and Polunin, 1997; Jennings and Kaiser, 1998; Hall, 1999; Gislason et al., 2000).

Northwestern Hawaiian Island Lobster Fishery

The Northwestern Hawaiian Islands (NWHI) is a series of islands, islets, banks, and reefs extending 1,500 nautical miles from Nihoa Island to Kure Atoll. Commercial and research lobster trapping in this region commenced concurrently in the mid-1970s. During the 1980s, the commercial trap fishery was one of Hawaii's most valuable demersal fisheries, valued at approximately $6 million per year (Polovina, 1993). This fishery is a multispecies fishery and primarily targets Hawaiian spiny lobster (*Panulirus marginatus*) and common slipper lobster (*Scyllarides squammosus*). Commercial catch peaked in 1985, and effort peaked in 1986 (Fig. 1); however, the commercial fishery was

closed in 2000 due to an increasing lack of confidence in the population models used for management decisions.  Research to advance the existing population models is presently underway (DiNardo and Wetherall, 1999).

The nature of the commercial fishery changed over time.  When the fishery started in the mid-1970s, one to two vessels targeted Hawaiian spiny lobster in the NWHI each year bringing them back to port alive for the live-lobster market.  Trips lasted about 10 days and coupled bottomfishing with lobster trapping with a total of less than 20 trips per year combined.  Trapping effort was relatively low, circa 50-100 trap hauls per vessel-day totaling less than 20,000 hauls per year.  The standard trap for the fishery was the two-chambered California lobster trap.  This was a wire trap with a 2x4-inch mesh.  In 1981, vessels began conducting trips dedicated solely to lobster trapping and processed the catch at sea, landing only frozen tails for an export market.  The fleet size increased in the early 1980s to as many as 15 vessels fishing in a single year.  Trapping effort on these trips increased markedly with trips frequently lasting 40-60 days and approximately 1,000 traps hauled per vessel-day.  By the mid-1980s, the gear of choice changed from the wire California trap to a stackable molded plastic trap with a 1x2-inch mesh.  This gear change allowed vessels to carry and fish more traps and also resulted in much higher slipper lobster catch rates.

Research trapping by NMFS used similar gear and techniques.  Efforts in the late 1970s and early 1980s were largely exploratory in nature, spread thinly throughout the Archipelago.  In 1986, a monitoring program was initiated whereby set sites around Necker Island and Maro Reef were visited annually using standardized gear and trapping techniques.

In this study, we analyzed the time series of NWHI lobster trap catches obtained on research cruises.  Changes in diversity and species abundance were evaluated and discussed with particular emphasis on changes that can be associated with fishing activities.

## METHODS

Field Operations

The National Oceanic and Atmospheric Administration (NOAA) Fisheries Honolulu Laboratory conducted fishery-independent lobster trapping operations in the NWHI since 1976.  As in the commercial fishery, two types of traps were used during this time.  Two-chambered California lobster traps with a 2x4-inch mesh were used from 1976 through 1991, and molded plastic traps with a 1x2-inch mesh were used from 1986 though the present.  Plastic trap escape vents, required to be opened for the commercial fishery, remained closed on the research cruises allowing for greater catchability of small organisms including small individuals of the target species.  During research operations, baited traps were set in the afternoon, soaked over night, and then hauled the next day.  All organisms captured were identified to the lowest taxonomic level possible, generally the species level, with total counts of each taxon recorded for each trap.  In 1986, the Honolulu Laboratory initiated a fixed-site, depth-stratified survey program.  Selected sites

were sampled annually during early summer at two banks in the NWHI, Necker Island and Maro Reef, with the exception of 1989, when no survey was conducted, and 2003, when only Maro Reef sites were visited. Two depth strata were targeted. Ten strings of 8 traps were set in 18-37 m at each survey site and two to four strings of 20 traps were set in 38-91 m at sites where these depths occurred. At sites where the deeper water was not present, all trap strings were set within the shallower range. From 1986 to 1991, wire traps were used for the strings of 8 traps, and plastic traps were used for the strings of 20 traps. Starting in 1992, plastic traps were used for all sets.

Data Analysis

Raw data from the fishery-independent trap surveys conducted from 1976 to 2003 were summarized by species, year, bank, site, depth, and gear type. Some taxa (e.g., hermit crabs, moray eels, and sharks) were poorly identified on a few earlier research cruises (e.g., to the genus or family level only), particularly on the 1991 cruise. For the purpose of analysis in this study, individuals of those poorly identified taxa within any site strata (bank/site/depth) were allotted amongst the probable species based on the relative abundances of those component species within that strata recorded for other years. Data for specific trapping sites at each bank were pooled into four bank/depth bins for diversity and abundance analysis. These bins are: Necker Island 18-37 m, Necker Island 38-91 m, Maro Reef 18-37 m, and Maro Reef 38-91 m. Data were excluded for years when less than 50 traps were fished within a particular bin.

Simpson's diversity (1/D), Simpson's measure of evenness ($E_{1/D}$), and Margalef's diversity (a measure of richness) indices were calculated as follows for the four sampling bins.

Simpson's Diversity Index (1/D):     $1/D = 1/\Sigma((n(n-1))/(N(N-1)))$
Simpson's Measure of Evenness:     $E_{1/D} = (1/D)/S$
Margalef's Diversity Index:     $D_{Mg} = (S-1)/\ln(N)$
where     n = number of individuals of a particular species
    N = total number of individuals of all species in the sample

and     S = total number of species in the sample

Catch-per-unit-effort (CPUE), in terms of number per trap-haul, was calculated for species groups based on those species that comprised at least 1.0% of the catch in plastic lobster traps (spiny lobster, slipper lobster, hermit crabs, calappid crabs, portunid crabs, moray eels, and *Heniochus diphreutes*). Two additional groups, octopus and the whitetip reef shark, *Triaenodon obesus*, were added to the analysis for reasons explained in the discussion section. In order to compare patterns of species with very different catch rates, CPUE values for each species were indexed by their median value. Indexing results in a 1.0 value representing the "normal" catch rate, 0.5 being one half normal, 6.0 being six times normal, etc. The indexed CPUE values were then graphed together to compare abundance patterns. Linear regressions were applied to each series of diversity and indexed CPUE values using Microsoft Excel data analysis tools. Significant regressions at the 95% confidence level, positive or negative, were considered as evidence of possible fishing impact.

**RESULTS AND DISCUSSION**

Selectivity

Both wire and plastic lobster traps are highly selective gears for lobsters. Wire traps set between 1976 and 1991 on research cruises caught a total of 82 species (Table 1). Of these species, the two target species of lobster accounted for 90.5% of the catch by number. Plastic trap catches from 1986 to 2003 contained 258 species (Table 2) of which 73.1% were the two target species. For both gears the two target species were most abundant in the catches. Also, two species of *Dardanus* hermit crabs were next in abundance for both gears, with the moray eel (*Gymnothorax steindachneri*) within the top ten in both cases. Ridgeback slipper lobster (*Scyllarides haanii*), a large reef fish (*Melichthys niger*), and adults of three bottomfish species (*Pristipomoides filamentosus*, *Epinephelus quernus*, and *Pseudocaranx cheilio*), rounded out the top ten for the wire traps, whereas three sand-dwelling crabs (*Calappa calappa*, *Charybdis hawaiiensis*, and *Ranina ranina*), and two small reef-fish species (*Heniochus diphreutes* and *Pervagor spilosoma*) did so for the plastic traps. It is interesting to note that, with the exception of juveniles of *Epinephelus quernus*, bottomfish species were not caught with the plastic traps. This may be a result of these species avoiding the plastic traps, similar to the behavior of avoiding structure, including plastic traps, observed by Moffitt and Parrish (1996) for juvenile *Pristipomoides filamentosus*.

The smaller mesh size of the plastic traps was likely responsible for the greater number of species captured, most of which were small species. These traps were nearly equal to wire traps in their ability to catch spiny lobster, but were much better at catching slipper lobster (Table 3). Although the number of species caught in the plastic traps was much greater than in the wire traps, this gear was still highly selective. The top nine species comprised 90% of the catch by number (Table 2). Of the remaining species, 181 of them (70% of the 258 species total) were represented in the catch by 18 or less individuals, which means they averaged only one individual caught per year of research trapping compared to an average catch of 4,114 targeted lobsters per year.

Diversity

Because the traps used in the NWHI lobster fishery were highly selective for target species, they did not provide a very accurate measurement of the diversity of the reef community on the lobster fishing grounds. However, changes in diversity indices measured by these traps over time could indicate whether fishing activity may have altered the diversity of the benthic community. Because the wire and plastic traps had different catchability characteristics for most species, the results could not be pooled across trap types, therefore only plastic trap results are included below. Unfortunately, diversity indices are strongly influenced by sample size (Kaiser, 2003; Magurran, 2004), and the sampling effort in this study fluctuated (generally increased) over time. The indices used in this study were selected for their resistance to sample size influences.

Results of the linear regressions for diversity indices and species abundances over time are listed in Table 3. The Simpson diversity indices obtained for three of the four bank-depth bins displayed significant trends (Fig. 2). At Necker Island the observed diversity increased over time for both depth bins, whereas at Maro Reef a significant decline was observed for the shallower depth bin. Richness (Margalef's diversity index) and evenness components were evaluated separately and can help explain the observed changes in the diversity indices. Margalef's index was selected as the measure of richness for this paper because of its resistance to sample size bias (Margurran, 2004). Despite this resistance, evaluation of species richness over time for the four bins showed a significant increase in all cases, largely mirroring changes in trapping effort and probably not reflecting actual increases in species richness in the benthic community. Regressions of effort and Margalef's indices were significantly positive for all bins (Table 4). The relationship between richness and trapping effort over time for Necker Island 18-37 m is shown in Figure 3. Significant decreases in species evenness were observed for both depths at Maro Reef and are likely due to the large increase in slipper lobster abundance described below. Changes in evenness for Necker Island, on the other hand, were not significant. No significant increase in the evenness component with the fishing down of abundant target species as reported by ICES (1996) and Rice (2000) was observed in our study. In light of the changes in richness and evenness components of the diversity indices, it is likely that increases measured for Necker can be attributed to increases in the richness component as a result of increased sampling effort. For Maro Reef, decreases in the evenness component may have counteracted the observed increases in the species richness indices leading to a significant decline in diversity for the 18-37-m depth bin and no significant change in the 38-91-m bin.

Relative Abundance

Only lobsters showed a significant decline in abundance (Table 4). Spiny lobster CPUE values show significant declines as expected for three of the four sampling bins. The exception was the deeper (38-91 m) bin at Maro Reef, where spiny lobsters were never particularly abundant, and the observed declines in this bin were not significant. Changes in slipper lobster abundance showed a different pattern. Necker 18-37 m slipper lobster CPUE significantly declined in a similar manner to that of spiny lobster, whereas declines in the deeper bin were not significant. Slipper lobster abundance at Maro Reef, however, showed increases, significant at the shallower depths but not the deeper (Fig. 4). This increase in abundance is likely a case of competitive replacement in response to the drastic drop in spiny lobster abundance at the shallower depths at Maro Reef; slipper lobsters were able to outpace the decline in abundance expected from commercial harvest.

All other species groups examined showed either a positive trend or no significant trend in abundance over time. The nontargeted crustaceans groups, hermit crabs, calappid crabs, and portunid crabs, all showed a positive trend in CPUE in the shallow bin at Necker. These increases may be due to competitive replacement in response to declining lobster abundance. Hermit crabs showed no significant trend in the other

sampling bins, calappid abundance increased in the 38-91-m bin at Necker, and portunids increased in both depth bins at Maro. The only reef-fish species in the top 90% of the catch, *Heniochus diphreutes*, showed no significant linear trends in abundance for any sampling bin. In spite of this, their pattern of abundance is interesting (Fig. 5). These fish were caught as recently settled juveniles, and their abundance in the catch for any year may reflect year-class recruitment strength. As can be seen, abundance fluctuated markedly between years, most notably at Maro. Changes in abundance of the whitetip reef shark are presented in Figure 6. It was included in this paper due to its interesting pattern. As can be seen, abundance was low for most of the study period, but has increased markedly in the last few years at both Necker Island and Maro Reef. This increase is not likely related to fishing activity (e.g., competitive replacement or scavenger enhancement) and remains unexplained. Finally, octopus abundance was evaluated due to its potential as an important prey item for the endangered Hawaiian monk seal (*Monachus schauinslandi*). As can be seen in Table 3, octopus are a relatively rare item in our trap catches with only 83 individuals captured in the 1986-2003 study period. Furthermore, examination of research CPUE data shows no significant decline or increase in abundance over time.

## CONCLUSION

In conclusion, lobster trapping activities have likely contributed to changes in abundance of a few species of the benthic community on the NWHI lobster fishing grounds, but do not appear to have resulted in major changes to the ecosystem. Significant declines in species abundance through direct removal (harvest) appear to be limited to the target species. Competitive replacement may have led to increases in abundance of several nontarget crab species and the targeted slipper lobster at Maro Reef. Direct damage to the benthic habitat by the traps has not been studied, but is not likely to be substantial due to the low relief, hard substrate that characterizes the fishing grounds (Parrish and Boland, 2004). Future researchers may be able to measure and document the resiliency of the lobster populations now that commercial fishing has stopped.

## ACKNOWLEDGEMENTS

Table 1. Species caught in wire traps, 1976-1991.

| Species | # | % | Cum % |
|---|---|---|---|
| *Panulirus marginatus* | 21749 | 81.6098 | 81.6098 |
| *Scyllarides squamosus* | 2368 | 8.8856 | 90.4953 |
| *Dardanus gemmatus* | 1034 | 3.8799 | 94.3752 |
| *Dardanus brachyops* | 374 | 1.4034 | 95.7786 |
| *Gymnothorax steindachneri* | 322 | 1.2083 | 96.9869 |
| *Pristipomoides filamentosus* | 80 | 0.3002 | 97.2871 |
| *Epinephelus quernus* | 70 | 0.2627 | 97.5497 |
| *Scyllarides haanii* | 68 | 0.2552 | 97.8049 |
| *Pseudocaranx dentex* | 56 | 0.2101 | 98.0150 |
| *Melichthys niger* | 52 | 0.1951 | 98.2101 |
| *Bodianus bilunulatus* | 45 | 0.1689 | 98.3790 |
| *Carcharhinus amblyrhynchos* | 37 | 0.1388 | 98.5178 |
| *Astopyga radiate* | 31 | 0.1163 | 98.6341 |
| *Carpilius convexus* | 30 | 0.1126 | 98.7467 |
| *Gymnothorax undulatus* | 29 | 0.1088 | 98.8555 |
| *Melichthys vidua* | 25 | 0.0938 | 98.9493 |
| *Ranina ranina* | 24 | 0.0901 | 99.0394 |
| *Dardanus* "purple leg" | 22 | 0.0826 | 99.1220 |
| *Dromidiopsis dormia* | 22 | 0.0826 | 99.2045 |
| *Dardanus sanguinocarpus* | 19 | 0.0713 | 99.2758 |
| *Parribacus antarcticus* | 13 | 0.0488 | 99.3246 |
| *Dardanus megistros* | 13 | 0.0488 | 99.3734 |
| *Seriola dumerili* | 13 | 0.0488 | 99.4221 |
| *Triaenodon obesus* | 11 | 0.0413 | 99.4634 |
| *Octopus cyanea* | 10 | 0.0375 | 99.5009 |
| *Octopus sp.* | 9 | 0.0338 | 99.5347 |
| *Gymnothorax flavimarginatus* | 8 | 0.0300 | 99.5647 |
| *Sargocentron spiniferum* | 8 | 0.0300 | 99.5947 |
| *Bodianus sp* | 8 | 0.0300 | 99.6248 |
| *Aluterus scriptus* | 7 | 0.0263 | 99.6510 |
| *Calappa calappa* | 5 | 0.0188 | 99.6698 |
| *Gymnothorax albimarginatus* | 5 | 0.0188 | 99.6886 |
| *Chaetodon miliaris* | 5 | 0.0188 | 99.7073 |
| *Panulirus penicillatus* | 4 | 0.0150 | 99.7223 |
| *Carpilius maculatus* | 4 | 0.0150 | 99.7373 |
| *Echinothrix calamaris* | 4 | 0.0150 | 99.7523 |
| *Gymnothorax berndti* | 3 | 0.0113 | 99.7636 |
| *Conger cinereus marginatus* | 3 | 0.0113 | 99.7749 |
| *Parupeneus porphyreus* | 3 | 0.0113 | 99.7861 |
| *Parupeneus insularis* | 3 | 0.0113 | 99.7974 |
| *Kyphosus bigibbus* | 3 | 0.0113 | 99.8086 |
| *Heniochus diphreutes* | 3 | 0.0113 | 99.8199 |
| *Luidia magnifica* | 2 | 0.0075 | 99.8274 |
| *Eucidaris metularia* | 2 | 0.0075 | 99.8349 |
| *Sargocentron xantherythrum* | 2 | 0.0075 | 99.8424 |
| *Caranx ignobilis* | 2 | 0.0075 | 99.8499 |
| *Parupeneus chrysonemus* | 2 | 0.0075 | 99.8574 |
| *Acanthurus olivaceus* | 2 | 0.0075 | 99.8649 |
| *Sufflamen fraenatus* | 2 | 0.0075 | 99.8724 |
| *Pervagor spilosoma* | 2 | 0.0075 | 99.8799 |
| *Pherecardia striata* | 1 | 0.0038 | 99.8837 |
| *Plesionika sp.* | 1 | 0.0038 | 99.8874 |
| *Parthenope contrarius* | 1 | 0.0038 | 99.8912 |
| *Lissocarcinus laevis* | 1 | 0.0038 | 99.8949 |
| *Conus quercinus* | 1 | 0.0038 | 99.8987 |
| *Conus vexillum* | 1 | 0.0038 | 99.9024 |
| *Leiaster leachi hawaiiensis* | 1 | 0.0038 | 99.9062 |
| *Linckia guildingi* | 1 | 0.0038 | 99.9099 |

Table 1. Species caught in wire traps, 1976-1991 (Con'td)

| Species | # | % | Cum % |
|---|---|---|---|
| *Linckia multifora* | 1 | 0.0038 | 99.9137 |
| *Ophiuroidea* | 1 | 0.0038 | 99.9174 |
| *Diadema paucispinum* | 1 | 0.0038 | 99.9212 |
| *Opheodesoma spectabilis* | 1 | 0.0038 | 99.9250 |
| *Bathycongrus sp.* | 1 | 0.0038 | 99.9287 |
| *Conger oligoporus* | 1 | 0.0038 | 99.9325 |
| *Myrichthys magnificus* | 1 | 0.0038 | 99.9362 |
| *Synodus capricornis* | 1 | 0.0038 | 99.9400 |
| *Physiculus rhodopinnis* | 1 | 0.0038 | 99.9437 |
| *Scorpaenodes corallinus* | 1 | 0.0038 | 99.9475 |
| *Segastapistes ballieui* | 1 | 0.0038 | 99.9512 |
| *Segastapistes galactacma* | 1 | 0.0038 | 99.9550 |
| *Priacanthus alalaua* | 1 | 0.0038 | 99.9587 |
| *Carangoides orthogrammus* | 1 | 0.0038 | 99.9625 |
| *Parupeneus pleurostigma* | 1 | 0.0038 | 99.9662 |
| *Kyphosus vaigiensis* | 1 | 0.0038 | 99.9700 |
| *Chaetodon fremblii* | 1 | 0.0038 | 99.9737 |
| *Polydactylus sexfilis* | 1 | 0.0038 | 99.9775 |
| *Thalassoma purpureum* | 1 | 0.0038 | 99.9812 |
| *Thalassoma ballieui* | 1 | 0.0038 | 99.9850 |
| *Coris ballieui* | 1 | 0.0038 | 99.9887 |
| *Acanthurus blochii* | 1 | 0.0038 | 99.9925 |
| *Thamnaconus garretti* | 1 | 0.0038 | 99.9962 |
| *Sphoeroides pachygaster* | 1 | 0.0038 | 100.0000 |

Table 2. Species caught in plastic traps, 1986-2003.

| Species | # | % | Cum % | Species | # | % | Cum % |
|---|---|---|---|---|---|---|---|
| *Panulirus marginatus* | 37277 | 36.79281 | 36.79281 | *Panulirus penicillatus* | 160 | 0.157922 | 96.7695 |
| *Scyllarides squamosus* | 36783 | 36.30522 | 73.09803 | *Parupeneus multifasciatus* | 156 | 0.153974 | 96.9235 |
| *Dardanus gemmatus* | 6297 | 6.215208 | 79.3132 | *Segastapistes ballieui* | 152 | 0.150026 | 97.0735 |
| *Dardanus brachyops* | 3816 | 3.766434 | 83.0797 | *Thalamita auauensis* | 143 | 0.141143 | 97.2147 |
| *Calappa calappa* | 2284 | 2.254333 | 85.3340 | *Parthenope contrarius* | 131 | 0.129298 | 97.3440 |
| *Charybdis hawaiensis* | 1801 | 1.777607 | 87.1116 | *Astopyga radiata* | 123 | 0.121402 | 97.4654 |
| *Gymnothorax steindachneri* | 1363 | 1.345296 | 88.4569 | *Chaetodon fremblii* | 96 | 0.094753 | 97.5601 |
| *Heniochus diphreutes* | 1134 | 1.11927 | 89.5762 | *Myrichthys magnificus* | 91 | 0.089818 | 97.6499 |
| *Ranina ranina* | 550 | 0.542856 | 90.1190 | *Gymnothorax albimarginatus* | 86 | 0.084883 | 97.7348 |
| *Pervagor spilosoma* | 468 | 0.461921 | 90.5810 | *Dendrochirus barberi* | 84 | 0.082909 | 97.8177 |
| *Sargocentron xantherythrum* | 464 | 0.457973 | 91.0389 | *Cirrhitops fasciatus* | 79 | 0.077974 | 97.8957 |
| *Carpilius convexus* | 464 | 0.457973 | 91.4969 | *Parupeneus insularis* | 79 | 0.077974 | 97.9737 |
| *Pseudanthias thompsoni* | 458 | 0.452051 | 91.9490 | *Homola dickinsoni* | 78 | 0.076987 | 98.0507 |
| *Scyllarides haanii* | 458 | 0.452051 | 92.4010 | *Carcharhinus amblyrhynchos* | 65 | 0.064156 | 98.1148 |
| *Parupeneus pleurostigma* | 443 | 0.437246 | 92.8382 | *Conger cinereus marginatus* | 63 | 0.062182 | 98.1770 |
| *Gymnothorax undulatus* | 406 | 0.400726 | 93.2390 | *Dardanus sanguinocarpus* | 63 | 0.062182 | 98.2392 |
| *Chaetodon miliaris* | 350 | 0.345454 | 93.5844 | *Luidia magnifica* | 61 | 0.060208 | 98.2994 |
| *Triaenodon obesus* | 342 | 0.337558 | 93.9220 | *Charybdis paucidentata* | 59 | 0.058234 | 98.3576 |
| *Canthigaster jactator* | 330 | 0.325714 | 94.2477 | *Nassarius hirtus* | 57 | 0.05626 | 98.4139 |
| *Aulostomus chinensis* | 325 | 0.320779 | 94.5685 | *Nassarius papillosus* | 56 | 0.055273 | 98.4691 |
| *Pherecardia striata* | 312 | 0.307947 | 94.8764 | *Octopus sp.* | 55 | 0.054286 | 98.5234 |
| *Dromidiopsis dormia* | 259 | 0.255636 | 95.1321 | *Torquigener sp.* | 52 | 0.051325 | 98.5748 |
| *Lutjanus kasmira* | 247 | 0.243792 | 95.3759 | *Gymnothorax flavimarginatus* | 48 | 0.047377 | 98.6221 |
| *Parribacus antarcticus* | 234 | 0.230961 | 95.6068 | *Dardanus megistros* | 48 | 0.047377 | 98.6695 |
| *Calappa pokipoki* | 220 | 0.217142 | 95.8240 | *Apogon maculiferus* | 45 | 0.044415 | 98.7139 |
| *Dardanus "purple leg"* | 218 | 0.215168 | 96.0391 | *Gymnothorax berndti* | 45 | 0.044415 | 98.7583 |
| *Carpilius maculates* | 212 | 0.209246 | 96.2484 | *Dairoides kusei* | 36 | 0.035532 | 98.7939 |
| *Lupocyclus quinquedentatus* | 202 | 0.199376 | 96.4477 | | | | |
| *Epinephelus quernus* | 166 | 0.163844 | 96.6116 | | | | |

Table 2. Species caught in plastic traps, 1986–2003 (Con'td)

| Species | # | % | Cum % |
|---|---|---|---|
| *Luzonichthys earlei* | 31 | 0.030597 | 98.8245 |
| *Pseudanthias bicolor* | 31 | 0.030597 | 98.8551 |
| *Enoplometopus occidentalis* | 31 | 0.030597 | 98.8857 |
| *Chromis ovalis* | 30 | 0.02961 | 98.9153 |
| *Gymnothorax melatremus* | 30 | 0.02961 | 98.9449 |
| *Fusinus sandvichensis* | 30 | 0.02961 | 98.9745 |
| *Plesionika sp.* | 30 | 0.02961 | 99.0041 |
| *Octopus cyanea* | 27 | 0.026649 | 99.0308 |
| *Priacanthus alalaua* | 26 | 0.025662 | 99.0564 |
| Nudibranchia (includes at least 1 *Halgerda terramfuensis*) | 26 | 0.025662 | 99.0821 |
| *Canthigaster rivulata* | 24 | 0.023688 | 99.1058 |
| *Thalamita picta* | 24 | 0.023688 | 99.1295 |
| *Bothus thompsoni* | 22 | 0.021714 | 99.1512 |
| *Vexillum pacificum* | 20 | 0.01974 | 99.1709 |
| *Cycloes granulose* | 20 | 0.01974 | 99.1907 |
| *Acanthurus olivaceus* | 19 | 0.018753 | 99.2094 |
| *Thalassoma ballieui* | 19 | 0.018753 | 99.2282 |
| *Gymnothorax meleagris* | 19 | 0.018753 | 99.2469 |
| *Echinothrix calamaris* | 19 | 0.018753 | 99.2657 |
| *Linckia multifora* | 19 | 0.018753 | 99.2844 |
| *Thalamita admete* | 19 | 0.018753 | 99.3032 |
| *Linckia guildingi* | 17 | 0.016779 | 99.3199 |
| *Canthigaster coronata* | 16 | 0.015792 | 99.3357 |
| *Cantherhines verecundus* | 16 | 0.015792 | 99.3515 |
| *Nassarius splendidulus* | 16 | 0.015792 | 99.3673 |
| *Scyllarus aurora* | 16 | 0.015792 | 99.3831 |
| *Gymnothorax eurostus* | 15 | 0.014805 | 99.3979 |
| *Coris ballieui* | 13 | 0.012831 | 99.4108 |
| *Myripristis chryseres* | 13 | 0.012831 | 99.4236 |

| Species | # | % | Cum % |
|---|---|---|---|
| Ophiuroidea | 13 | 0.012831 | 99.4364 |
| *Progeryon mus* | 13 | 0.012831 | 99.4492 |
| *Fusinus michaelrogersi* | 12 | 0.011844 | 99.4611 |
| *Nassarius gaudiosus* | 12 | 0.011844 | 99.4729 |
| *Lissocarcinus laevis* | 12 | 0.011844 | 99.4848 |
| *Plectroglyphidodon johnstonianus* | 11 | 0.010857 | 99.4956 |
| *Parupeneus chrysonemus* | 11 | 0.010857 | 99.5065 |
| *Synodus ulae* | 11 | 0.010857 | 99.5174 |
| *Mithrodia fisheri* | 11 | 0.010857 | 99.5282 |
| *Trizopagurus strigatus* | 11 | 0.010857 | 99.5391 |
| *Turbo sandwicensis* | 10 | 0.00987 | 99.5489 |
| *Justitia longimana* | 10 | 0.00987 | 99.5588 |
| *Heterocarpus ensifer* | 10 | 0.00987 | 99.5687 |
| *Sargocentron diadema* | 9 | 0.008883 | 99.5776 |
| *Eucidaris metularia* | 9 | 0.008883 | 99.5864 |
| *Odontodactylus hawaiiensis* | 9 | 0.008883 | 99.5953 |
| *Cirrhitus pinnulatus* | 8 | 0.007896 | 99.6032 |
| *Dascyllus albisella* | 8 | 0.007896 | 99.6111 |
| *Chaetodon kleinii* | 8 | 0.007896 | 99.6190 |
| *Conger oligoporus* | 8 | 0.007896 | 99.6269 |
| *Bursa luteostoma* | 8 | 0.007896 | 99.6348 |
| *Thalamita wakensis* | 8 | 0.007896 | 99.6427 |
| *Lahaina ovata* | 8 | 0.007896 | 99.6506 |
| *Aniculus maximus* | 8 | 0.007896 | 99.6585 |
| *Calotomus zonarcha* | 7 | 0.006909 | 99.6654 |
| *Priacanthus meeki* | 7 | 0.006909 | 99.6723 |
| *Gymnothorax nudivomer* | 7 | 0.006909 | 99.6792 |
| *Squalus mitsukurii* | 7 | 0.006909 | 99.6861 |
| *Huenia pacifica* | 7 | 0.006909 | 99.6930 |

Table 2. Species caught in plastic traps, 1986–2003 (Con'td)

| Species | # | % | Cum % |
|---|---|---|---|
| *Portunus sanguinolentis* | 6 | 0.005922 | 99.6990 |
| *Melichthys niger* | 5 | 0.004935 | 99.7039 |
| *Centropyge potteri* | 5 | 0.004935 | 99.7088 |
| *Seriola dumerili* | 5 | 0.004935 | 99.7138 |
| *Scorpaenodes littoralis* | 5 | 0.004935 | 99.7187 |
| *Myripristis kuntee* | 5 | 0.004935 | 99.7236 |
| *Ariosoma marginatum* | 5 | 0.004935 | 99.7286 |
| *Pentaceraster cumingi* | 5 | 0.004935 | 99.7335 |
| *Chlorodiella laevissima* | 5 | 0.004935 | 99.7384 |
| *Paromola alcocki* | 5 | 0.004935 | 99.7434 |
| *Calotomus carolinus* | 4 | 0.003948 | 99.7473 |
| *Chromis hanui* | 4 | 0.003948 | 99.7513 |
| *Chromis vanderbilti* | 4 | 0.003948 | 99.7552 |
| *Parupeneus porphyreus* | 4 | 0.003948 | 99.7592 |
| *Mulloidichthys vanicolensis* | 4 | 0.003948 | 99.7631 |
| *Mulloidichthys flavolineatus* | 4 | 0.003948 | 99.7671 |
| *Segastapistes galactacma* | 4 | 0.003948 | 99.7710 |
| *Iracundus signifier* | 4 | 0.003948 | 99.7750 |
| *Hippocampus sp.* | 4 | 0.003948 | 99.7789 |
| *Bathycongrus sp.* | 4 | 0.003948 | 99.7829 |
| *Pyrosomata* | 4 | 0.003948 | 99.7868 |
| *Leiaster leachi hawaiiensis* | 4 | 0.003948 | 99.7908 |
| Atyidae (includes at least 1 *Haminoea curta*) | 4 | 0.003948 | 99.7947 |
| *Bulla vernicosa* | 4 | 0.003948 | 99.7986 |
| *Fusinus midwayensis* | 4 | 0.003948 | 99.8026 |
| *Calcinus laurentae* | 4 | 0.003948 | 99.8065 |
| *Bothus mancus* | 3 | 0.002961 | 99.8095 |
| *Apogon kallopterus* | 3 | 0.002961 | 99.8125 |
| *Scorpaenopsis brevifrons* | 3 | 0.002961 | 99.8154 |
| *Scorpaenodes corallinus* | 3 | 0.002961 | 99.8184 |
| *Rhinopias xenops* | 3 | 0.002961 | 99.8214 |
| *Pristilepis oligolepis* | 3 | 0.002961 | 99.8243 |
| *Physiculus rhodopinnis* | 3 | 0.002961 | 99.8273 |
| *Antennarius commerson* | 3 | 0.002961 | 99.8302 |
| *Gymnothorax javanicus* | 3 | 0.002961 | 99.8332 |
| *Bohadschia paradoxa* | 3 | 0.002961 | 99.8362 |
| *Culcita novaeguineae* | 3 | 0.002961 | 99.8391 |
| *Mitrella bella* | 3 | 0.002961 | 99.8421 |
| *Pinaxia versicolor* | 3 | 0.002961 | 99.8450 |
| *Drupa grossularia* | 3 | 0.002961 | 99.8480 |
| *Bursa rhodostoma* | 3 | 0.002961 | 99.8510 |
| *Lophozozymus dodone* | 3 | 0.002961 | 99.8539 |
| *Thalamita spinifera* | 3 | 0.002961 | 99.8569 |
| *Scylla serrata* | 3 | 0.002961 | 99.8598 |
| *Portunus pubescens* | 3 | 0.002961 | 99.8628 |
| *Daldorfia rathbuni* | 3 | 0.002961 | 99.8658 |
| *Hyastenus sp.* | 3 | 0.002961 | 99.8687 |
| *Galathea spinosorostris* | 3 | 0.002961 | 99.8717 |
| *Fungia scutaria* | 3 | 0.002961 | 99.8746 |
| *Canthigaster epilampra* | 2 | 0.001974 | 99.8766 |
| *Sufflamen fraenatus* | 2 | 0.001974 | 99.8786 |
| *Bothus pantherinus* | 2 | 0.001974 | 99.8806 |
| *Thalassoma purpureum* | 2 | 0.001974 | 99.8825 |
| *Oxycheilinus bimaculatus* | 2 | 0.001974 | 99.8845 |
| *Cheilodactylus vittatus* | 2 | 0.001974 | 99.8865 |
| *Paracirrhites arcatus* | 2 | 0.001974 | 99.8885 |
| *Chaetodon multicinctus* | 2 | 0.001974 | 99.8904 |
| *Sebastapistes coniorta* | 2 | 0.001974 | 99.8924 |

Table 2. Species caught in plastic traps, 1986-2003 (Con'td)

| Species | # | % | Cum % | Species | # | % | Cum % |
|---|---|---|---|---|---|---|---|
| *Scorpaenopsis diabolus* | 2 | 0.001974 | 99.8944 | *Scarus sp.* | 1 | 0.000987 | 99.9447 |
| *Pterois sphex* | 2 | 0.001974 | 99.8964 | *Coris venusta* | 1 | 0.000987 | 99.9457 |
| *Neoniphon sammara* | 2 | 0.001974 | 99.8983 | *Bodianus sp* | 1 | 0.000987 | 99.9467 |
| *Sargocentron punctatissimum* | 2 | 0.001974 | 99.9003 | *Amblycirrhitus bimacula* | 1 | 0.000987 | 99.9477 |
| *Sargocentron spiniferum* | 2 | 0.001974 | 99.9023 | *Apolemichthys arcuatus* | 1 | 0.000987 | 99.9487 |
| *Antennarius pictus* | 2 | 0.001974 | 99.9043 | *Forcipiger flavissimus* | 1 | 0.000987 | 99.9497 |
| *Synodus falcatus* | 2 | 0.001974 | 99.9062 | *Kyphosus vaigiensis* | 1 | 0.000987 | 99.9506 |
| *Synodus amaranthus* | 2 | 0.001974 | 99.9082 | *Kyphosus bigibbus* | 1 | 0.000987 | 99.9516 |
| *Enchelycore pardalis* | 2 | 0.001974 | 99.9102 | *Mulloidichthys pfluegeri* | 1 | 0.000987 | 99.9526 |
| *Opheodesoma spectabilis* | 2 | 0.001974 | 99.9122 | *Naucrates doctor* | 1 | 0.000987 | 99.9536 |
| *Stichopus horrens* | 2 | 0.001974 | 99.9141 | *Apogon erythrinus* | 1 | 0.000987 | 99.9546 |
| *Diadema paucispinum* | 2 | 0.001974 | 99.9161 | *Dactyloptena orientalis* | 1 | 0.000987 | 99.9556 |
| *Acanthaster planci* | 2 | 0.001974 | 99.9181 | *Caracanthus typicus* | 1 | 0.000987 | 99.9566 |
| *Pleurobranchus sp.* | 2 | 0.001974 | 99.9201 | *Neoniphon aurolineatus* | 1 | 0.000987 | 99.9576 |
| *Conus pertusus* | 2 | 0.001974 | 99.9220 | *Sargocentron tiere* | 1 | 0.000987 | 99.9585 |
| *Morula granulate* | 2 | 0.001974 | 99.9240 | *Brotula multibarbata* | 1 | 0.000987 | 99.9595 |
| *Bursa rosa* | 2 | 0.001974 | 99.9260 | *Synodus capricornis* | 1 | 0.000987 | 99.9605 |
| *Strombus vomer hawaiensis* | 2 | 0.001974 | 99.9279 | *Gymnothorax ypsilon* | 1 | 0.000987 | 99.9615 |
| *Lybia edmondsoni* | 2 | 0.001974 | 99.9299 | *Scuticaria okinawae* | 1 | 0.000987 | 99.9625 |
| *Etisus splendidus* | 2 | 0.001974 | 99.9319 | *Pectinidae* | 1 | 0.000987 | 99.9635 |
| *Actaea nodulosa* | 2 | 0.001974 | 99.9339 | *Aplysia sp.* | 1 | 0.000987 | 99.9645 |
| *Carpilodes rubber* | 2 | 0.001974 | 99.9358 | *Terebra thaanumi* | 1 | 0.000987 | 99.9655 |
| *Lyreidus tridentatus* | 2 | 0.001974 | 99.9378 | *Terebra chlorata* | 1 | 0.000987 | 99.9664 |
| *Diodon holocanthus* | 1 | 0.000987 | 99.9388 | *Terebra gouldi* | 1 | 0.000987 | 99.9674 |
| *Thamnaconus garretti* | 1 | 0.000987 | 99.9398 | *Conus textile* | 1 | 0.000987 | 99.9684 |
| *Acanthurus nigrofuscus* | 1 | 0.000987 | 99.9408 | *Conus pulicarius* | 1 | 0.000987 | 99.9694 |
| *Acanthurus triostegus sandvicensis* | 1 | 0.000987 | 99.9418 | *Conus abbreviatus* | 1 | 0.000987 | 99.9704 |
| *Gobiidae* | 1 | 0.000987 | 99.9428 | *Conus striatus* | 1 | 0.000987 | 99.9714 |
| *Exallias brevis* | 1 | 0.000987 | 99.9437 | *Latirus nodatus* | 1 | 0.000987 | 99.9724 |

Table 2. Species caught in plastic traps, 1986-2003 (Con'td)

| Species | # | % | Cum % |
|---|---|---|---|
| *Prodotia iostomus* | 1 | 0.000987 | 99.9734 |
| *Murex pele* | 1 | 0.000987 | 99.9743 |
| *Bursa granularis* | 1 | 0.000987 | 99.9753 |
| *Strombus helli* | 1 | 0.000987 | 99.9763 |
| *Cerithium sp.* | 1 | 0.000987 | 99.9773 |
| *Pseudosquilla oculata* | 1 | 0.000987 | 99.9783 |
| *Pilumnus sp* | 1 | 0.000987 | 99.9793 |
| *Pilodius areolatus* | 1 | 0.000987 | 99.9803 |
| *Pilodius flavus* | 1 | 0.000987 | 99.9812 |
| *Neoliomera immigrans* | 1 | 0.000987 | 99.9822 |
| *Xanthias glabrous* | 1 | 0.000987 | 99.9832 |
| *Lophozozymus pulchellus* | 1 | 0.000987 | 99.9842 |
| *Lophozozymus intonsus* | 1 | 0.000987 | 99.9852 |
| *Percnon abbreviatum* | 1 | 0.000987 | 99.9862 |
| *Thalamita crenata* | 1 | 0.000987 | 99.9872 |
| *Thalamita coeruleipes* | 1 | 0.000987 | 99.9882 |
| *Thalamita kukenthali* | 1 | 0.000987 | 99.9891 |
| *Thalamita alcocki* | 1 | 0.000987 | 99.9901 |
| *Charybdis erythrodactyla* | 1 | 0.000987 | 99.9911 |
| *Portunus nipponensis* | 1 | 0.000987 | 99.9921 |
| *Osachila japonica* | 1 | 0.000987 | 99.9931 |
| *Lambrachaeus ramifer* | 1 | 0.000987 | 99.9941 |
| Leucosiidae | 1 | 0.000987 | 99.9951 |
| *Paromola japonica* | 1 | 0.000987 | 99.9961 |
| *Munida sp.* | 1 | 0.000987 | 99.9970 |
| *Saron marmoratus* | 1 | 0.000987 | 99.9980 |
| *Oplophorus gracilirostris* | 1 | 0.000987 | 99.9990 |
| Amphipoda | 1 | 0.000987 | 100.0000 |

Table 3. Mean catch rates of spiny and slipper lobster by gear type (number of lobsters per trap haul).

| | Mean CPUE 1986-88 | |
| --- | --- | --- |
| | Wire | Plastic |
| Spiny | 2.62 | 2.64 |
| Slipper | 0.20 | 1.19 |

Table 4. Significant changes in diversity and major species abundance through time.

| | Necker 18-37 | | | Necker 38-91 | | | Maro 18-37 | | | Maro 38-91 | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | slope | r squared | p | slope | r squared | p | slope | r squared | p | slope | r squared | p |
| **Diversity Indices** | | | | | | | | | | | | |
| **Simpson's Index 1/D** | 0.18 | 0.67 | 0.0002 | 0.34 | 0.67 | 0.0002 | -0.078 | 0.38 | 0.01 | 0.026 | 0.02 | 0.61 |
| **Simpson's Evenness E$_{1/D}$** | -0.002 | 0.18 | 0.11 | 0.0003 | 0.00 | 0.87 | -0.006 | 0.73 | 0.00002 | -0.014 | 0.62 | 0.0005 |
| **Margalef's Index** | 0.44 | 0.91 | 0.00000005 | 0.43 | 0.74 | 0.00004 | 0.164 | 0.40 | 0.008 | 0.240 | 0.60 | 0.0006 |
| **Effort vs Margalef's Index** | 0.003 | 0.74 | 0.00004 | 0.007 | 0.90 | 0.00000008 | 0.004 | 0.48 | 0.003 | 0.021 | 0.75 | 0.00003 |
| **Abundance Indices** | | | | | | | | | | | | |
| **Spiny Lobster** | -0.10 | 0.60 | 0.0004 | -0.14 | 0.61 | 0.0004 | -1.188 | 0.51 | 0.001 | -0.207 | 0.18 | 0.09 |
| **Slipper Lobster** | -0.06 | 0.37 | 0.01 | -0.07 | 0.19 | 0.09 | 0.081 | 0.78 | 0.000002 | 0.044 | 0.22 | 0.06 |
| **Hermit Crabs** | 0.06 | 0.43 | 0.006 | 0.02 | 0.03 | 0.51 | 0.022 | 0.04 | 0.44 | 0.039 | 0.03 | 0.52 |
| **Calappid Crabs** | 0.24 | 0.64 | 0.0002 | 0.14 | 0.60 | 0.0004 | 0.021 | 0.03 | 0.49 | 0.071 | 0.23 | 0.05 |
| **Portunid Crabs** | 0.08 | 0.37 | 0.01 | -0.35 | 0.09 | 0.26 | 0.064 | 0.31 | 0.02 | 0.077 | 0.35 | 0.01 |
| ***Heniochus*** | 0.04 | 0.00 | 0.84 | -0.28 | 0.08 | 0.30 | 0.937 | 0.08 | 0.26 | 0.438 | 0.07 | 0.31 |
| **Moray Eels** | -0.04 | 0.21 | 0.08 | -0.01 | 0.01 | 0.69 | -0.023 | 0.13 | 0.16 | -0.015 | 0.01 | 0.73 |
| **Whitetip Reef Shark** | 0.48 | 0.54 | 0.001 | 0.10 | 0.45 | 0.005 | 0.232 | 0.37 | 0.009 | -0.108 | 0.16 | 0.11 |
| | All Banks 10-20 | | | All Banks 21-50 | | | | | | | | |
| **Octopus** | -0.0001 | 0.08 | 0.29 | -0.0003 | 0.10 | 0.26 | | | | | | |
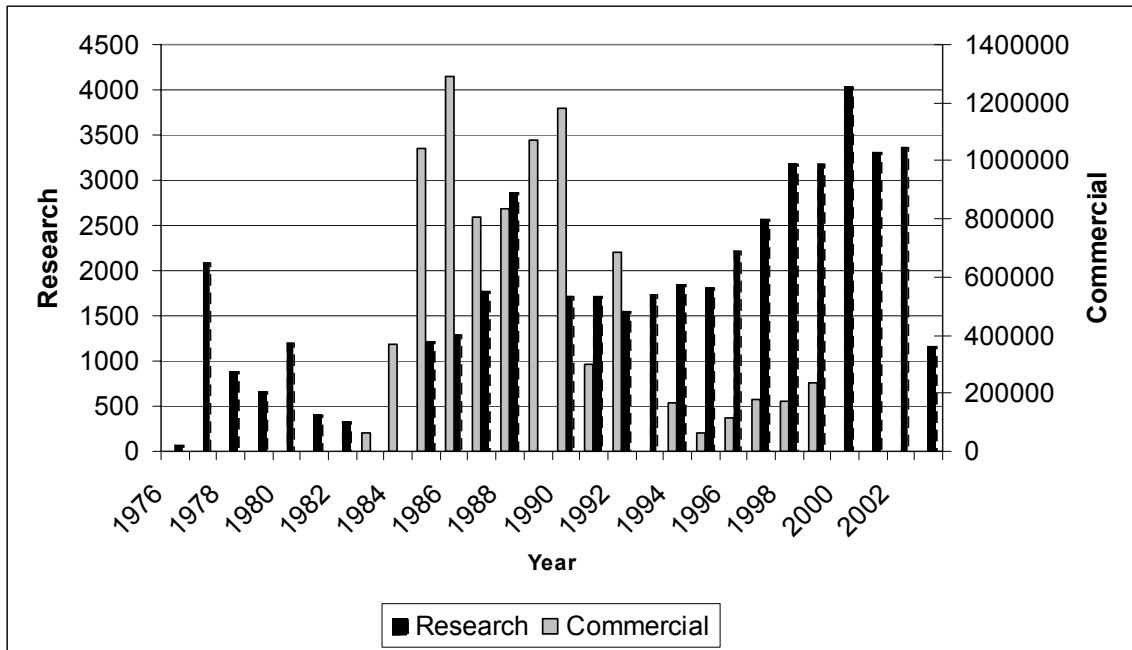
**Figure 1**. Commercial and research lobster trapping effort in trap hauls. (Commercial effort data is not available prior to the implementation of a Federal logbook system in mid-1983).
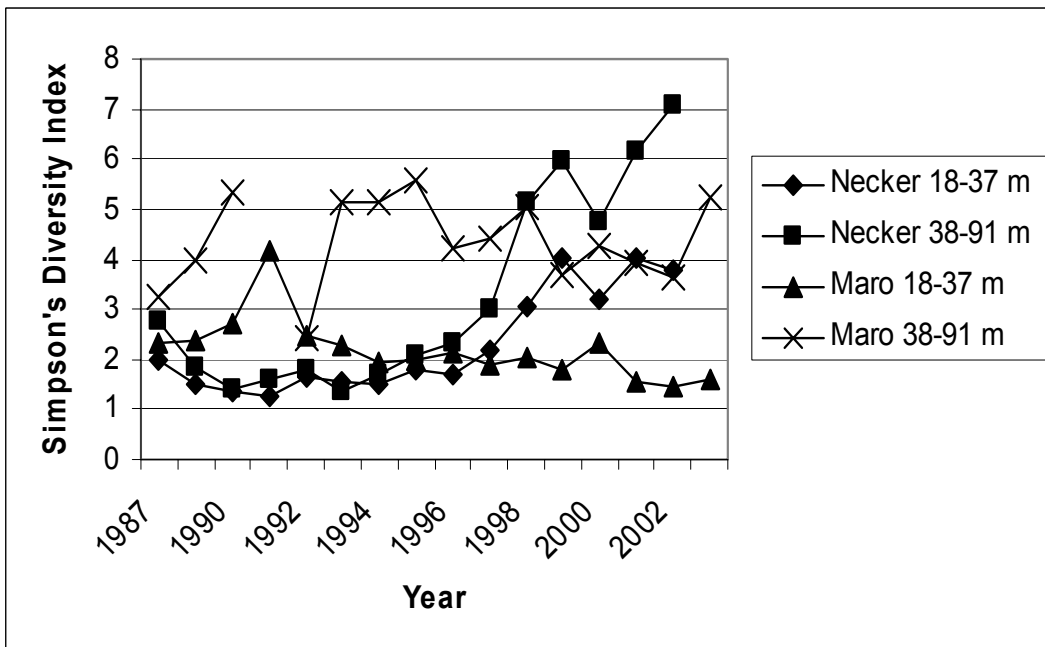


**Figure 2**. Diversity indices.
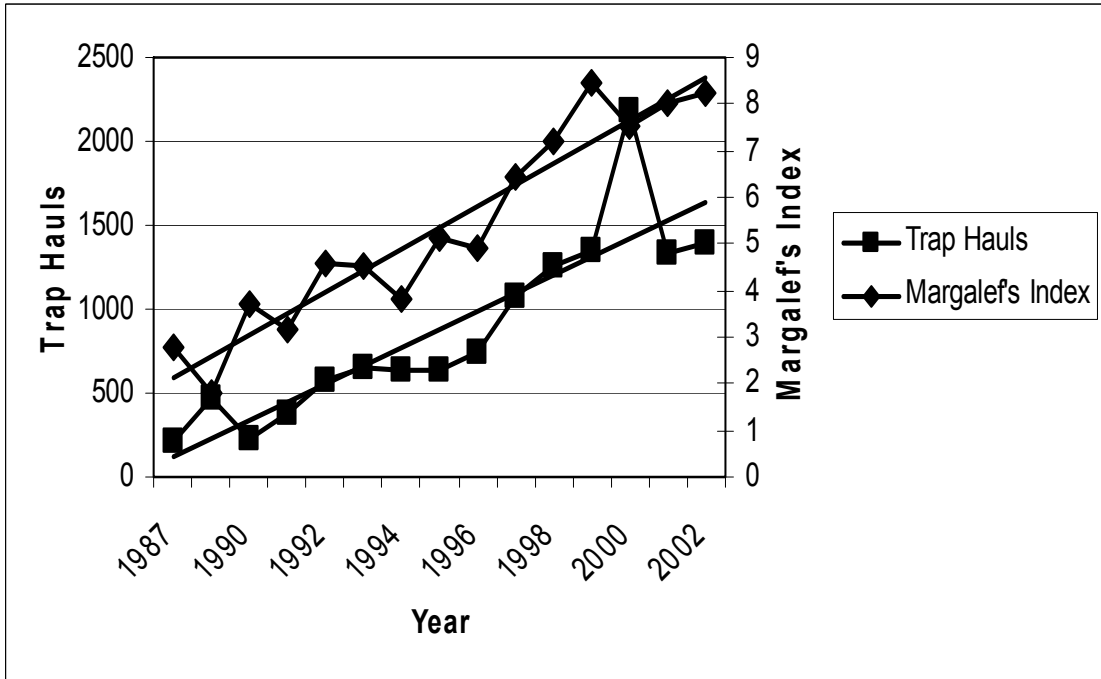
**Figure 3**. Species richness and trapping effort .
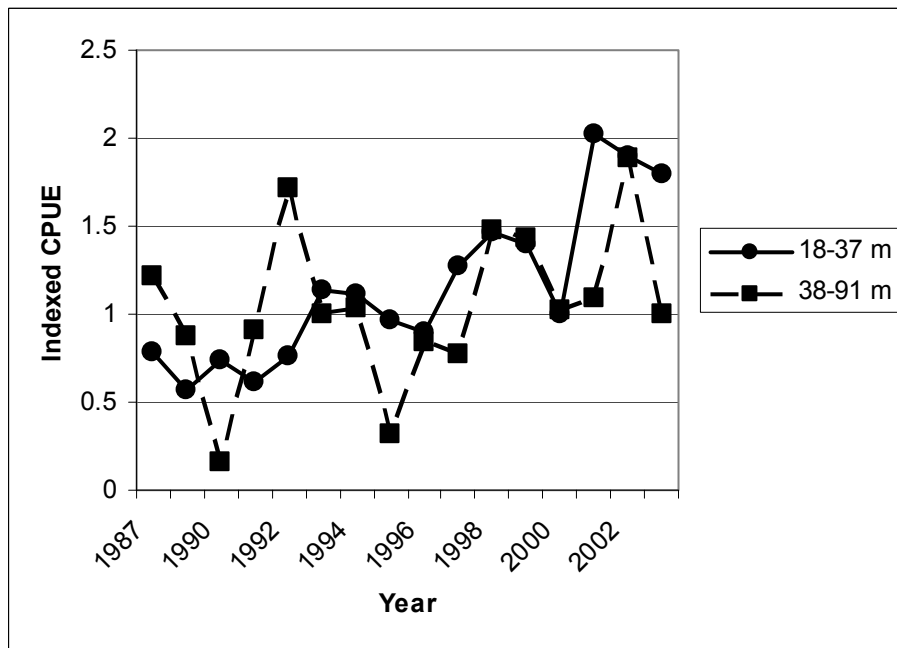


**Figure 4.** Indexed CPUE for slipper lobster at Maro Reef
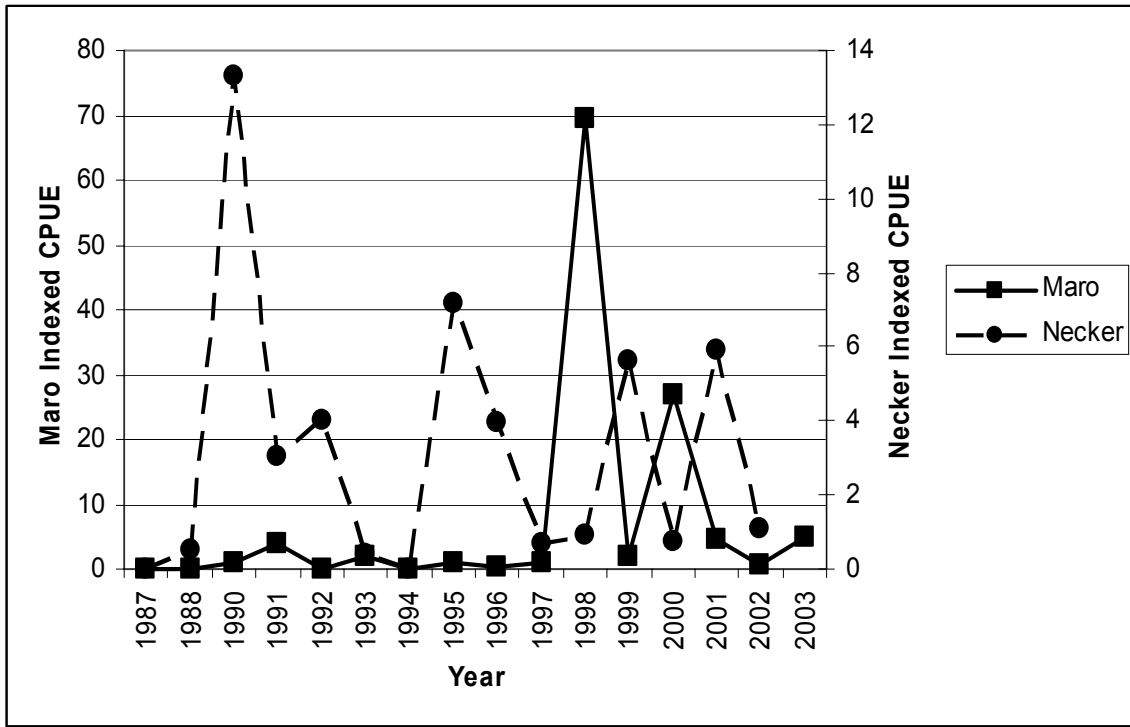
**Figure 5**. Indexed CPUE for *Heniochus dipheutes.*
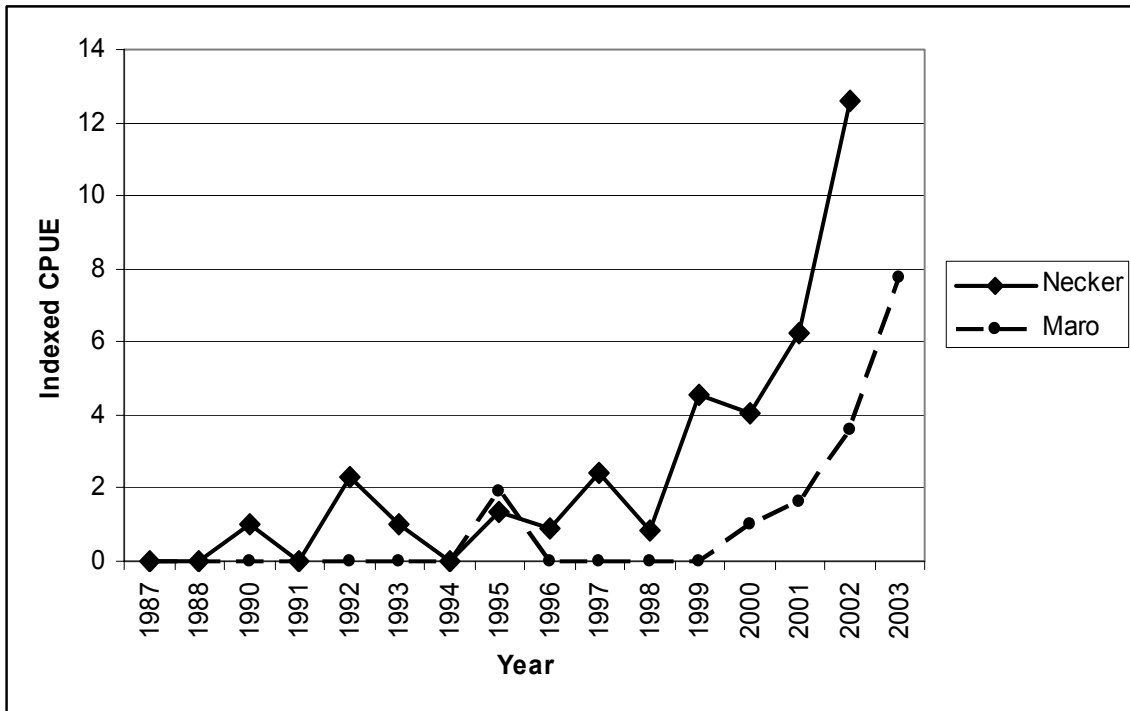


**Figure 6**. Indexed CPUE for whitetip reef shark.

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# PREDATION, ENDEMISM, AND RELATED PROCESSES STRUCTURING SHALLOW-WATER REEF FISH ASSEMBLAGES OF THE NWHI

BY

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## ABSTRACT

Data on distribution, abundance, and related patterns, reflecting key ecological processes such as predation, are herein summarized for the shallow-water (< 18-m) reef fishes of the Northwestern Hawaiian Islands (NWHI). This summary is based on the results of two complementary series of relatively recent underwater diver surveys conducted by the Pacific Islands Fisheries Science Center (PIFSC), National Marine Fisheries Service, National Oceanic and Atmospheric Administration (NOAA) and allied-agency personnel that began in the early 1990s and extended through 2004. The first series of surveys began in 1992 at French Frigate Shoals and 1993 at Midway Atoll as a re-characterization of a decade-prior baseline assessment conducted by the U.S. Fish and Wildlife Service (USFWS). These surveys were repeated yearly from 1995 through 2000. A second series of assessment surveys began in 2000 and extended through 2001 and 2002. The first series thus is an intensive long-term but spatially limited characterization that complements a spatially extensive but relatively short-term characterization for all ten emergent NWHI reefs in the second series. Among the more important patterns linked to predation and related processes that have been revealed recently are: a nearly three-fold greater standing biomass of shallow-water reef fishes in the NWHI (versus the Main Hawaiian Islands, MHI) that primarily reflects the near extirpation of apex predatory reef fishes in the MHI and a large reduction in secondary carnivores; the importance of wave-sheltered habitats as juvenile nurseries for many species and the value of atolls that provide disproportionate amounts of sheltered habitat; the heretofore unquantified extent of endemism (e.g., > 50% by numerical abundance) in NWHI reef fishes and its geographic increase with latitude-longitude to maxima at the three northernmost atolls; and the effects of apex predators on the body size distribution of prey reef fishes and the size-at-sex change in protogynous parrotfishes in the NWHI. These findings have identified the NWHI as one of the few remaining predator-dominated coral-reef ecosystems and an important part of an archipelago with a unique and strongly endemic fish fauna.

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## INTRODUCTION

Predation is a keystone process in marine ecosystems (Hixon, 1991), especially in near-pristine systems like the NWHI that have been minimally impacted by humans. Many perceived patterns within an ecosystem represent responses at various scales—from individuals to population and assemblage levels of organization—to the fundamental ecological processes that structure it, and careful examination of patterns can provide insight into these processes. In this paper we identify conspicuous patterns related to the major structuring process of predation and several other processes indirectly related to predation. In so doing, we hope to broaden appreciation by fishery and coastal resource managers, and the general public, of the unique value of the NWHI as a natural, predation-structured ecosystem and the need to conserve, protect, and learn from it.

## PATTERNS RELATED TO PREDATION

There are many phenomena whose patterns clearly attest, directly or indirectly, to predation as a major structuring agent. Among the most obvious are those related to the relative magnitude of conspicuous elements of the fish faunas (apparent to an *in situ* diver-observer) at shallow, conventional diving depths on NWHI and MHI reefs. Our observations of these patterns have provided insights into the population and community processes that structure the NWHI shallow coral-reef ecosystem.

Observations of NWHI reef fishes have been accrued over two series of partially overlapping monitoring and assessment-monitoring surveys during the periods 1992-2000 and 2000-2004. The first series of surveys was conducted by the PIFSC and began in 1992 at French Frigate Shoals (FFS) and 1993 at Midway Atoll. Its objective was to track the temporal dynamics of the shallow-reef fish forage base of monk seals (*Monachus schauinslandi*) at FFS and Midway by, first, re-characterizing and then subsequently monitoring the densities of fishes at stations established a decade prior during an initial baseline assessment conducted by the USFWS. These monitoring surveys were repeated yearly from 1995 through 2000. A second series of fish resource assessment surveys were initiated by the PIFSC, the NOAA National Ocean Survey (NOS) Coastal Oceans and National Marine Sanctuary Program, and other allied agencies (State of Hawaii Department of Land and Natural Resources, Division of Aquatic Resources) in 2000 and was extended through 2001 and 2002. These surveys were followed in 2003 and 2004 by the first two of a continuing series of annual surveys dedicated to monitoring a representative subset of stations. Briefly stated, a combination of quantitative (transect-delimited, stationary diver), and qualitative (Rapid Visual Assessment), nondestructive visual surveys have been conducted, with method linked to the type of estimate and to the size and mobility of different groups of fishes. Reef sites and survey methods are specified by DeMartini et al. (1996, 2002) and Friedlander and DeMartini (2002).

The most conspicuous of the patterns documented by these *in situ* observations is the strikingly higher numerical and biomass densities and greater average body sizes of reef fishes in the NWHI compared to the MHI, particularly for large jacks, reef

sharks, and other apex predators (Fig. 1). Also notable is the overall reduced numbers and biomass of lower trophic level fishes in the MHI, including lower-level carnivores (Fig. 2). The smaller proportion of lower-level carnivore (versus herbivore) biomass in the MHI is likely due to the greater extraction of the former by line fishing and selective gillnetting as well as spearfishing. The lesser abundance of apex predators as well as lower-trophic-level fishes in the MHI is likely the result of overexploitation by humans in the MHI (Friedlander & DeMartini, 2002). Were it not for extraction, reef-fish productivity in the MHI should be higher (not lower) than in the NWHI as a result of greater terrigenous nutrient input and more diverse juvenile nursery habitats at the vegetated, high windward islands; other anthropogenic stressors insufficiently explain the lower standing stocks of reef fishes in the MHI (Friedlander and DeMartini, 2002; Friedlander and Brown, 2004).

Perhaps the strongest evidence for the controlling influence of apex predation on the structure of fish assemblages in the NWHI is provided by data on the size, composition, and spatial distribution of prey species. In the early 1990s, differences were first noted between FFS and Midway in the relative abundance of herbivores and carnivores and in the distribution of fish numbers and biomass among barrier reef and lagoonal patch reef habitats—with large-bodied herbivores prevailing on barrier reefs and relatively small-bodied (< 10 cm Total Length) carnivores dominating numerically on patch reefs (DeMartini et al., 1996). Size structure data collected during re-assessment surveys in 2000-02 provided further insights into the effects of apex predators on their shallow-water reef fish prey: protogynous (female-to-male sex-changing) labroid fishes (primarily parrotfishes), the adult sexes of which conspicuously differ in body coloration, are preferred prey of the giant trevally (also called white ulua or ulua aukea, *Caranx ignobilis*; Sudekum et al., 1991). The giant trevally is the dominant apex predator in the NWHI, and the species is particularly abundant on exposed fringing and barrier reefs (Friedlander and DeMartini, 2002). Among the three northernmost atolls of the NWHI, body sizes at coloration (sex) change of labroids are larger (Fig. 3), and overall size distributions are skewed larger in labroids (Fig. 4) and other prey fishes (Fig. 5) at Midway Atoll (all $p < 0.001$), where giant trevally are fewer compared to Pearl and Hermes Atoll (PHR), where they are more abundant (Fig. 6; $p < 0.001$; DeMartini et al., 2005). Interestingly, prey size distributions are also skewed larger at Kure Atoll ($p < 0.001$), where giant trevally are even fewer than at Midway, likely reflecting over three decades (ending in 1992) of extraction and disturbance of trevally by resident Coast Guard tending Kure's Loran station (DeMartini et al., 2005). The differences in giant trevally abundance we observed among these three northernmost atolls in 2000-02 were similar to those observed between FFS and Midway during the 1990s (DeMartini et al., 2002), including the early 1990s when recreational extraction of trevally at Midway was not prohibited. Giant and bluefin trevally (or omilu, *Caranx melampygus*) were then more frequently encountered by divers (and hence likely more abundant) at FFS versus Midway, and the magnitude of this general difference increased (as ulua sightings decreased) subsequent to 1996 (Fig. 7). In 1996, a recreational catch-and-release fishery was begun at Midway after the Midway Naval Air Station was closed and the Atoll became a USFWS National Wildlife Refuge, and the observed further decrease in ulua sightings at Midway likely represent declines in the adult ulua populations, changes in ulua behavior (conditioned aversion to boats and divers), or both (DeMartini et al., 2002).
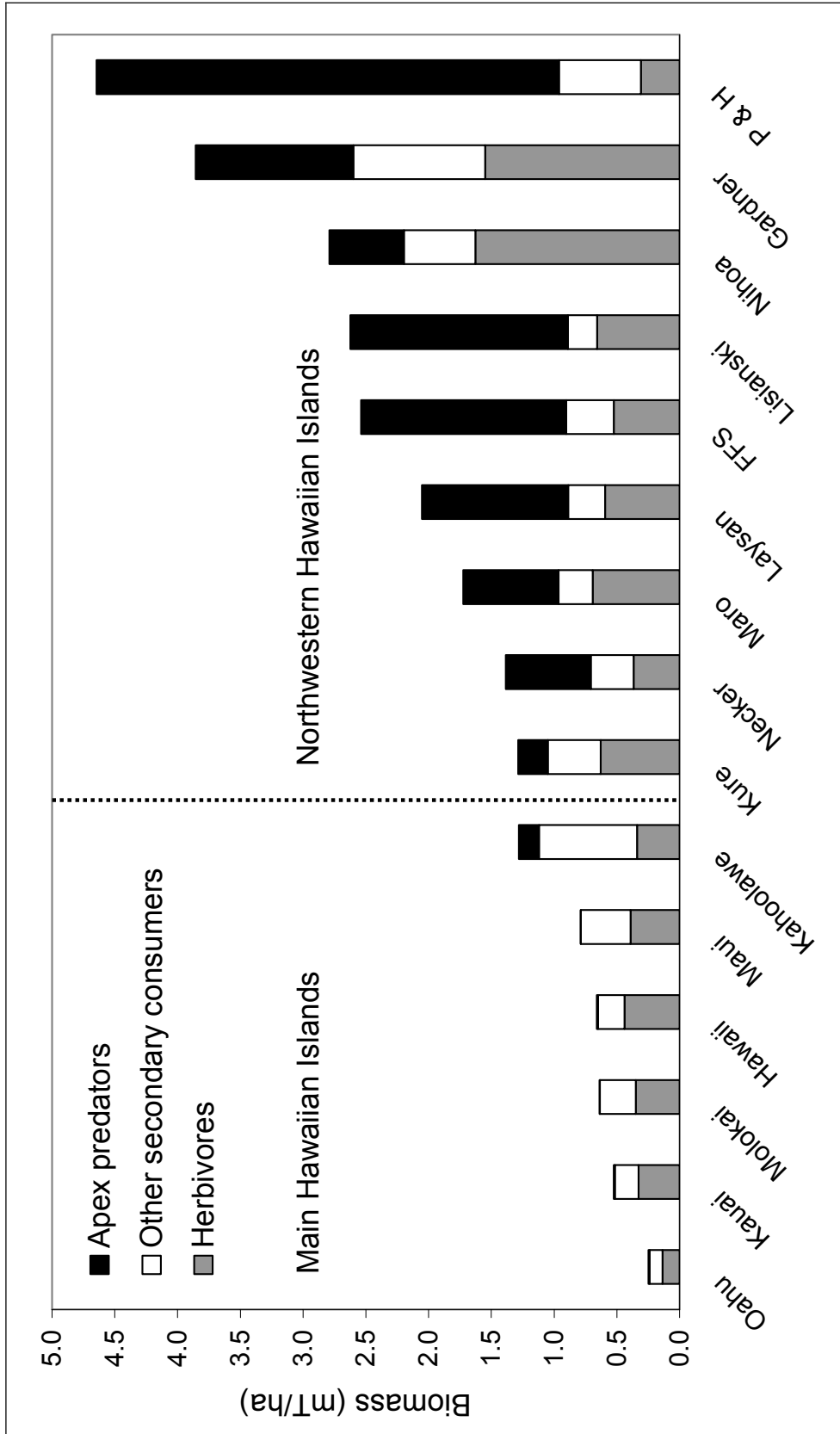
**Figure 1** Histograms of ranked (from left to right, lowest to highest) total grand mean biomass density and grand mean reef fish biomass density by trophic level for all reefs in the MHI and the NWHI, based on belt transects made during initial surveys in the year 2000. Data collected at stations in similarly wave-exposed habitats (e.g., forereefs at atolls) only were compared. Protected areas were weighted by area of coverage. FFS = French Frigate Shoals; P&H = Pearl & Hermes. Source: Adapted from Figure 3 of Friedlander and DeMartini (2002).
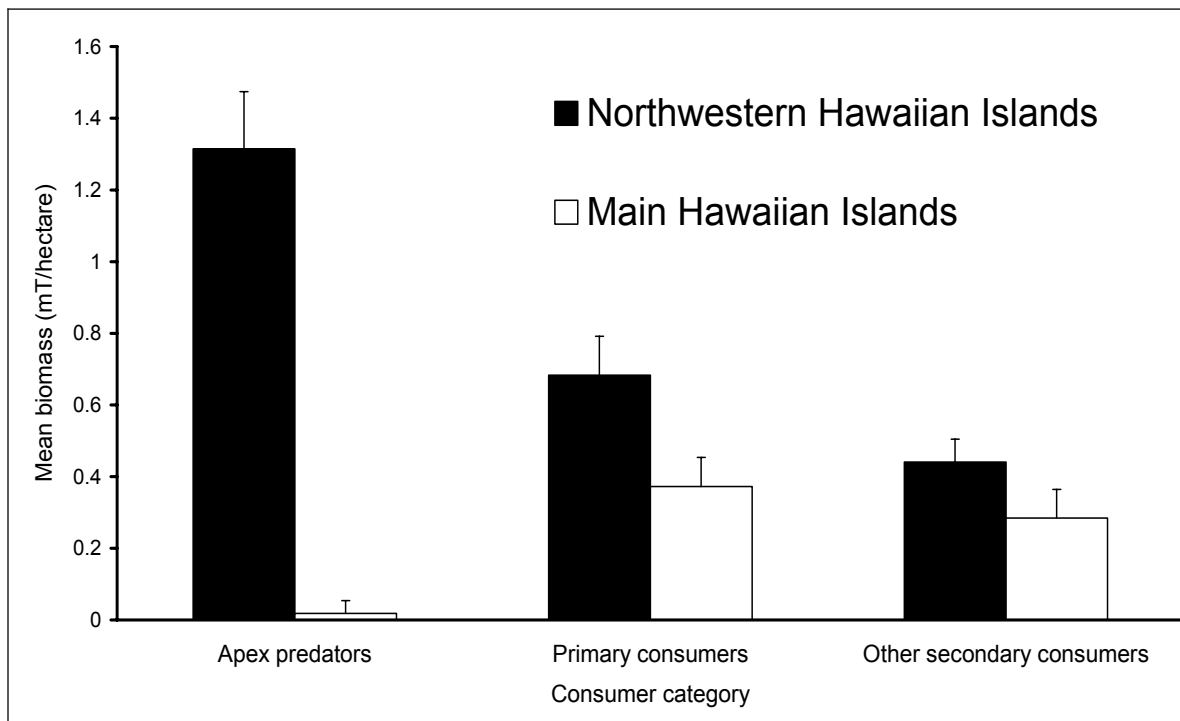
**Figure 2**. Trophic comparisons of fish assemblages in the NWHI and MHI. Source: Figure 17.5 of Sladek-Nowlis and Friedlander (2005); based on data in Table 1 of Friedlander and DeMartini (2002).
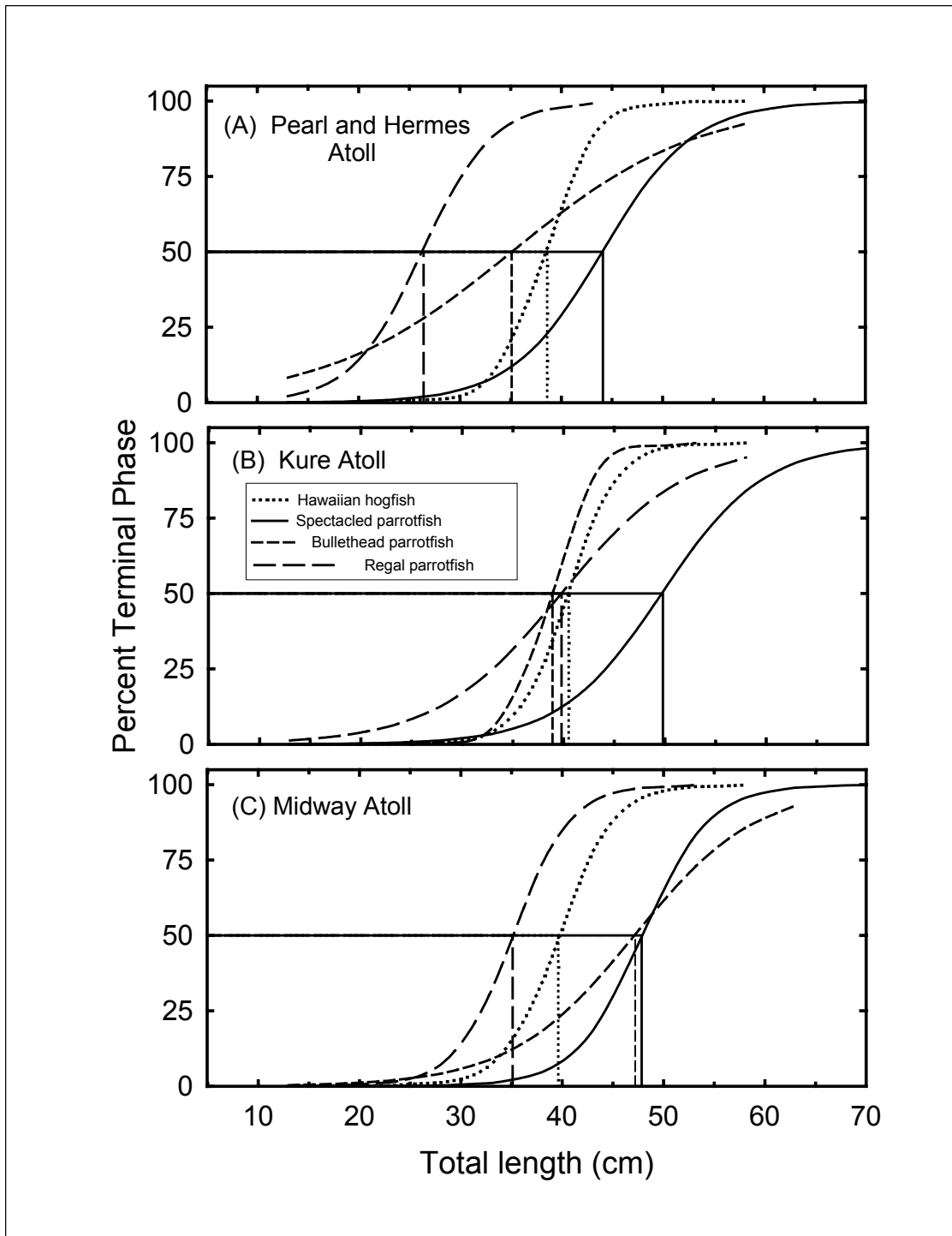
**Figure 3**. Logistic spline curves (predicted fits) of the percentage Terminal Phase (of all individuals observed–both Initial female and Terminal male phases) by 5-cm Total Length (TL) class, for each of four major species of labroids (one labrid plus three scarids), at (A) Pearl and Hermes, (B) Kure, and (C) Midway Atolls in the NWHI during September−October of 2000 and 2002. Vertical lines indicate estimated body length at which 50% of individuals are Terminal Phase. Source: Figure 1 of DeMartini et al. (2005).
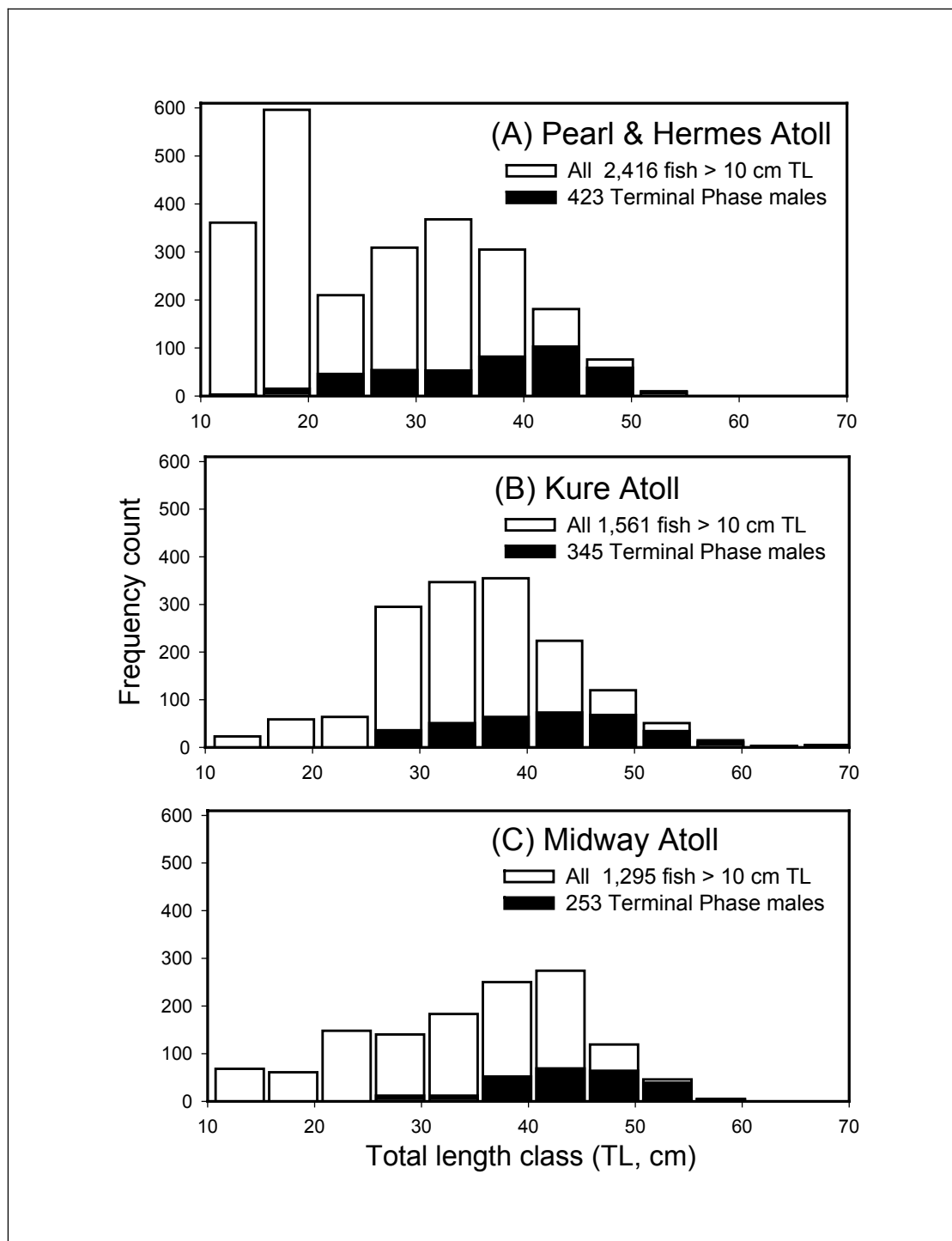
**Figure 4**. Body size (Total length, TL) frequency distributions of the aggregate of eight species of select (large-bodied, conspicuously dichromatic) labroids ≥10 cm TL, comprising four labrids and four scarids, observed by divers on Belt Transects and Stationary Point Count surveys at (A) Pearl and Hermes, (B) Kure, and (C) Midway Atolls in the NWHI during September−October of 2000 and 2002. Tallies are partitioned by Initial and Terminal phase individuals. Source: Figure 2 of DeMartini et al. (2005).
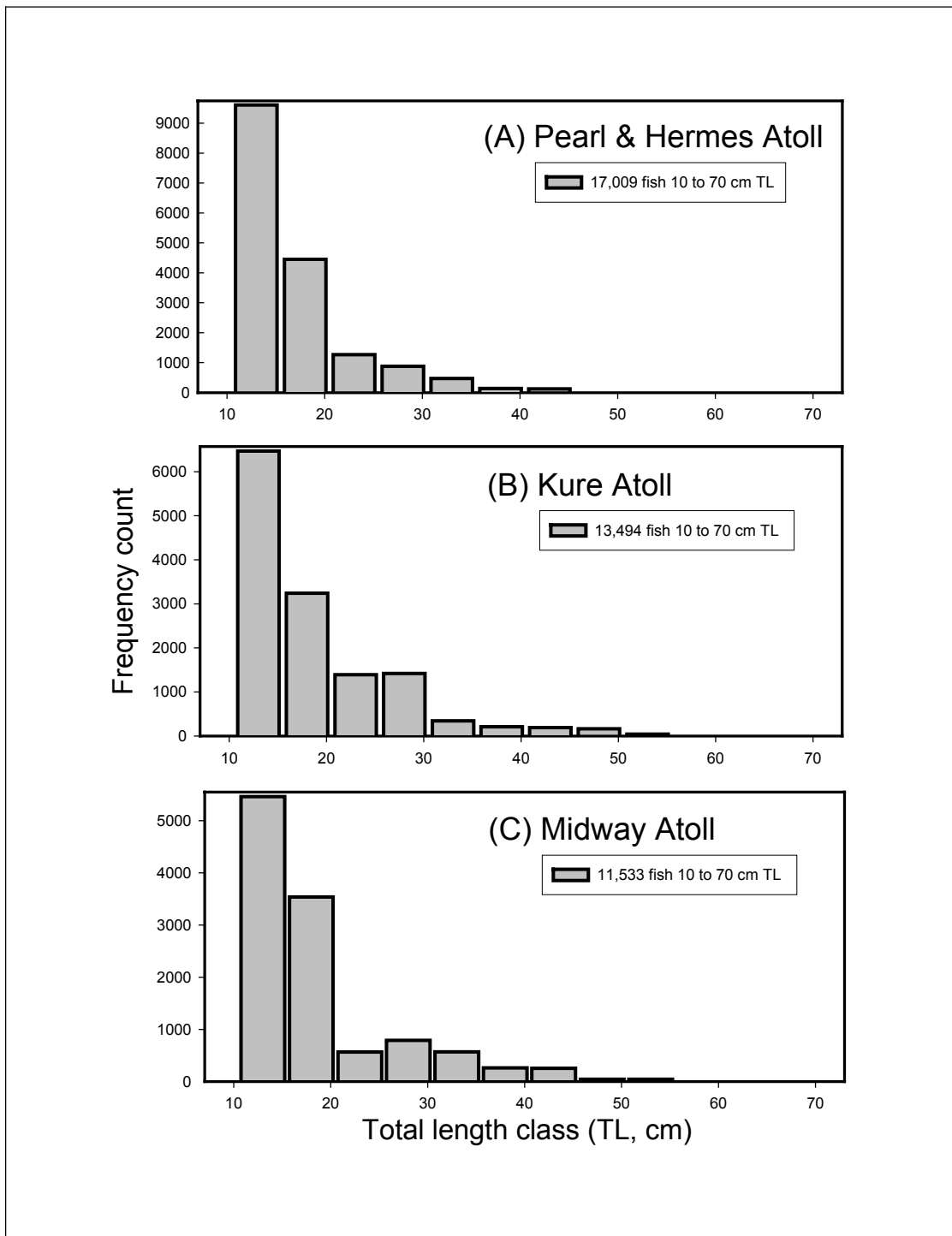
**Figure 5**. Body size (total length, TL) frequency distributions of the aggregate of all other taxa of prey reef fishes ≥10 cm TL observed by divers on belt transects at (A) Pearl and Hermes, (B) Kure, and (C) Midway Atolls in the NWHI during September−October of 2000 and 2002. Note different scales of y-axes in the various panels. Source: Figure 3 of DeMartini et al. (2005).
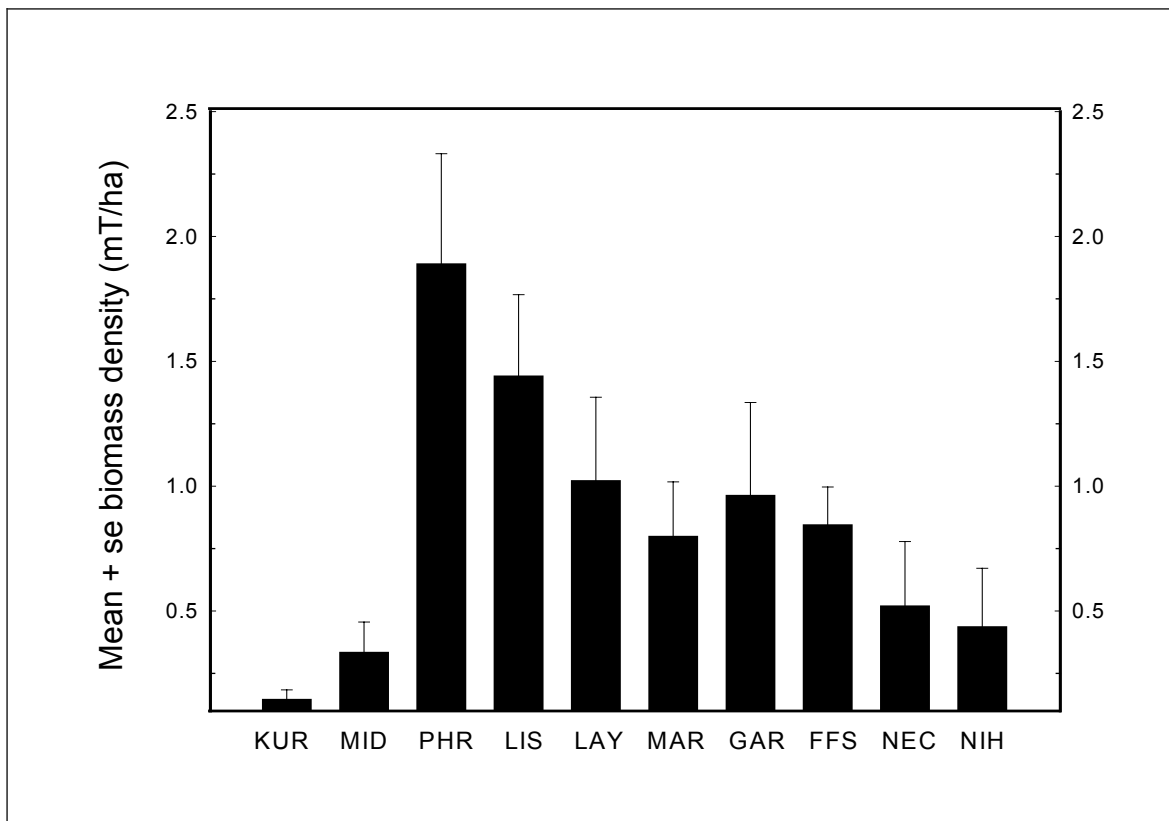
**Figure 6**. Geographic pattern of apex predator biomass density (averaging 70% giant trevally) at the 10 emergent NWHI reefs surveyed during September−October of 2000 and 2002. Estimates for these comprehensive surveys, based on standard belt transects (described by DeMartini and Friedlander, 2004) were sufficiently precise to justify presentation of standard error (se) bars. Source: Figure 8 of DeMartini and Friedlander (2004).

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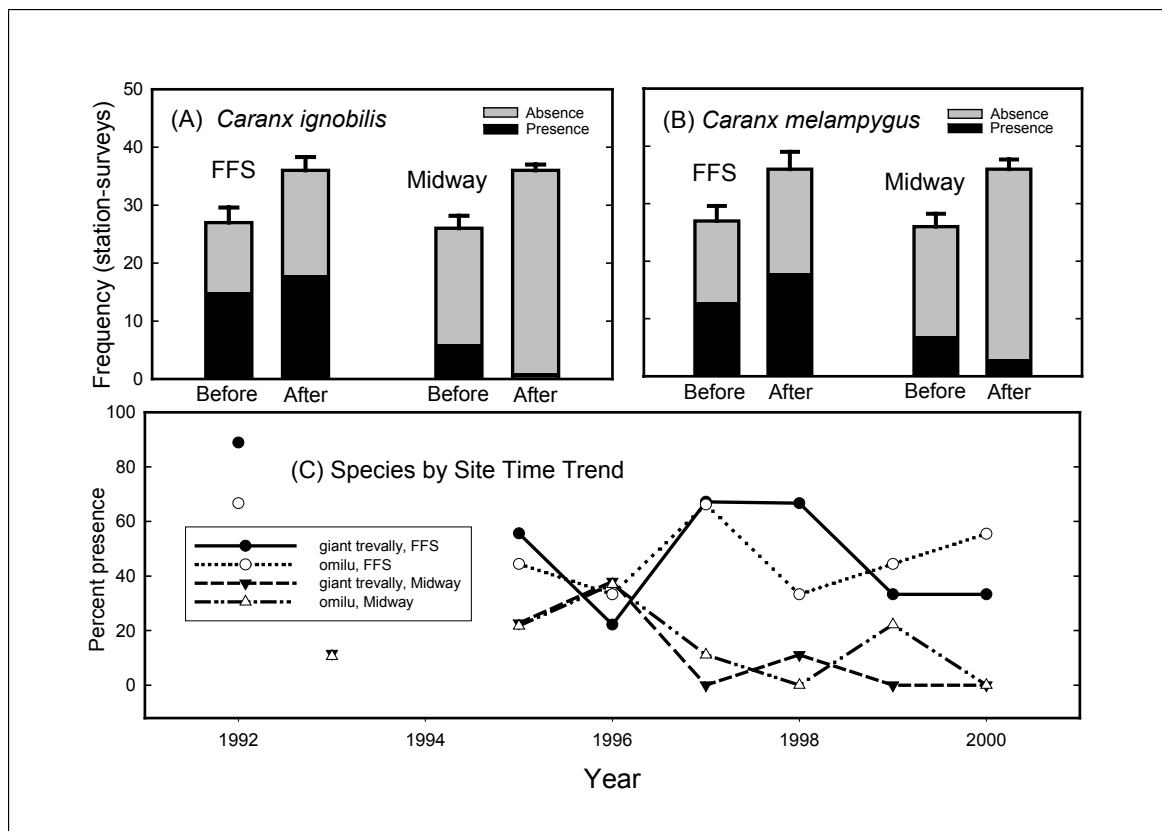


**Figure 7.** Relative presence-absence of (A) giant trevally (*Caranx ignobilis*) and (B) bluefin trevally (*C. melampygus*) at FFS and Midway stations during 1992 (FFS) or 1993 (Midway) through 1995-2000 pooled. The stacked presence-absence bars indicate species subtotals up to and including 1996 ("Before") versus after 1996 ("After") at each site. Panel C plots percent presence at stations on each survey. Vertical lines atop histograms are 1 se. Source: Figure 6 of DeMartini et al. (2002).

Most likely, the difference between FFS and Midway in the abundance of jacks is primarily the result of persistent fishing-associated mortality and disturbance at the latter and minimal extraction at the former (DeMartini et al., 2005).

Our observations of predator effects on prey size composition and life history have several significant implications for an ecosystem-based approach to fishery management in the Hawaiian Archipelago. First, *in situ* observations instead of destructive sacrifice (necessary for gonadal examination) might prove useful for estimating size at sex change in labroids, one important parameter in stock assessment for this major group of reef fishes. Second, size spectra and related metrics (Graham et al., 2005; DeMartini et al., 2005) may be used to assess functional change on NWHI reefs. In particular, indices of exploitation based on prey size frequency distributions have the potential to be developed as an effective proxy for predation intensity (predator abundance).

Several other major patterns (shelter use and the planktonic dispersal of organisms

among reefs), indirectly related to predation, are also clearly evident in the NWHI fish assemblage data. Refuging behavior and the use of habitat for shelter are major anti-predator adaptations of reef fishes (Hixon and Beets, 1993; Friedlander and Parrish, 1998). DeMartini (2004) documented the habitat-specific spatial distributions of juvenile and other small-bodied fishes particularly susceptible to predation and recognized the importance of backreef, lagoonal patch reef, and other sheltered (wave-protected) habitats as nursery areas for juvenile reef fishes in the NWHI (Fig. 8). This study, based on re-analyses of data collected at FFS and Midway Atoll during the 1990s, has contributed substantially to development of both "essential fish habitat" (EFH) and "habitat areas of particular concern" (HAPC) concepts in recognizing the greater per-unit-area value of atolls due to their larger proportion of sheltered juvenile nursery habitats (DeMartini, 2004).

The planktonic dispersal of reef fishes is an important process linked to the persistence of benthic reef populations besieged by continuing sources of natural mortality that include predation and physical disturbances like habitat-destructive hurricanes and other major storm events. Endemism must be importantly related to the dispersal and connectivity of reef-fish populations in Hawaii and is remarkably high for shallow reef fishes throughout the Archipelago, particularly in the NWHI (DeMartini and Friedlander, 2004). Percentage endemism based on a typical species-presence criterion is about one-fifth higher (30% versus 25%) in the NWHI versus MHI (DeMartini and Friedlander, 2004). The latter MHI value, also based on *in situ* diver observations, is indistinguishable from the best present estimate of 23% for Hawaiian fishes based on comprehensive specimen sources including market sampling, poison stations, and other sources for museum collections (Randall, 1998). Endemism is even more strongly expressed in terms of standing stock per unit area in the NWHI—both biomass (mean 37%) and especially numerical (mean 52%) densities increase with latitude throughout the islands even though species-presence-based measures of endemism lack latitudinal pattern in the NWHI (Fig. 9; DeMartini and Friedlander, 2004). These recent observations of a latitudinal effect on standing stock-based endemism were foreshadowed by an analogous pattern observed previously at FFS and Midway Atoll (Fig. 10; DeMartini, 2004).

Greater endemism upchain in the NWHI may be related to consistently higher rates of replenishment by young-of-the-year (recruitment of benthic "yoy") upchain following dispersal as pelagic larvae and/or juveniles (DeMartini and Friedlander, 2004). This was first indicated by survey data collected during the 1990s at FFS and Midway (DeMartini et al., 2002; DeMartini, 2004). During this period, there was consistently higher recruitment of young-of-the-year (yoy) life stages of fishes at Midway Atoll versus FFS despite the generally greater densities of older-stage fishes at FFS (Fig. 11). During 2000-02, recruit fish densities were generally greater upchain to the northwest (versus downchain) and a larger number of endemic (versus non-endemic) species recruited to a greater extent upchain in the NWHI (Table 1; DeMartini and Friedlander, 2004). The observed greater abundance and recruitment of endemics upchain were not importantly complicated by species composition or within-species adult body size differences (DeMartini and Friedlander, 2004).

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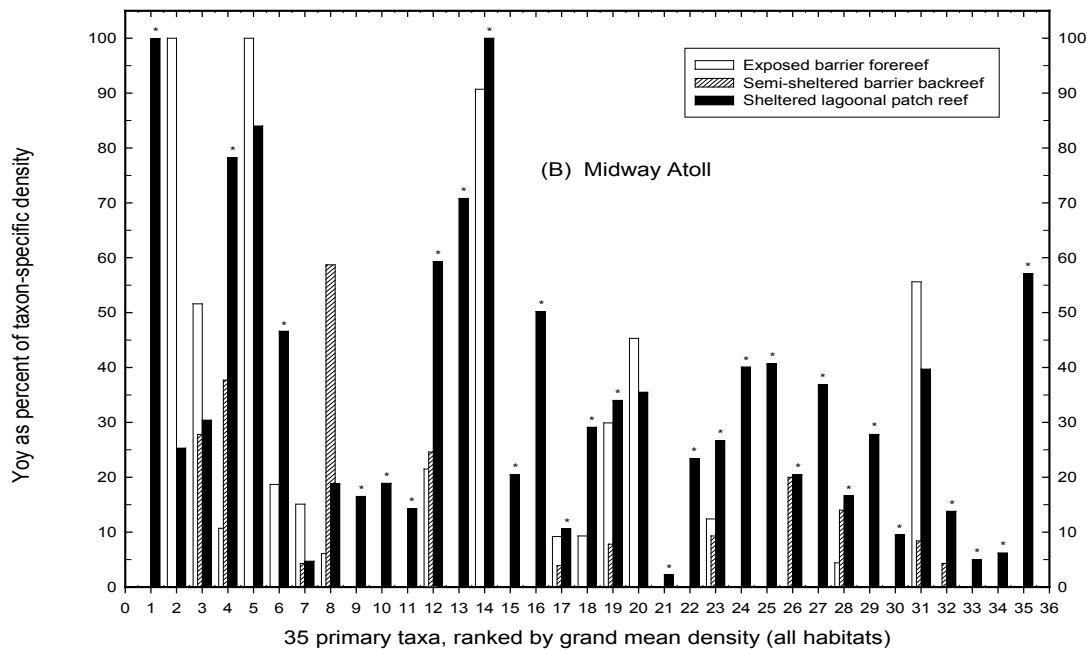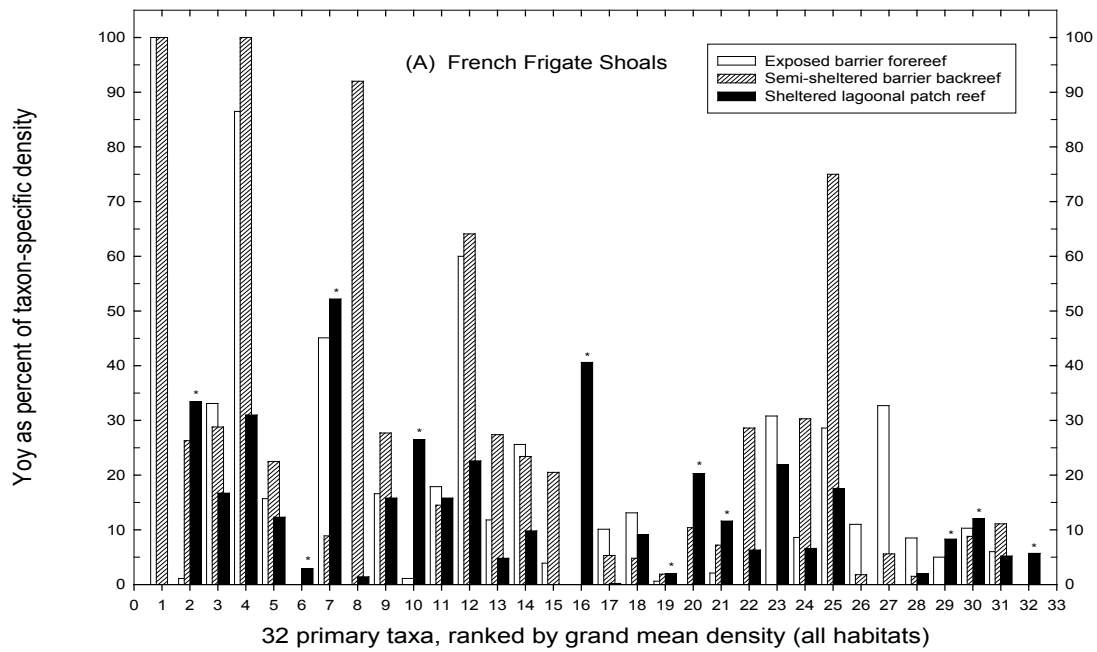


**Figure 8.** Bar histograms of the percentage contribution of yoy to overall yoy plus older-stage densities for each primary (common and abundant) taxon at (A) FFS and (B) Midway Atoll. Estimates are numbered, ordered, and partitioned by habitat. Taxa with nominally highest yoy percentages at sheltered patch reefs are noted by asterisk; see DeMartini (2004) for names of taxa. Source: Figure 3 of DeMartini (2004).
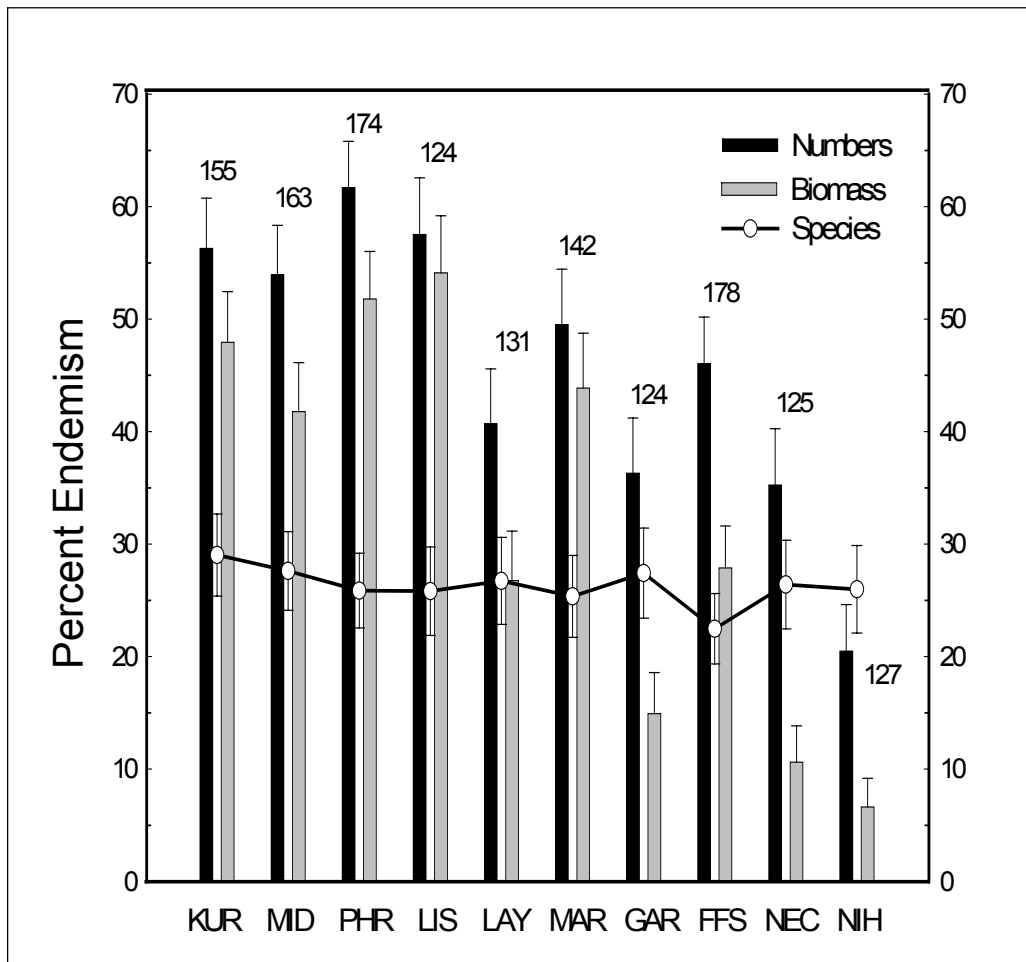
**Figure 9.** Various measures of percentage endemism (based on species occurrence, and on numerical and biomass densities) at each of ten emergent NWHI reefs, illustrating patterns of endemism with latitude-longitude. Occurrence data are indicated by line graph and density data by histograms. Vertical lines indicate se of estimates. Species richness (number of species) is noted by a number atop each set of histograms. Source: Figure 2 of DeMartini & Friedlander (2004).
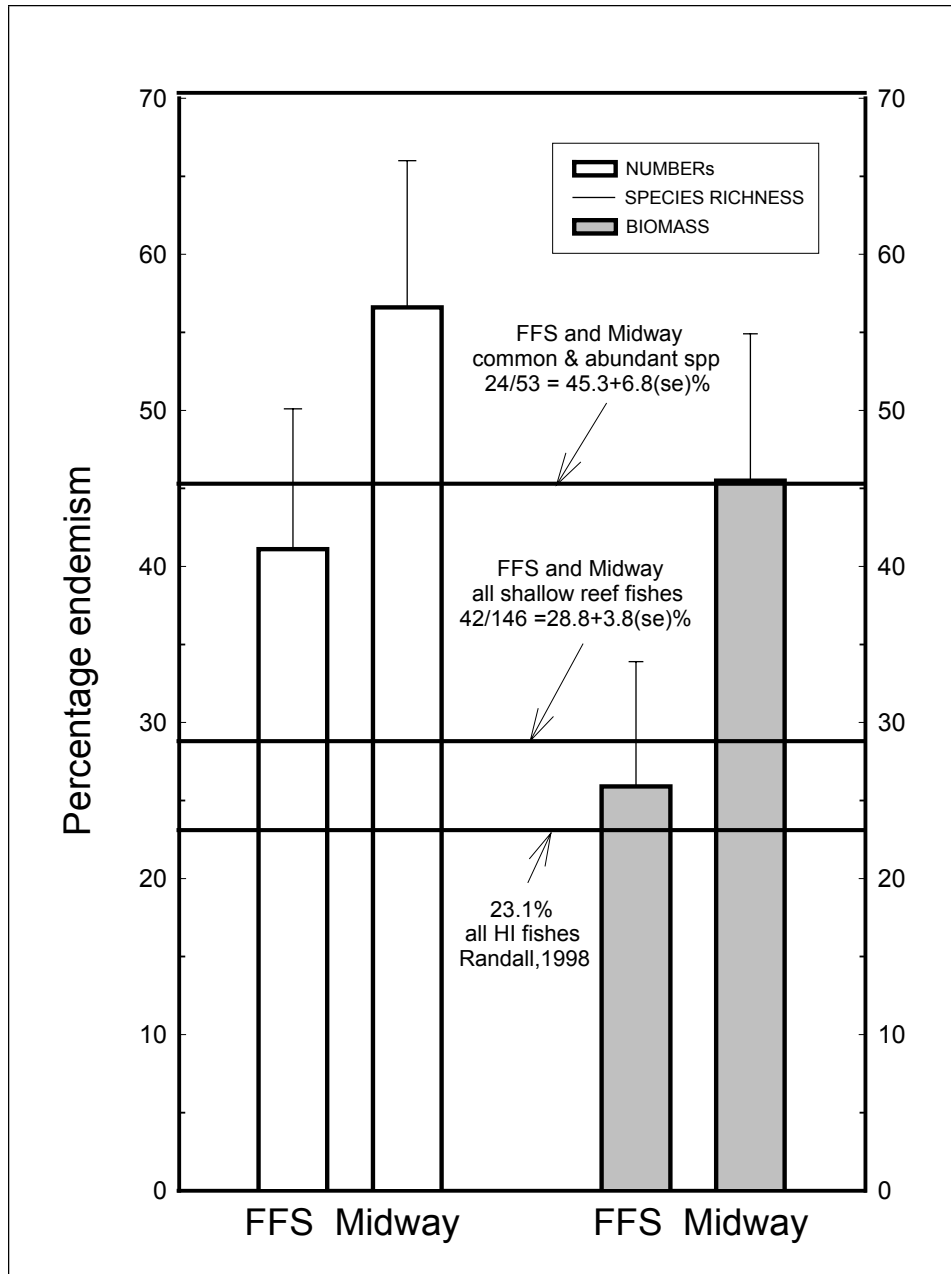
**Figure 10**. Bar histograms depicting percentage endemism based on numerical and biomass densities estimated on yearly diver surveys at FFS and Midway Atoll during the period from 1992/93-2000, inclusive. Arrows indicate three lines referring to species diversity (richness): for all Hawaiian fishes (Randall 1998), for all shallow reef fishes surveyed by DeMartini et al. (2002), and for only the most common and abundant fishes surveyed by DeMartini et al. (2002). Source: Figure 4 of DeMartini (2004).
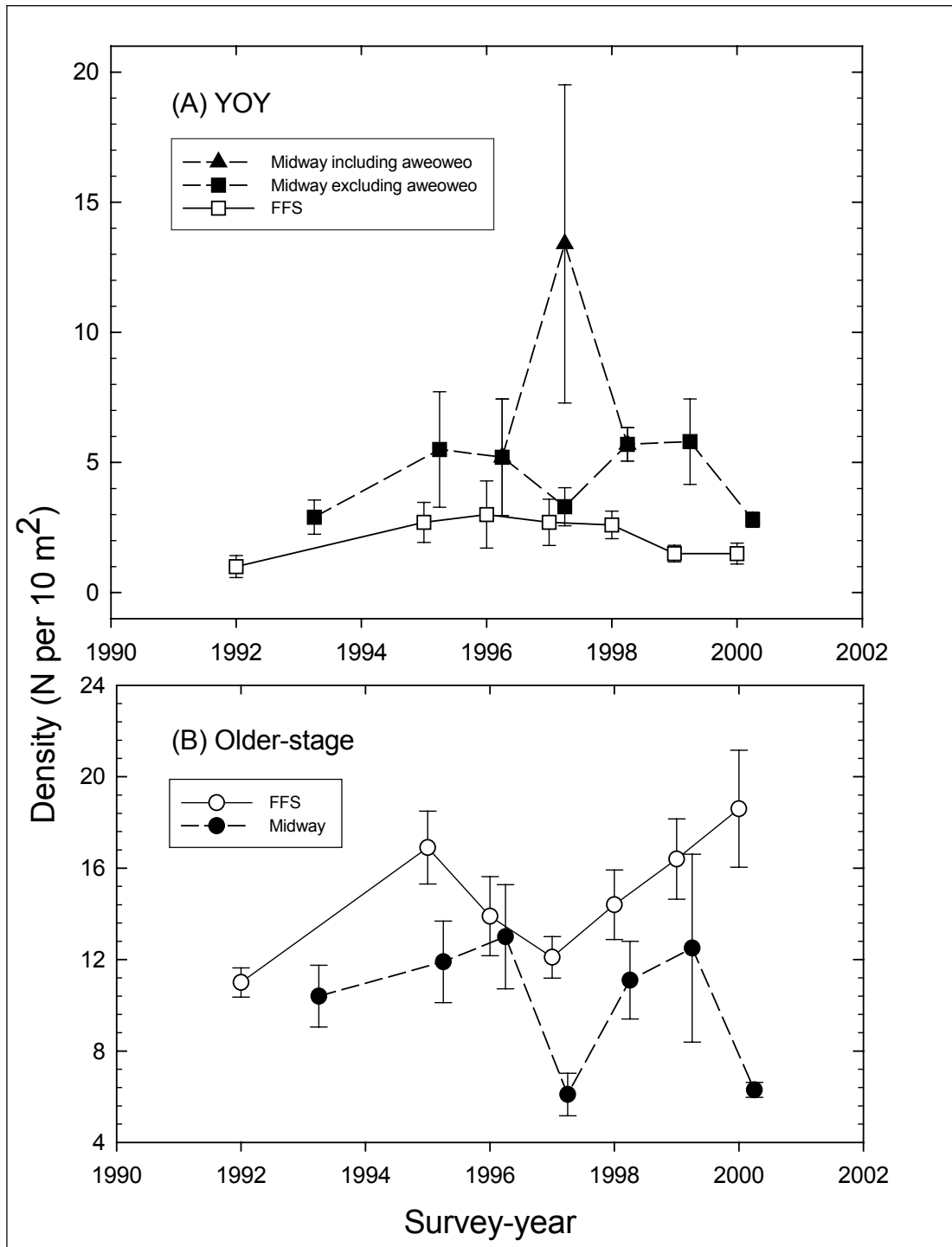
**Figure 11**. Time series of the estimated mean numerical density of (A) yoy and (B) older-stage fishes of all taxa at FFS and Midway during each survey year. Aweoweo = *Priacanthus meeki*. Each vertical bar represents 1 se of the estimated survey year grand mean for both major habitats. Source: Figure 1 of DeMartini (2004).

Table 1. Data classification and Chi-square test results evaluating signed (positive, negative) correlations and trends in a recruit index (numerical density ratio of yoy to larger-sized, older individuals comprising a species' reef-population) versus latitude for component species of endemic and non-endemic taxa. Source: Table 4 of DeMartini and Friedlander (2004).

| Distribution of correlations/trends | | | Chi-square statistics |
|---|---|---|---|
| | Pos | Neg | Both | |
| Endemic | 13 | 2 | 15 | $\chi^2 = 4.08$ |
| Non-Endemic | 9 | 10 | 19 | df = 1 |
| Both | 22 | 12 | 34 | $0.05 > p > 0.02$ |

## THE SIGNIFICANCE OF PREDATION IN THE NWHI ECOSYSTEM

That predation is a major structuring agent in marine ecosystems is not a novel conclusion, and the shallow reef ecosystem of the NWHI is no exception. Our recent observations confirm and extend those made by Hobson (1984) and J.D. Parrish and USFWS co-workers (Norris and Parrish, 1988; Parrish et al., 1985, 1986) on the first NWHI diver surveys during the late 1970s and early to mid-1980s. Characterizing the extent and magnitude of piscivory on shallow NWHI reefs was a major focus of the USFWS studies, and these included a series of field experiments for assessing the effects of lower-level piscivores on patch-reef fish assemblages in the lagoon at Midway Atoll (Schroeder, 1989). An allied study (Schroeder, 1987) evaluated the effects of several shelter resource variables on the recruitment of fishes at these patch reefs.

Predation as a structuring process, of course, is not limited to shallow-reef areas, or just to fish assemblages in the NWHI. Parrish and Boland (2004), for example, recently described the over-arching influence that apex predators have on the distribution and abundance of substrate-associated fishes atop the summits (30-40 m) of deeper banks in the NWHI. Studies of the foraging habitat, feeding behavior, and diet of monk seals (Parrish et al., 2000; Goodman-Lowe, 1998) attest to the historical (if not present—due to depressed population level) importance of monk seals as predators that interact competitively with predatory fishes such as jacks and sharks and, to some extent, that serve as the prey of some larger sharks. Huge seabird populations exist in the NWHI, and the effects of seabird predation on the population dynamics of squid and small fishes, including the near-surface planktonic stages of many reef fishes, may be considerable (Harrison et al., 1983).

## CONCLUSIONS AND SUGGESTED FUTURE RESEARCH

Clearly, coral reef fish assemblage structure is routinely controlled by so-called "top-down" predation in the NWHI, even if a "bottom-up" (nutrient input) process is sometimes responsible for regime shifts in overall ecosystem productivity (Polovina et al., 1994). The effects of apex predation, primarily by giant trevally, are pervasive: they structure prey population sizes and age distributions and strongly influence the reproductive and growth dynamics of harvestable fishes (such as parrotfish) as well as smaller-bodied, lower-trophic-level fishes on shallow NWHI reefs. Habitat utilization is related to refuging from predation, and the important nursery function of predator-inaccessible shallows and other wave-protected, finely structured regions at atolls cannot be overemphasized, especially when selecting sites for the establishment of no-take marine protected areas (MPAs). Finally, the inter-related processes of dispersal and recruitment cannot be overlooked because they represent the mechanisms used to counter local extirpation resulting from predation and physical disturbance. All of these processes—dispersal, recruitment, and predation—are linked, importantly if indirectly, to the present structure and function of the strongly endemic fish fauna of the NWHI.

The fish assemblages of oceanic islands such as the NWHI, like the ecosystems in which they are imbedded, are sensitive to human perturbations of the predatory hierarchy (DeMartini et al., 1999). Our appreciation of the pervasive influence of predation on the structure and behavior of reef fish and other assemblages within the NWHI ecosystem is, in a trivial sense, an "artifact" of the near-pristine nature of the NWHI. In the MHI, as in other human-impacted reef ecosystems, we no longer have an intact, naturally functioning system left to observe. We must continue to promote good stewardship of the NWHI ecosystem.  In part this will require persistent dedication to responsible research that, to the extent possible, minimizes human disturbance while increasing our understanding of the functional structure of reef ecosystems.

Some logical suggestions for further research involving NWHI reef fishes include: (1) characterizing the strength of coral and other habitat linkages among reef fishes and other key fauna and flora; (2) obtaining extended time series describing the inter-annual variations in population replenishment for fish (as well as corals, algae, and key macroinvertebrates); (3) pursuing studies of genetics and trace element markers present in reef-fish otoliths that together can provide complementary insights into the evolutionary and present-day structure of their stocks; (4) conducting controlled field experiments (if such can be accomplished while maintaining responsible stewardship) that further quantify the influence of apex predators, especially giant trevally, on prey assemblage structure and function; and (5) comparative evaluations of the spatial and temporal dynamics of primary productivity and nutrient and detrital flux on NWHI and MHI reefs.

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# SHARKS AND JACKS
# IN THE NORTHWESTERN HAWAIIAN ISLANDS
# FROM TOWED-DIVER SURVEYS 2000 - 2003

BY

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## ABSTRACT

Sharks (Carcharhinidae) and jacks (Carangidae) were surveyed using towed divers at the atolls and banks of the Northwestern Hawaiian Islands (NWHI) during annual surveys from 2000 to 2003. We compared numerical and biomass densities of these predators among reefs, among habitats within atolls (forereef, backreef, channel, and lagoon) and banks (insular and exposed), and mapped the spatial distribution of predators at the reefs where they were most abundant. Shark and jack densities were both very high at two of the three pinnacles in the chain, Necker and Gardner Pinnacle. Otherwise, shark densities were highest at Maro Reef and Midway Atoll, and jack densities were highest at Pearl and Hermes Atoll and Lisianksi-Neva Shoals. Galapagos sharks (*Carcharhinus galapagensis*) and gray reef sharks (*C. amblyrhynchos*) were observed most frequently in forereef habitats within atolls, and on exposed reefs within banks. Whitetip reef sharks (*Triaenodon obesus*) showed no significant habitat preferences on either atolls or banks. Giant trevally (*Caranx ignobilis*), bluefin trevally (*C. melampygus*), and amberjack (*Seriola dumerili*) were most frequently observed in forereef habitats within atolls, although the difference was significant only for amberjack. Jack densities were similar on exposed and insular reefs within banks. Maps of the spatial distribution of Galapagos sharks at Maro Reef and Midway Atoll and giant and bluefin trevally at Pearl and Hermes and Lisianski Island-Neva Shoals showed localized hotspots (areas of high density) within these habitats. We conclude that towed-diver surveys provide an effective method to assess shark and jack populations at the remote, expansive atolls and banks of the NWHI. Continued tow surveys will enable us to monitor the status of these important apex predators in an ecosystem relatively undisturbed by humans.

## INTRODUCTION

In the remote Northwestern Hawaiian Islands (NWHI), human impacts on the shallow coral reef ecosystems have been relatively minimal, and large mobile predators are abundant (Sudekum et al., 1991; Friedlander and DeMartini, 2002). Worldwide,

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many coral reefs currently have far fewer apex predators than were historically present (Jackson, 1997; Jennings and Kaiser, 1998; Pauly et al., 1998; Jackson et al., 2001). Reefs of the Main Hawaiian Islands (MHI) are a case in point (Shomura, 1987). Recent surveys found very few jacks or sharks in the MHI (Friedlander and DeMartini, 2002; Friedlander et al., 2003), in contrast to the impressive densities of predators encountered in the older, more remote, northwestern part of the Hawaiian Archipelago (Friedlander and DeMartini, 2002).

The objective of our study was to complete a comprehensive initial assessment of shark and jack populations at the 10 major reefs of the NWHI. We recorded numerical and biomass densities, as well as spatial distribution, using towed-diver surveys. Relative densities of apex predators were compared across several spatial scales to address the following questions:

1. Do median counts differ among reefs based on all relevant data for jacks and sharks?
2. Are shark and jack species equally represented in all of the habitats available at a reef?

Coral-reef ecosystems in remote areas such as the NWHI are in a more natural state than reefs subjected to significant fishing pressure, habitat degradation, pollution, runoff, and other anthropogenic stressors in the MHI. The NWHI reefs have the potential to provide insight into how a healthy ecosystem operates, especially concerning the role of predators on coral reefs. Mobile predators have a strong effect on the abundance, diversity, and behavior of other coral-reef residents (Parrish et al., 1985; Sudekum et al., 1991; Norris and Parrish, 1998; Stevens et al., 2000; Dulvy et al., 2004). Sharks and jacks prey on bony and cartilaginous fishes, cephalopods, crustaceans, and gastropods (Wass, 1971; Okamoto and Kawamoto, 1980; Randall, 1980; Sudekum et al., 1991; Weatherbee et al., 1997; Meyer et al, 2001).  We initiated a comprehensive, quantitative documentation of predator abundance and distribution to provide necessary baseline data. These data will help decipher patterns of apex predator abundance and distribution, and could provide insight into the predation process structuring lower trophic levels (Friedlander and DeMartini, 2002; DeMartini and Friedlander, 2004; DeMartini et al., 2005).


**MATERIALS AND METHODS**


Survey Sites

A total of 331 towed-diver fish surveys were completed during annual NWHI cruises from 2000 to 2003 organized by the Coral Reef Ecosystem Division (CRED) of the Pacific Islands Fisheries Science Center (PIFSC), National Oceanic and Atmospheric Administration (NOAA), Honolulu, Hawaii. The towed-diver surveys covered 865 linear kilometers of reef habitat at 10 different locations (Fig. 1), generally during late summer or early fall. Surveys were conducted at four atolls (French Frigate Shoals, Pearl and Hermes Atoll, Midway Atoll, and Kure Atoll), three banks (Maro Reef, Laysan

Island, and Lisianski Island-Neva Shoals), and three pinnacles (Necker, Nihoa, and Gardner Pinnacles). Atolls and banks were designated according to geomorphological reef structure (NOAA, 2003). Atolls were characterized by a distinctive barrier reef and lagoon. Banks were characterized by a shelf of submerged reef without any of the classic barrier-reef-and-lagoon structure of an atoll. Pinnacles were considered separately from banks based on their unique geomorphological characteristic of basaltic rock elevated above sea level and to accommodate survey logistical limitations. We were constrained by diver physiology and survey protocol to the small area of relatively shallow reef (<30 m) directly surrounding the elevated basalt pinnacles.

Atolls and banks do not have the same habitats and were treated separately for the smaller-scale comparisons. To compare habitats within atolls, the following reef zone classifications were used: forereef, backreef, lagoon, and channel. Towed-diver surveys completed along the outward-facing part of the barrier reef, next to open ocean, were designated as forereef. Towed-diver surveys conducted along the inward-facing section of the barrier reef were designated as backreef. Tows along reefs and sand areas in the center of the atoll were considered lagoon surveys. Channel tows were those that primarily cut across openings or interruptions in the barrier reef. To compare habitats within banks, we designated reefs as exposed or insular. Tows along the outermost edge of the bank were called exposed and those on the interior (i.e., not directly adjacent to open ocean) as insular.

These remote reefs were accessed by the NOAA ships *Townsend Cromwell* and *Oscar Elton Sette*. The towed-diver surveys were part of CRED's comprehensive, multidisciplinary Pacific Reef Assessment and Monitoring Program (Pacific RAMP). Concurrent data were collected on corals, algae, reef fishes, invertebrates, oceanographic conditions, and benthic habitat.

Towed-Diver Fish Surveys

Surveys for large mobile predators were conducted using towed divers in order to search large areas of reef in a limited period. We used a modified version of the manta board (Done et al., 1981; Kenchington, 1984), modeled after prototypes used in the NWHI to classify spiny lobster habitat (Parrish and Polovina, 1994). Towboards were mounted with an underwater digital video camera, Seabird Electronics temperature depth recorders (a SBE39 set to record at 5-sec intervals), timing devices, and observer data sheets. In addition, the fish towboard carried a magnetic-switch telegraph for communication with personnel on the surface.

Towed-diver surveys covered an average of ~2.5 km linear distance per tow. Two divers were towed behind a skiff on a 60-m line at a speed of approximately 1.5 knots. One diver served as a fish observer and recorded all fish ≥ 50-cm total length (TL) (Zgliczynski et al., 2004). The second diver recorded benthic habitat characteristics and conspicuous, ecologically important macro-invertebrates (Hill and Wilkinson, 2004). Divers attempted to maneuver the towboards ~1 m off the bottom, avoiding obstacles and abrupt ascents as necessary. Surface support personnel located in the towing vessel used a handheld GPS unit to record waypoints at the beginning and end of each survey as well

as a track throughout the tow (5-sec interval).

The towed-diver fish survey protocol was designed specifically for quantifying large mobile predators. The fish observer recorded all fishes ≥ 50-cm TL that occurred within a 10-m swath in front of the diver (5-m to either side of the diver and 10-m forward). Fishes were identified to species level, and the number present was recorded in size bins of 50 to 75-cm TL, 75 to 100-cm TL, 100 to 150-cm TL, 150 to 200-cm TL, 200 to 250-cm TL, and >250-cm TL. The standard survey was composed of ten 5-min segments. During each 5-min segment, fishes within the 10-m swath were recorded for 4 min, followed by a 1-min count of all fishes ≥ 50-cm TL observed within the limits of visibility in a 360° arc. Data analyzed for this paper included only the quantitative 4-min transect data. The 1-min counts were not amenable to density estimates as the survey area was not as easily quantified. These data will be analyzed later for information on maximum numbers of predators encountered per tow survey.

Analyses

Data on individual fish sightings were used to calculate numerical and biomass densities, which were the basis of all statistical comparisons. Numerical density was calculated by dividing the number of fish by the transect area (tow length x 10-m width). Biomass was calculated using length-weight conversion formulas with species-specific values derived from studies in the tropical Pacific (Kulbicki et al, 1993; Letourneur et al., 1998; Hawaii Cooperative Fishery Unit, unpublished data; www.fishbase.org). Tow length was accurately computed in ArcView using the track recorded during the tow with a layback model applied (R. Hoeke, unpublished data).

Nonparametric statistics were used to test for differences in numerical and biomass densities among groups because all datasets failed tests for normality. We used Kruskal-Wallis (K-W) one-way analysis of variance (ANOVA) on ranks to compare large-scale differences among reefs, mesoscale differences among habitats within atolls (forereef vs. backreef vs. lagoon vs. channel) and within banks (exposed vs. insular reefs). When K-W ANOVA showed a significant difference, we used a K-W multiple comparison z-value test to detect which groups were different from each other. The effects of reef and habitat were tested separately with two one-way ANOVAs on rank. We did not use a Friedman's 2-way ANOVA because the dataset was doubly unbalanced, with habitats not represented at all reefs and unequal numbers of tow surveys in each habitat. To account for multiple testing of the dataset, an adjusted significance level of α=0.025 was applied for statistical tests of higher-order taxa (i.e., at the family level), and α=0.016 for tests at the species level.

For comparisons among reefs, only exposed habitats were included to make the comparison equitable among atolls, banks, and pinnacles. For comparisons among habitats, only those habitats specific to atolls or banks were used, depending on the group of reefs being tested. Reefs were pooled for the habitat analysis by geomorphology (atoll or bank) with the condition that densities not differ significantly among pooled reefs in the *post-hoc* multiple comparison test (K-W z-test) performed after the inter-reef K-W ANOVA.

Maps of the spatial distribution of biomass were created in ArcView 3.3. The biomass calculations for each species were geo-referenced using the aforementioned layback model. Biomass values were linked to the geographic midpoint of each 5-min tow segment. These values were displayed on the IKONOS image of the atoll or bank using a size-graduated scale of symbols to visually represent comparative biomass of shark and jack species across the areas surveyed.

## RESULTS

Fish Assemblage

Five species of sharks were observed during towed-diver surveys in the NWHI (Table 1). Sharks were exclusively from the Family Carcharhinidae and included midwater reef-associated sharks such as Galapagos (*Carcharhinus galapagensis*), gray reef (*C. amblyrhynchos*), and tiger sharks (*Galeocerdo cuvier*), as well as a benthic species, the whitetip reef shark (*Triaenodon obesus*). In addition, blackfin reef sharks (*C. limbatus*) were recorded during non-quantitative surveys in low-visibility lagoon areas at Pearl and Hermes. The three most common sharks (Galapagos, gray reef, and whitetip reef sharks) accounted for 90% of the quantitative shark observations.

Nine species of jacks (Family Carangidae) larger than 50-cm TL were observed during towed-diver surveys (Table 1). The most common jacks were giant trevally (*Caranx ignobilis*), bluefin trevally (*C. melampygus*), and greater amberjack (*Seriola dumerili*). These three jack species accounted for 91% of the quantitative jack observations.

Comparisons Among Reefs

The mean density of sharks (all species combined) differed significantly among reefs in both numbers and biomass (Table 2). Shark densities ranged from 0 to 1.8 sharks per ha (57 kg/ha). Necker had significantly higher densities and Laysan had significantly lower densities of sharks than most other reefs (Table 3). Gardner, Midway, and Maro Reef also had relatively high shark densities compared to the other reefs (Fig. 2).

The mean density of jacks (all species combined) also differed significantly among reefs in both numbers and biomass (Table 2). Jack densities ranged from 0 to 4.4 jacks per ha (95 kg/ha). Pearl and Hermes Atoll and Lisianski-Neva Shoals had significantly higher densities of jacks than most other reefs (Table 3). Gardner, Necker, and Kure also had high jack densities, while Midway Atoll and Maro Reef had comparatively low densities (Fig. 3).

Comparisons Among Habitats

*Within Atolls.* The four atolls (French Frigate Shoals, Pearl and Hermes, Midway, and Kure Atoll) were pooled for habitat analysis for both sharks and jacks because

densities did not differ significantly among atolls during *post-hoc* multiple comparison tests (Table 3).

Only one of the three major shark species showed a significant difference in densities among atoll habitats (Table 2). Galapagos sharks were the most abundant shark at NWHI atolls and were recorded in all four reef zones (forereef, backreef, channel, lagoon). Densities of Galapagos sharks were significantly higher in channel and forereef habitats (Table 4), with a peak mean of 0.35 sharks per ha (16.14 kg per ha) in the channels. Gray reef sharks were also recorded at all four atoll habitats, though they were rarely encountered in the channels. Gray reef sharks were most abundant in forereef habitats (Fig. 4), where the mean density was 0.10 gray reefs per ha (7.09 kg per ha). Whitetip reef sharks were recorded at all four atoll habitats without any significant difference among habitats, with an average density of 0.11 sharks per ha (2.36 kg per ha). Whitetip reef sharks were not recorded by towed divers at the two northernmost atolls, Midway and Kure, but were relatively common at all of the other banks, atolls, and pinnacles.

The three major jack species appeared to be distributed unevenly among atoll habitats (Fig. 4), but only amberjack demonstrated a statistically significant difference (Table 2), undoubtedly because variance was high and the power of tests low for the other two species. The mean density of giant trevally was 2.23 fish per ha (37.42 kg per ha) on forereefs, compared to 0.21 fish per ha (6.32 kg per ha) in channels. Bluefin trevally were observed more frequently on forereef habitats with a mean of 0.83 fish per ha (2.90 kg per ha), although they were scarce in backreef and lagoon habitats. Amberjack were significantly more abundant on the forereef than on the backreef or lagoon reefs (Table 4; Fig. 4), with an overall mean of 0.18 fish per ha (2.28 kg per ha).

*Within Banks.* The three NWHI banks (Maro Reef, Lisianski Island-Neva Shoals, and Laysan) were pooled for within-bank habitat comparisons for shark species because densities (for the family) did not differ significantly among banks (p>0.025). For jack species, Lisianski Island-Neva Shoals and Laysan were pooled but Maro Reef was excluded because its jack densities differed significantly from other banks (p<0.025, Table 3).

The density of one of the three shark species was significantly higher on outside-facing, exposed bank reefs than on more insular, protected reefs (Table 2; Fig. 5). Galapagos were the most abundant shark at NWHI banks. Galapagos sharks were recorded exclusively in exposed reef habitats, with a mean density of 0.49 sharks per ha (24.26 kg per ha). Gray reef sharks were also recorded in greater numbers on exposed reef habitats although the difference was not significant, with an overall mean of 0.08 gray reefs per ha (2.49 kg per ha). Whitetip reef sharks were spread more evenly across bank reef habitats and did not differ significantly in density between exposed and insular reefs, with an overall mean of 0.10 whitetips per ha (1.90 kg per ha).

The three major species of jacks showed no significant difference in densities between exposed and insular bank habitats (Table 2; Fig. 5). Overall, giant trevally were the most abundant jack by number and biomass, with a mean density of 0.93 fish per ha (26.14 kg per ha). Bluefin trevally were the second most common jack on bank reef

habitats with a mean of 0.27 fish per ha (2.06 kg per ha). Amberjack were relatively scarce on NWHI banks, recorded at mean density levels of 0.02 fish per ha (0.10 kg per ha).

Maps of Spatial Distribution

*Shark Species.* The three major shark species were mapped at the atoll and bank where sharks were most abundant (Midway Atoll and Maro Reef). At Midway Atoll, Galapagos shark biomass was concentrated along the south and southeast forereef, as well as the western channels (Fig. 6). Gray reef shark biomass was scattered more evenly along the east and southeast forereef, with a single observation on the south backreef. No whitetip reef sharks were observed at Midway during towed-diver surveys. At Maro Reef, Galapagos shark biomass was high at all four corners of the bank, especially the northeast and southeast outer reefs (Fig. 6). Gray reef shark biomass was sparser, with a few sharks in the southeast, and one sighting along the lower northwest corner. Whitetip reef sharks were generally observed singly, and their biomass was distributed relatively evenly across Maro Reef.

*Jack Species.* The three major jacks were likewise mapped by species at the atoll and bank where jacks were most abundant (Pearl and Hermes Atoll and Lisianski Island-Neva Shoals). At Pearl and Hermes Atoll, giant trevally biomass was extremely high and was scattered throughout forereef and backreef habitats all around the atoll (Fig. 7). Giant trevally biomass was especially high in the northeast corner on the outside of the barrier, as well as along the east forereef, and the south central forereef. Bluefin trevally biomass was distributed differently, with the majority of biomass concentrated in the southeast corner, where the barrier reef is breached by numerous channels. Amberjack biomass was more evenly distributed with individuals recorded along the south, southwest, and northwest reefs outside the barrier. At Lisianski Island-Neva Shoals, jack biomass was scattered throughout the bank's outer reefs. The highest concentrations of giant trevally were in the northwest adjacent to the island, and of bluefin trevally in the southeast corner of Neva Shoals (Fig. 7). No amberjacks were observed during towed-diver fish surveys at Lisianski.

## DISCUSSION

Based on 2000-03 towed-diver surveys, apex predator densities were highest at Gardner Pinnacles and Necker. These two pinnacles show the intense concentrations of biomass that can occur around an abrupt topographical feature such as a seamount or pinnacle (Boehlert and Genin, 1987). Our towed-diver surveys documented the high biomass of predators occupying the area immediately surrounding the pinnacle, but we did not survey the bank surrounding the pinnacles due to diving depth constraints. This bias should be taken into account when comparing predator densities at these pinnacles to those obtained for the other reefs, where we surveyed a variety of habitats.

Three of the four atolls surveyed had similar patterns of shark and jack distribution. Kure, French Frigate Shoals, and Pearl and Hermes Atoll all had moderate to high levels of jacks, and moderate levels of sharks, with jack biomass outweighing shark biomass. This is consistent with results of previous studies using standard belt transect methods, based on which jacks were the dominant apex predator by biomass at NWHI atolls (Friedlander and DeMartini, 2002). Pearl and Hermes Atoll was the most extreme case with the greatest numerical and biomass densities of jacks in the NWHI. The latter is consistent with previous estimates (Friedlander and DeMartini, 2002; DeMartini et al., 2005), although the mean densities of apex predators estimated using towed-diver surveys in the present paper are lower than those estimated previously using belt transects and stationary point counts (Friedlander and DeMartini, 2002; Parrish and Boland, 2004; DeMartini et al., 2005). In part this reflects the differing data parameters (i.e., which size classes and families were included) and time periods used for the characterizations, but it also reflects the different biases inherent in the various methods. Densities estimated using towed-diver surveys are not directly comparable to results from survey methods such as belt transects (Brock, 1954; Brock, 1982) or stationary point counts (Bohnsack and Bannerot, 1986). Temporal and spatial comparisons using a given survey method are still valid, however, and it may be informative to compare the direction and magnitude of future trends in abundance and biomass using different survey methods.

Relatively few jacks were encountered at Midway, and this represented the lone exception to the general pattern of jacks being dominant over sharks by biomass at atolls. The scarcity of jacks may be related to the recreational fishing that has occurred at Midway during the past 50 years (Green, 1997). The atoll served as a military base for over four decades, and Midway-Phoenix Corporation operated eco-tourism ventures there from 1996 to 2000, including recreational scuba diving and a catch-and-release trophy fishery for giant trevally. Fishing activities may have affected the jack populations at Midway by removing individuals directly, by indirectly making them more susceptible to shark predation or physiological death after release in an exhausted state, or both. Alternatively, or additionally, the catch-and-release fishery and diving operation may have affected the behavior of jacks by promoting emigration to greater depths or by causing them to develop a conditioned aversion to boats and divers (e.g., Kulbicki, 1998). Each of the latter two factors might result in jacks being underrepresented on diver surveys. A combination of chronic, prior extraction and recent indirect mortality, plus conditioned aversion, is most likely (DeMartini et al., 2002).

Midway had the highest densities of sharks in the NWHI, in contrast to other atolls in the chain which generally had moderate densities. One possibility is that Midway's shark populations have responded functionally to competitive release with increased reproductive output. Another, non-mutually exclusive possibility is that adult sharks have immigrated to Midway in response to the depressed abundance of jacks. Now that sportfishing and persistent daily diving have been discontinued, it will be interesting to see if the jack populations increase at Midway and, if so, whether shark densities decrease. Understanding the movements of sharks and jacks to and from Midway will probably require the use of acoustic tags or sonic transmitters (e.g., Holland et al., 1999) to track individual animals, research that has already been initiated by the Hawaii

Institute of Marine Biology (HIMB) shark research group (Lowe et al., 2006).

The three banks surveyed each had unique patterns of apex predator density. The largest bank in the chain, Maro Reef, had higher densities of sharks than jacks, which matched the general pattern observed in a previous study of NWHI banks (Parrish and Boland, 2004). Neva Shoals, an extensive bank associated with Lisianski Island, had the opposite pattern, with high densities of jacks and very few sharks. The smaller reef associated with Laysan Island had low densities of both types of apex predator. Differences in habitat may explain some of the variation in densities and relative proportions of apex predators at these three banks. The reef around Laysan Island is relatively featureless, with low relief, and much of it is covered in turf algae. Lisianski Island-Neva Shoals and Maro Reef have much greater topographical complexity, with reticulated reefs and submerged pinnacles (NOAA, 2003). However, in surveys of deeper bank summits in the NWHI, Parrish and Boland (2004) found that the number of apex predators did not differ with scales of relief, although density of most other fishes did, perhaps in response to predators. Future analysis, which will include mapping predator densities in relation to oceanographic parameters, may give us greater insight into the variation in jack and shark distribution among banks.

Habitat preferences were well defined in the midwater reef-associated sharks. Galapagos and gray reef sharks at atolls were found mainly in forereef habitats and sometimes in the channels (Galapagos only), and on banks they were concentrated on the exposed reefs. Other investigations have found fish abundance in general to be higher on the forereef than other habitats (e.g., Sedberry and McGovern, 1995). Gray reef shark distribution at Maro and Midway was dispersed, with solitary individuals rather than aggregations as reported for other atolls (McKibben and Nelson, 1986; Economakis and Lobel, 1998) and in the NWHI by previous researchers (Taylor, 1993). These aggregations were predominantly female and linked to breeding-related behaviors. Our surveys were conducted during late summer and early fall rather than spring when the majority of aggregations were observed.

Whitetip reef sharks (a benthic species) were scattered throughout atoll and bank habitats. Maps of their distribution on Maro Reef showed mostly solitary individuals spaced at regular intervals across the reef. There are reports that whitetip reef sharks may be somewhat site attached, returning to a home cave between foraging excursions (Randall, 1977). Whitetips were recorded at all reefs south of and including Pearl and Hermes. While there were rare sightings of whitetip reef sharks at Midway and Kure during previous studies (Schroeder and Parrish, 2005), these atolls appear to lie just north of an undetermined distributional limit, perhaps related to winter water temperatures.

The habitat use of jack species was more difficult to specify. On banks, the three major species of jacks showed no preference for insular or exposed reefs. At atolls, the three major species of jacks were observed most often in forereef habitats, although the difference was significant only for amberjack. Amberjack were generally recorded as solitary individuals and were spaced relatively evenly throughout the habitats they occupied.

Giant trevally were often recorded in large, roving groups, although also observed singly. The two different modes of travel are probably related to prey spacing- e.g.,

grouped and single trevally have greater success foraging on schooled and isolated prey, respectively (Major, 1978). Plots of jack distributions at Lisianski Island-Neva Shoals indicated possible hotspots of giant trevally biomass on the leeward (western) reef near the island, and at the southernmost point of the shoals. Giant trevally biomass was greater along most of the forereef and much of the backreef of Pearl and Hermes, with highest concentrations along the windward side (east and northeast). The spatial distribution of giant trevally is likely to be dynamic as this species demonstrates long-term and long-distance movements at the scale of whole island reefs (Wetherbee et al., 2004), and at perhaps larger spatial scales.

Bluefin trevally biomass was most concentrated at the southwest corner of Pearl and Hermes Atoll, a distribution pattern that may be relatively persistent because site fidelity is strong in this species (Holland et al., 1996). Studies of bluefin trevally at Johnston Atoll showed that they prey heavily on spawning fishes using midwater and ambush hunting techniques (Sancho, 2000; Sancho et al., 2000). Bluefin trevally may be using similar strategies to feed on midwater planktivores, which are abundant along the southwest forereef of PHR. The forereef in the southwest corner of PHR is pockmarked with narrow channels and reef passes, and bluefin trevally may elect to hunt in these channels, a behavior that was well documented at an atoll in the Indian Ocean (Potts, 1980).

In summary, these baseline abundances provide the necessary starting point for understanding the population fluctuations of jacks and sharks that abound on the reefs of the NWHI and that, as apex predators, are important determinants of fish assemblage structure in these reef ecosystems (DeMartini and Friedlander, 2006). As monitoring surveys begin, it will be interesting to see if shark and jack hotspots within each reef are predictable from year to year. In general, it would be useful to evaluate whether relative abundances of the different predator species fluctuate temporally to appreciable extents. Towed-diver surveys potentially provide an effective method to assess the abundances of patchily distributed shark and jack predators at the remote, expansive atolls and banks of the NWHI. Continued towed-diver surveys will enable us to monitor the status of these important apex predators in an ecosystem relatively undisturbed by humans.

## ACKNOWLEDGEMENTS
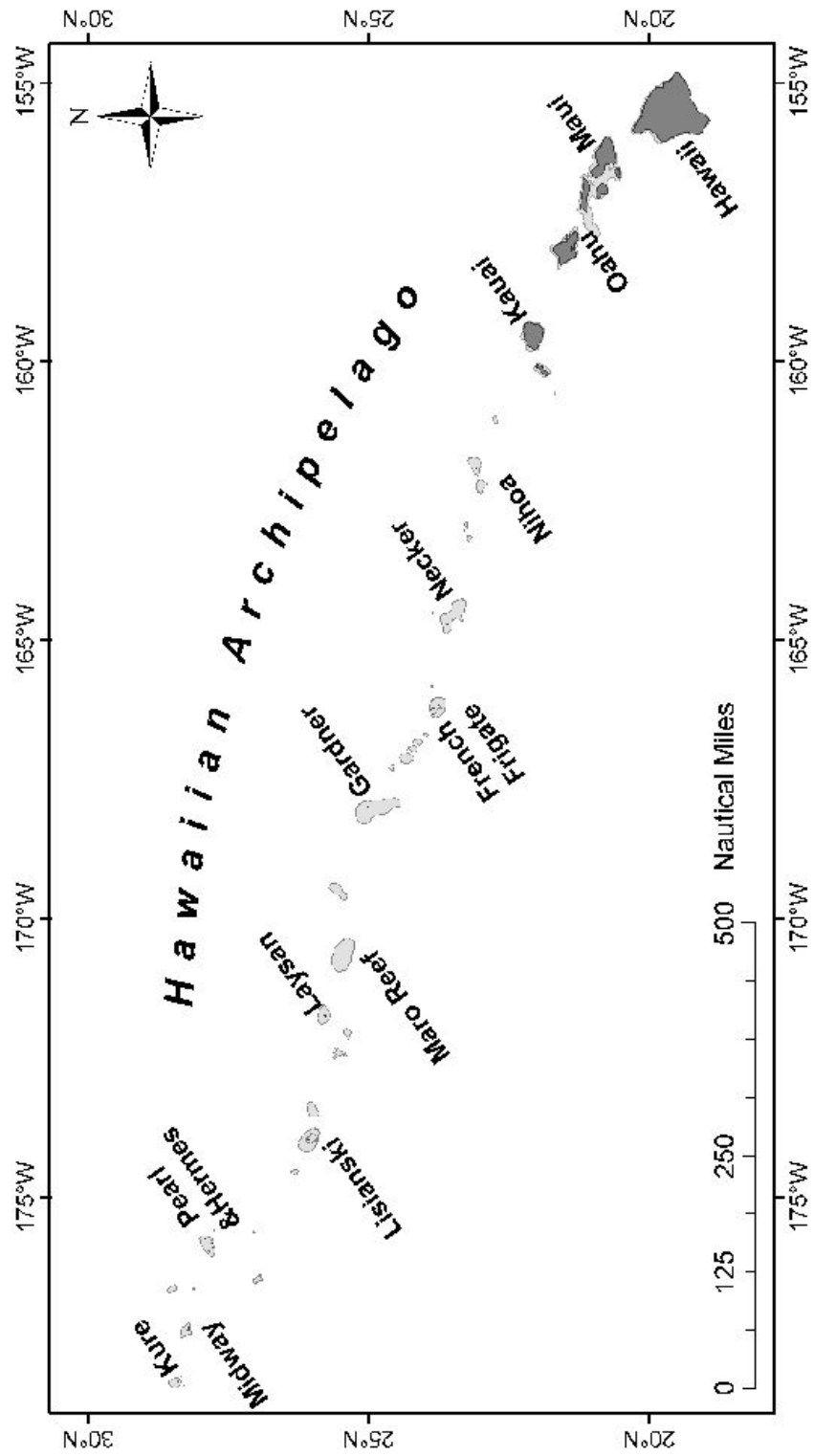
**Figure 1**. Map of the Hawaiian Archipelago, showing the Northwestern Hawaiian Islands study sites in relation to the main Hawaiian Islands.
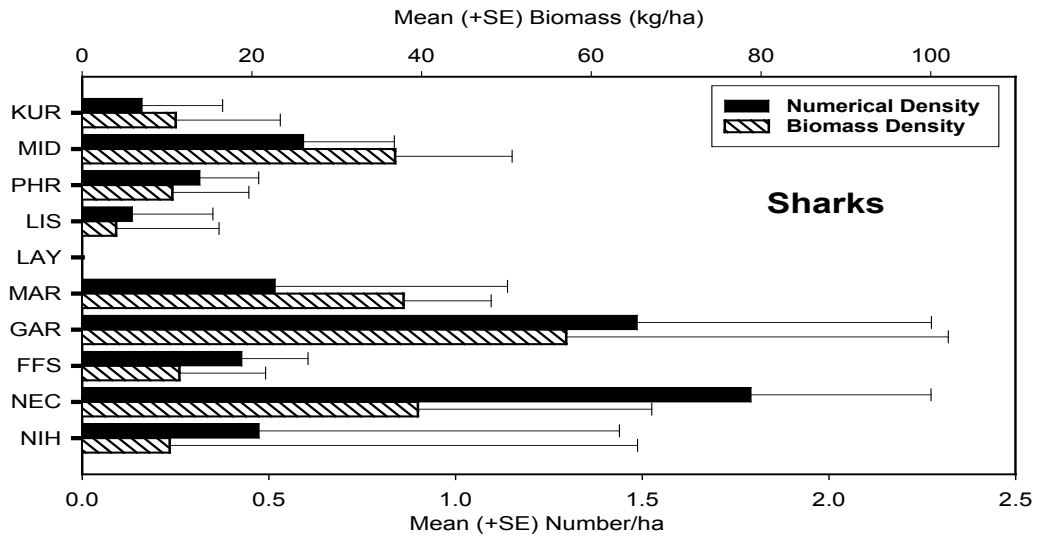
**Figure 2.** Mean numerical and biomass densities of sharks (Family Carcharhinidae) on NWHI reefs, listed from north to south.
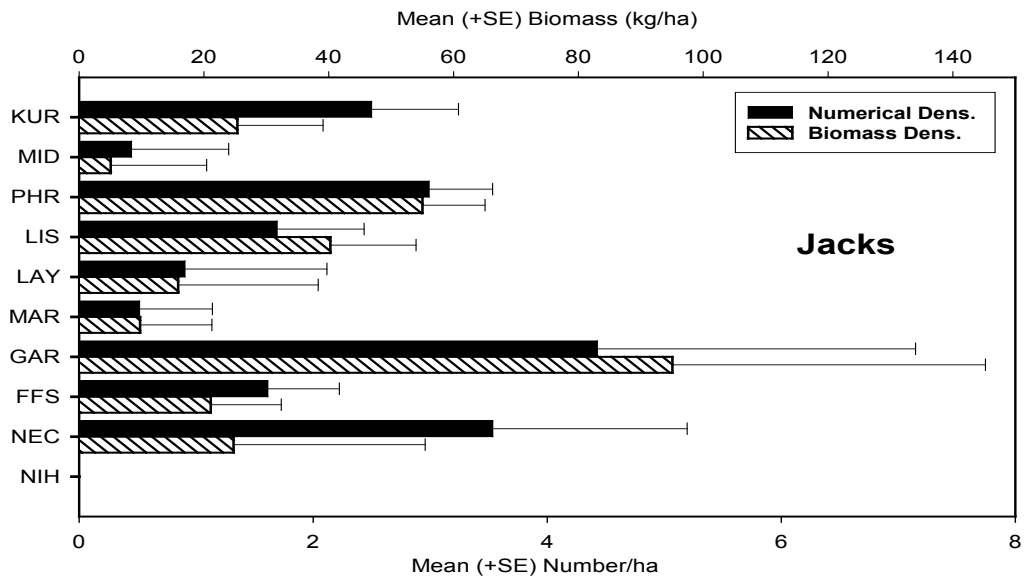


**Figure 3.** Mean numerical and biomass densities of jacks (Family Carangidae) on NWHI reefs, listed from north to south.
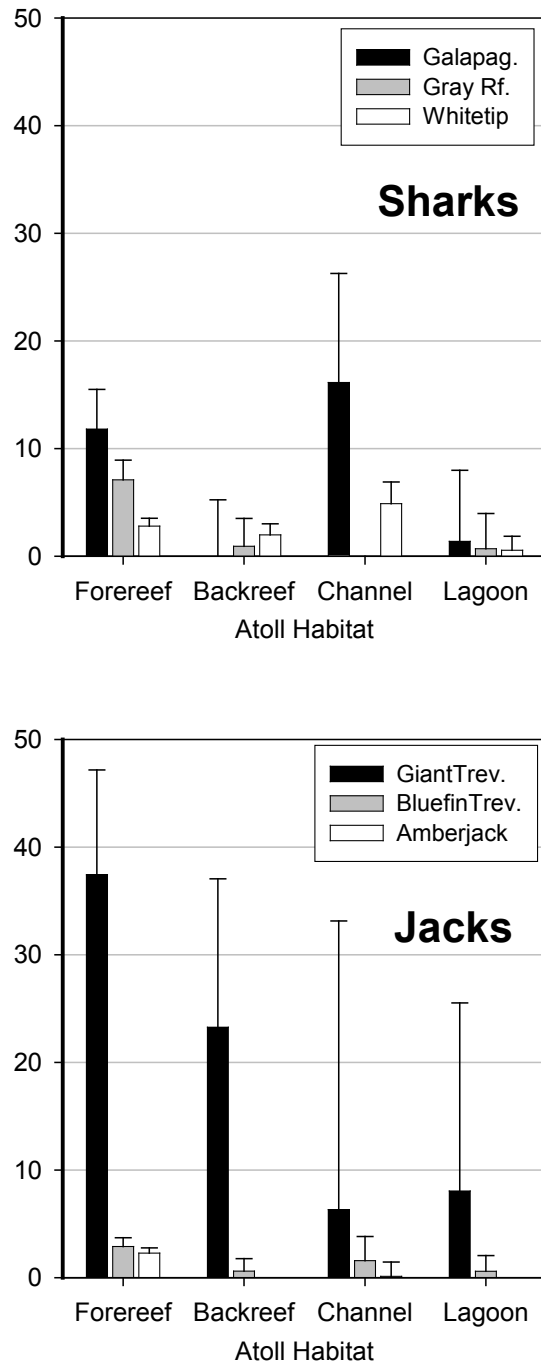
**Figure 4.** Mean biomass densities of top three shark and jack species on reef zone habitats within atolls (forereef, backreef, lagoon, and channel).
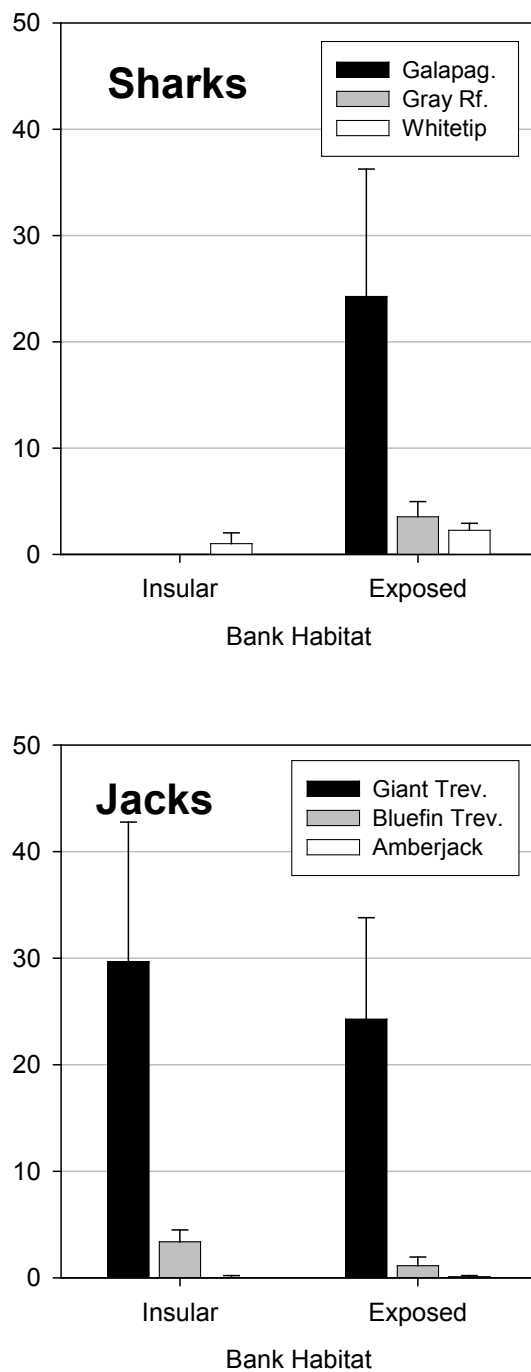
**Figure 5.** Mean biomass densities of top three shark and jack species in habitats within banks (insular and exposed reefs).
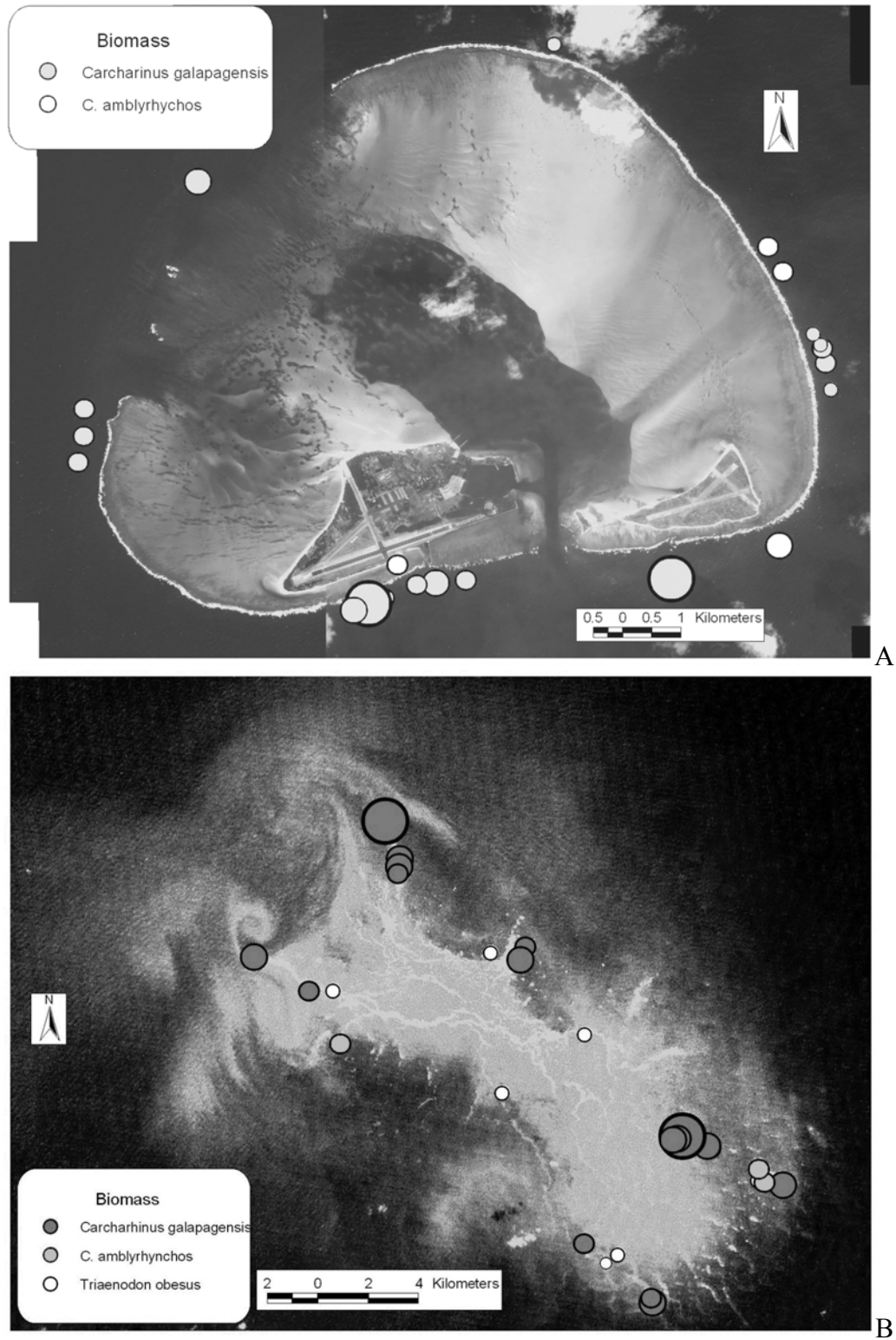
**Figure 6**. Spatial distribution of shark biomass by species at Midway Atoll (A) and Maro Reef (B) from towed-diver surveys (2000 to 2003). No whitetips were observed at Midway.
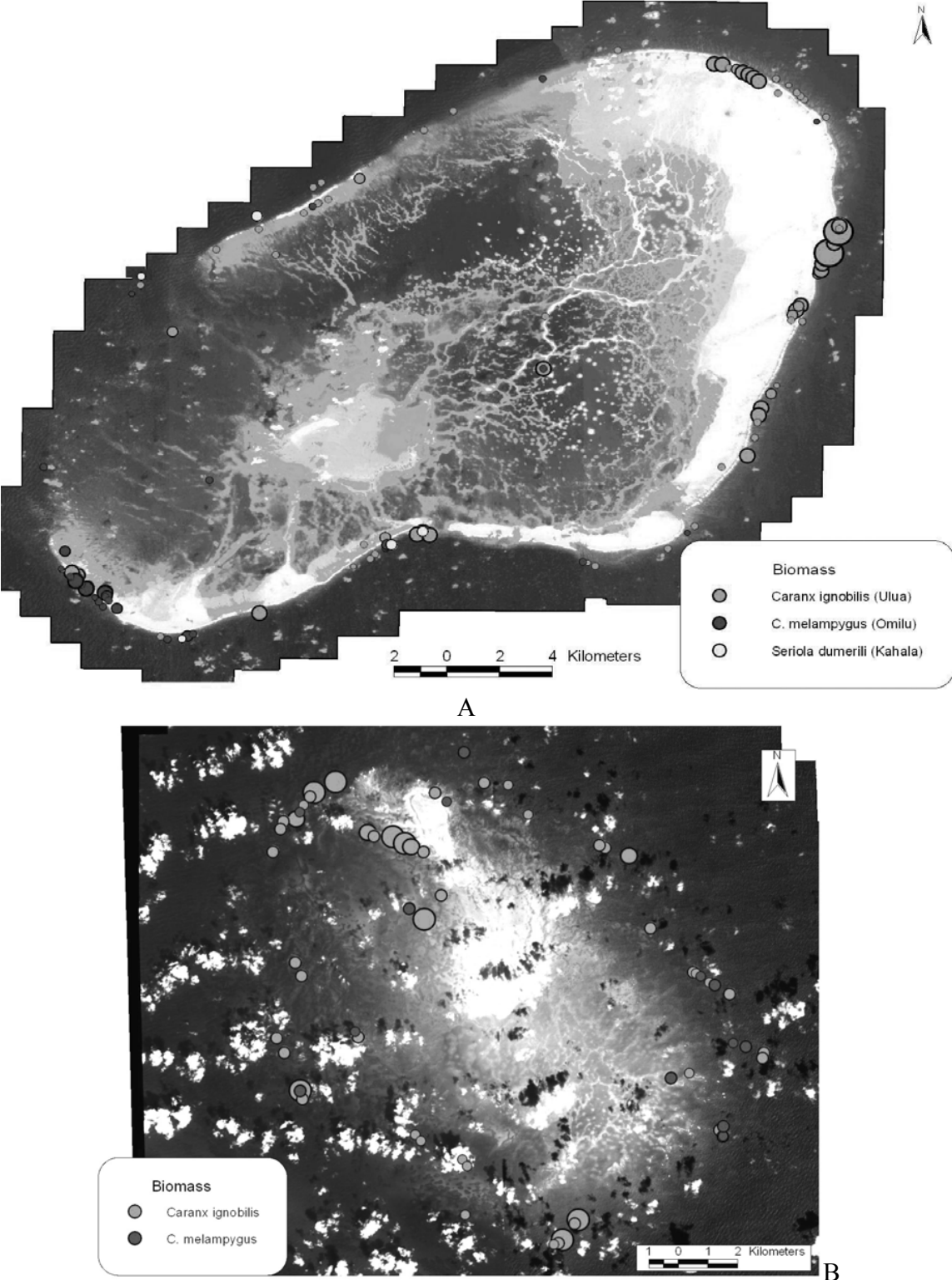
**Figure 7.** Spatial distribution of jack biomass by species at Pearl and Hermes Atoll (A) and Lisianski-Neva Shoals (B) from towed-diver surveys (2000 to 2003). No amberjack were observed at Lisianski-Neva

Table 1. Species of sharks and jacks recorded on NWHI towed-diver surveys. Species are listed within each family in decreasing order of total number of individuals (≥50-cm TL) observed during quantitative portions of towed-diver surveys. (* species seen only during non-quantitative portions of towed-diver surveys)

| Family/Species | Common name | Hawaiian/local name | Total $n$ |
|---|---|---|---|
| Carcharhinidae | | | |
| *Carcharhinus galapagensis* | Galapagos shark | mano | 171 |
| *Triaenodon obesus* | whitetip reef shark | mano lalakea | 99 |
| *C. amblyrhynchos* | gray reef shark | mano | 51 |
| *Galeocerdo cuvier* | tiger shark | niuhi | 1 |
| *C. limbatus* | blackfin shark | mano | * |
| Carangidae | | | |
| *Caranx ignobilis* | giant trevally | ʻulua aukea | 1004 |
| *C. melampygus* | bluefin trevally | ʻōmilu | 269 |
| *Psuedocaranx dentex* | thicklipped jack | butaguchi | 80 |
| *Seriola dumerili* | greater amberjack | kāhala | 60 |
| *Carangoides ferdau* | barred jack | ulua | 54 |
| *Elagatis bipinnulata* | rainbow runner | kamanu | 34 |
| *Caranx lugubris* | black trevally | ulua laʻuli | 2 |
| *Carangoides orthogrammus* | island jack | ulua | * |
| *Caranx sexfasciatus* | bigeye trevally | pake ulua | * |

Table 2. Statistical results of comparisons among reefs and among habitats. Results are given from one-way Kruskal-Wallis ANOVA on ranks for numerical (n/ha) and biomass (kg/ha) densities of sharks and jacks. For the among reefs comparison only data from habitats common to all reefs was used. An adjusted p-value of p<0.025 was used for tests on higher-order taxa and p<0.016 for tests on species-level taxa (*significant).

| Comparison | K-W ANOVA $\chi^2$ | df | P-value |
|---|---|---|---|
| **Among Reefs** | | | |
| Carcharhinidae | | | |
| Abundance | 34.32 | 9 | <0.001* |
| Biomass | 25.33 | 9 | <0.003* |
| Carangidae | | | |
| Abundance | 46.49 | 9 | <0.001* |
| Biomass | 49.59 | 9 | <0.001* |
| **Within Atolls: Forereef vs Backreef vs Lagoon vs Channel** | | | |
| Carcharhinidae | | | |
| gray reef shark | | | |
| Abundance | 10.10 | 3 | 0.018 |
| Biomass | 9.16 | 3 | 0.027 |

<u>Table 2. Continued</u>.

| | | | |
|---|---|---|---|
| Galapagos shark | | | |
| Abundance | 13.64 | 3 | 0.003* |
| Biomass | 13.83 | 3 | 0.003* |
| whitetip reef shark | | | |
| Abundance | 5.65 | 3 | 0.130 |
| Biomass | 5.07 | 3 | 0.167 |
| Carangidae | | | |
| giant trevally | | | |
| Abundance | 6.55 | 3 | 0.088 |
| Biomass | 4.56 | 3 | 0.207 |
| bluefin trevally | | | |
| Abundance | 5.33 | 3 | 0.149 |
| Biomass | 7.11 | 3 | 0.068 |
| amberjack | | | |
| Abundance | 16.37 | 3 | <0.001* |
| Biomass | 15.39 | 3 | 0.001* |

**Within Banks: Insular vs Exposed Reefs**

| | | | |
|---|---|---|---|
| Carcharhinidae | | | |
| gray reef shark | | | |
| Abundance | 4.03 | 1 | 0.045 |
| Biomass | 4.03 | 1 | 0.045 |
| Galapagos shark | | | |
| Abundance | 6.53 | 1 | 0.011* |
| Biomass | 6.53 | 1 | 0.011* |
| whitetip reef shark | | | |
| Abundance | 1.10 | 1 | 0.294 |
| Biomass | 0.64 | 1 | 0.423 |
| Carangidae | | | |
| giant trevally | | | |
| Abundance | 0.20 | 1 | 0.653 |
| Biomass | 0.71 | 1 | 0.426 |
| bluefin trevally | | | |
| Abundance | 0.35 | 1 | 0.552 |
| Biomass | 0.38 | 1 | 0.538 |
| amberjack | | | |
| Abundance | 0.19 | 1 | 0.662 |
| Biomass | 0.19 | 1 | 0.662 |

Table 3. Statistical results of *post-hoc* multiple comparisons (Kruskal-Wallis z-value test) of reefs (listed by number on left), by family. Numerical density (N) and biomass density (Bio) were compared among reefs. Reefs that differed significantly are listed (adjusted p=0.025). A dash (--) indicates no difference between listed reef and any other reef.

| | Reef differences | | | |
| --- | --- | --- | --- | --- |
| | Shark N | Shark Bio | Jack N | Jack Bio |
| 1-NIH | -- | -- | 2,3 | -- |
| 2-NEC | 3,5,6,7,8,9,10 | 3,5,6,7,8,10 | 1,3,5,6,9,10 | 5,9 |
| 3-FFS | 2,6 | 2,6 | 2,7,8 | 2,7,8 |
| 4-GAR | 6 | 6 | 1,5,9 | 5 |
| 5-MAR | 2 | 2 | 2,4,7,8 | 7,8 |
| 6-LAY | 2,3,4,8,9 | 2,3,4,5,8,9 | 2 | 7,8 |
| 7-LIS | 2 | 2 | 3,5,9,10 | 3,5,6,9,10 |
| 8-PHR | 2,6 | 2,6 | 2,3,5,10 | 2,3,5,6,10 |
| 9-MID | 2,6 | 6 | 2,4,7,8 | 2,7,8 |
| 10-KUR | 2 | 2 | 2,7,8 | 7,8 |

Table 4. Statistical results of *post-hoc* multiple comparisons (Kruskal-Wallis z-value test) of habitats (listed by number on left), by species. Densities of the top three jack and shark species were compared among habitats. Abundance and biomass results were identical. Habitats that differed significantly are listed (adjusted p=0.016). A dash (--) indicates no difference between listed habitat and any other habitat.

| | Habitat differences | | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | Sharks | | | Jacks | | |
| | GreyReef | Galapagos | Whitetip | GiantTrev | BluefinTrev | Amberjack |
| 1-Forereef | 2 | 2 | -- | -- | -- | 2,3 |
| 2-Backreef | 1 | 1,4 | -- | -- | -- | 1 |
| 3-Lagoon | -- | -- | -- | -- | -- | 2 |
| 4-Channel | -- | 2 | -- | -- | -- | -- |

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# USING ACOUSTIC TELEMETRY MONITORING TECHNIQUES TO QUANTIFY MOVEMENT PATTERNS AND SITE FIDELITY OF SHARKS AND GIANT TREVALLY AROUND FRENCH FRIGATE SHOALS AND MIDWAY ATOLL

BY

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## ABSTRACT

The Northwestern Hawaiian Islands (NWHI) host a variety of large vertebrate animals including seabirds, green sea turtles (*Chelonia mydas*), Hawaiian monk seals (*Monanchus schauislandi*), and large teleost fish such as trevally (Family Carangidae) and several species of sharks. The air-breathing vertebrates have been the subjects of relatively continuous and well-funded research programs over the past several decades, and many aspects of their biology in the NWHI have been documented fairly well. However, studies directed at understanding the biology and ecology of large teleost fishes and sharks in the NWHI have lagged substantially behind research conducted on birds, turtles and seals. In the summer of 2000, an array of autonomous acoustic receivers was deployed at French Frigate Shoals (FFS) in the NWHI as part of a project investigating the movement patterns of tiger sharks (*Galeocerdo cuvier*) within the atoll, particularly in relation to the high seasonal abundance of potential prey (birds, turtles, seals). Shortly after the establishment of the initial array of monitors in 2000, additional monitors were deployed in an effort to monitor the movements of Galapagos sharks (*Carcharhinus galapagensis*) at FFS, particularly at locations where monk seal pups had been preyed upon by these sharks. The scope of the monitoring study was further expanded to Midway Atoll during summer of 2001 to monitor movements of Galapagos sharks near seal haul-out beaches and to examine survivorship and behavior of giant trevally (*Caranx ignobilis*) captured and released in a commercial sport fishing operation conducted within the Midway National Wildlife Refuge. For each study, experimental animals were captured and surgically fitted with long-life, individually-coded acoustic transmitters. During nearly 4 years of acoustic monitoring at FFS and 2 years of monitoring at Midway, a total of over 45,000 detections of sharks and fish with transmitters were recorded on acoustic monitors. These data enable an assessment of long-term movement patterns of these large predators within the NWHI. Each species investigated demonstrated somewhat repeated and predictable behavioral patterns that provide a basis for improved understanding of determinants of behavior and for enhanced management of these animals and prey (birds, seals, turtles) with which they may interact.

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## INTRODUCTION

The Northwestern Hawaiian Islands (NWHI) support a wide variety of large marine vertebrates and are a well known breeding grounds for seabirds, green sea turtles (*Chelonia mydas*), and the endangered Hawaiian monk seal (*Monanchus schauislandi*) (Gerrodette and Gilmartin, 1990; Gilmartin and Eberhardt, 1995). The nearshore waters surrounding these islands are also home to several species of large, predatory fishes and sharks. Concern over negative human impacts on NWHI seabird, sea turtle, and monk seal populations has resulted in substantial efforts to monitor and rebuild populations of these animals (Gilmartin and Eberhardt, 1995). Establishment of NWHI field camps and permanent field stations has enabled long-term studies of these populations, and many aspects of the behavior, feeding, reproduction, and population dynamics of these species have been characterized (Rice and Kenyon, 1962; Harrison et al., 1984; Gilmartin and Eberhardt, 1995).

Despite their abundance (Friedlander and DeMartini, 2002), importance in trophic interactions as apex predators (Polovina, 1984), and possible impact on protected and endangered species populations (Balazs and Whittow, 1979; Alcorn and Kam, 1986; Lowe et al., 1996), studies on the biology and ecology of the large predatory fishes (sharks and trevally) of the NWHI have lagged considerably behind those of seabirds, turtles and seals. Much of the research that has been conducted on large marine fishes in the NWHI has been limited to islands with sufficient infrastructure (i.e., field stations, small boats, and ready access) to support seasonal or short-term field work (French Frigate Shoals and Midway), or has been conducted from research ships briefly visiting various islands within the NWHI (Tricas et al., 1981; Sudekum et al., 1991). Because of their solely aquatic nature, these fishes cannot be observed, captured, or monitored as easily as air-breathing vertebrates that spend periods of time either on land or at the surface.

Standard techniques typically used to assess and monitor fish populations in other locations are not effective in the NWHI for several reasons: 1) the remoteness of the NWHI adds greatly to the cost of fieldwork and transportation to study sites and reduces the effectiveness of methods that rely typically on local recreational or commercial fisheries; 2) the limited availability of suitable boating facilities within the NWHI and the often difficult sea conditions severely restrict use of small boats that are needed to access these fishes; 3) there are extensive fishing restrictions within the boundaries of the NWHI and Midway Atoll National Wildlife Refuge because of potential interactions with endangered monk seals; and 4) diver surveys are limited to only daytime observations and are often biased because divers tend to attract some of the large predatory fishes and may repel others.

Because of the limitations of various fishery techniques, telemetry has become increasingly popular for remote monitoring of fish populations (Voegeli et al., 2001; Simpfendorfer et al., 2002; Heupel et al., 2004; Lowe and Bray, 2006). Acoustic telemetry monitoring utilizes autonomous receivers to continuously "listen" for the presence or absence of organisms fitted with uniquely coded transmitters, and to store these data for long periods of time. Placement of autonomous receivers along a coastline, in channels, or in arrays can allow for relatively long-term (>1 year) monitoring of

movement patterns and fidelity to an area. Unlike conventional tag and recapture methods, acoustic monitoring allows for repeated "electronic" recaptures without the need for continuous fishing efforts and in some instances may be a more effective tool for monitoring population dynamics of species such as sharks and trevally that are difficult to study (Voegeli et al., 2001).

We used an array of autonomous acoustic receivers to monitor the movement patterns and site fidelity of tiger sharks (*Galeocerdo cuvier*), Galapagos sharks (*Carcharhinus galapagensis*), and giant trevally (*Caranx ignobilis*) around specific islands at FFS and Midway Atoll from 2000 to 2004. The objectives of this paper are to demonstrate whether these large predatory fishes show any affinity to islands containing common semi-terrestrial prey (i.e., seabirds, sea turtles, and monk seals) and to illustrate the utility of acoustic monitoring for studying the movement patterns of large fishes in remote locations over varying spatial scales.

## METHODS

Study Sites

This study was conducted at two atolls within the NWHI: French Frigate Shoals (FFS) from 2000 to 2004, located midway along the Hawaiian Archipelago (23° 52.3' N latitude, 166° 14.4' W longitude); and Midway Atoll from 2001 to 2003, near the northwestern end of the chain (28° 15' N latitude, 177° 20' W longitude). At FFS, our base of operation was the U.S. Fish and Wildlife Service (USFWS) field station on Tern Island, and at Midway operations were conducted in cooperation with USFWS and Midway Phoenix Corporation from Sand Island.

Fishing and Tagging

Sharks were caught using handlines baited with dead birds or fish. Handlines were monitored continuously during all fishing efforts. Our fishing methods used large hooks (14/0) and large baits in order to target larger sharks, although several species of smaller sharks (gray reef sharks – *Carcharhinus amblyrhynchos* and whitetip reef sharks (*Triaenodon obesus*) were occasionally caught at FFS. All tiger and Galapagos sharks caught were brought along side of the 6-m boat, and a rope was placed around their tail. Once sharks were restrained, they were inverted and placed in tonic immobility, at which point each was measured, sexed, tagged with an external identification tag (M-capsule tags or spaghetti type dart tags) in the dorsal musculature, and fitted with a coded acoustic transmitter.

At FFS the majority of fishing for tiger sharks was conducted near the center of the atoll at East Island, whereas Galapagos sharks were targeted primarily at Trig Island, along the perimeter of the atoll (Fig. 3). During the final 2 years of operations at FFS, we were not permitted to fish within 800 m of Trig Island or to use chum in attempts to attract sharks to baited hooks. The same methods used to fish for Galapagos and tiger sharks at FFS were employed at Midway Atoll; however, giant trevally were caught via trolling or by dunking fresh bait from a boat.

Transmitters and Autonomous Acoustic Receivers

To determine longer-term site fidelity of sharks and trevally to islets at FFS and Midway, individuals were fitted with coded acoustic transmitters (V16-R256 random coded, 69.0 kHz, Vemco). Sharks caught on handlines were brought along side the boat and placed in tonic immobility (Fig. 1a, b). Coded transmitters were implanted surgically into the body cavity of sharks through a small incision (4 cm), and the wound was closed with 4-5 interrupted sutures. Transmitters were coated with a combination of beeswax (30%) and paraffin wax (70%) to reduce immune response (Holland et al., 1999). Each transmitter emitted a uniquely coded acoustic signal at random intervals between 40-70 seconds and had battery lives of up to 4 years.

Giant trevally were anaesthetized with MS-222 (0.2 g/L, 30 to 45 s immersion time), placed on a foam pad and measured (fork length (FL) in cm). A coded transmitter (V16-R256 random coded, 69.0 kHz) coated with beeswax/paraffin was implanted surgically into the body cavity of each fish (Fig. 1c). Before surgery the scalpel blade and transmitter were immersed in iodine solution, and the incision site was swabbed with iodine solution. A small (20 mm) incision was made through the peritoneal wall into the posterior region of the body cavity. This site was chosen to avoid damage to internal organs from transmitter insertion. The transmitter was inserted into the body cavity through the incision, which then was sutured closed. Each fish was also tagged externally with a serially numbered, 10-cm plastic dart identification tag (Hallprint, South Australia), resuscitated by towing or swimming it alongside the boat until fully responsive, and then released (Fig. 2).

An array of autonomous acoustic receivers (VR1 model, Vemco) was placed at locations around various islands within FFS and Midway. These receivers are designed to listen for coded transmitters and to record the date and time of arrival and departure of individual sharks and trevally. At FFS, 10 receivers were placed around Tern, Trig, Round, East, Shark, and Gin Islands at depths easily reached by free diving (average depth of monitors was 2.5 m below the surface) (Fig. 3a). At Midway, five receivers were placed adjacent to Sand and Eastern Islands, in the main boat channel and on the outer reef at a dive site named "Fish Hole" (Fig. 3b). USFWS personnel recovered three of these receivers in summer 2004, but were unable to relocate the receiver from Fish Hole.

All receivers were secured to the benthos using sand screws and swiveling stainless steel rods. Foam floats were used to buoy acoustic receivers and attachment gear (Fig. 4). This design was chosen to reduce the risk of monk seal entanglement in the equipment arrays. The majority of receivers remained in place for many years with this design, although several floats were lost, and all floats that were still attached to monitors showed evidence of shark bites.

Acoustic range of each receiver varied depending on water depth, tide, and neighboring reef structure. Range tests at several sites indicated transmitter detection ranges of up to 400 m; however, at most locations the range was on the order of 20-50 m due to shallow depth and proximity of a reef or an island. Receivers were downloaded every 4 to 7 months by the research team or by USFWS personnel.

Site Fidelity and Movement Analysis

Degree of site fidelity and extent of use of a particular area was determined by the amount of time a fish spent in proximity to a particular receiver and by the number of detections at each location. Annual catch rates (CPUE) and recapture rates were determined for each island. Extent of movement within the acoustic receiver array at all islands was determined by measuring the linear distance between the two most distant receivers where tagged sharks or giant trevally were detected.

**RESULTS**

French Frigate Shoals

*Catch Data*. During four summers (2000-2003) and one fall (2002), a total of 477 h were spent fishing at East and Trig Islands, with 190.5 h spent fishing around East Island. A total of 34 sharks were caught at FFS, including tiger, Galapagos, whitetip reef, and grey reef sharks. Of the 34 sharks caught, 4 Galapagos and 13 tiger sharks were fitted with coded acoustic transmitters (Table 1). With the exception of a few whitetip reef and gray reef sharks, only tiger sharks were caught at East Island, whereas many of the sharks caught and observed at Trig Island were Galapagos sharks. The CPUE for tiger sharks in all fishing at East Island was 0.052 sharks $h^{-1}$. In 2002 and 2003, very little time was spent fishing at East Island (7.5 h), and no tiger sharks were caught. In previous years, tiger sharks were frequently observed preying on fledging albatross chicks in the mornings, when the winds appeared to provide the best opportunities for the young birds to fly. In 2003, we sighted very few tiger sharks at East Island, although this trip was conducted during August, when nearly all albatross have fledged from East Island. No Galapagos sharks were seen or caught at East Island.

During 2002-2003, the majority of fishing effort was focused in the vicinity of Trig Island in an attempt to target Galapagos sharks. A total of 274 h was spent fishing near Trig Island. Although tiger sharks were rarely seen at Trig Island, over all years we caught one small, one medium and two large-sized tiger sharks (178, 259, 394, and 397 cm TL), three of which were captured in October of 2002 (Table 1). A total of four Galapagos sharks were also captured at Trig Island. CPUEs for tiger sharks and Galapagos were identical (0.015 sharks $h^{-1}$). Galapagos sharks were the most common large sharks observed at Trig Island; however, their occurrence appeared to vary widely on both a daily and annual basis.

The total fishing effort in all years of this study resulted in the capture, tagging, and instrumentation with transmitters of 13 tiger sharks and 4 Galapagos sharks. Ten gray reef sharks were also caught during this time period but were only tagged with standard identification tags, and none of the whitetip reefs sharks caught were tagged. All tiger sharks caught were females, of which ~70% appeared notably rotund and may have been pregnant. The average total length of tiger sharks caught was 350 ± 7 cm (± sd), and, based on available reproductive data, it is likely that all except two sharks were mature (Wetherbee et al., 1994). The four Galapagos sharks captured at Trig were relatively large and had an average total length of 248 ± 2 cm (Table 1).

*Acoustic Monitoring.* All of the 13 tiger sharks tagged at FFS were detected by acoustic receivers. Tiger sharks were detected a total of 38,886 times during the course of this project. Two tiger sharks (ID tag #005 and #011) were not detected on receivers until 26 and 11 months, respectively, following tagging and release. Of the nine tiger sharks tagged at East Island, all were detected at East Island as well as at islands other than East Island (Trig, Gin, Round, Shark, and Tern Island) throughout the year at FFS. Based on the number of acoustic detections (hits) recorded by different receivers, the amount of time sharks spent in proximity to certain islands varied considerably. A vast majority of the hits from tiger sharks were recorded in June and July at East Island, whereas tiger sharks spent proportionally more time around Tern Island in the winter months (Fig. 5). With the exception of the monitors at East Island, detections were usually brief, suggesting that sharks were passing through an area when detected. Tiger sharks also showed distinct temporal patterns of visits to the various islands, particularly at East Island, where they were typically detected during summer months in the mornings. One tiger shark (#005) tagged at East Island, FFS in July 2000 was detected by an array of acoustic receivers off the Kona coast (approx. 1,190 km straight-line distance) from January-March 2003. Another tiger shark (#008) tagged at East Island, FFS in July 2000 was detected by our array of acoustic receivers off Midway (approx. 1,280 km straight-line distance) from September-December 2002 (Table 1).

Of the four Galapagos sharks tagged, three were detected by acoustic receivers at FFS, yielding a total of 2,891 detections during the entire study. These sharks were detected primarily by monitors at Trig Island, followed by Tern Island, and only a few brief detections at Shark and East Islands. The occurrence of Galapagos sharks at Trig Island varied seasonally, with fewest detections recorded between February and July, and an elevated number of detections between August and January (Fig. 6). Detections at Tern Island, as well as Shark and East Islands, also were highest between September and February (Fig. 6). The number of detections at different times of day for all Galapagos sharks pooled indicated that these sharks visited Trig throughout the day, but more frequently at night. At other islands (Tern and Shark), Galapagos sharks also were detected more frequently during nighttime hours (Fig. 6).

Midway

*Acoustic Monitoring.* The Midway Atoll Galapagos shark data are skewed by VR1 receiver coverage due to difficulties in getting to Midway Atoll in order to download and rebattery receivers. The batteries in several VR1 receivers deployed in summer 2001 failed in May 2002 and were not replaced until September 2002. Only three of five VR1 receivers deployed in September 2002 were recovered successfully by USFWS personnel. The two VR1s that were lost (Fish Hole, Main Channel) were historically the receivers with the most Galapagos shark detections. The combination of these events meant that no data were available for the heavily utilized Fish Hole and Channel locations after May 2002.

Six Galapagos sharks were detected by the array of underwater receivers at Midway Atoll over periods ranging from 55 to 749 days (Table 2). Based on detections at receivers spread across the atoll, sharks were detected at receivers ranging from 1 to 9

km apart. The movements of all six sharks overlapped, with each individual being most frequently detected at the Fish Hole and Channel locations (Fig. 7). Five sharks showed a day-night habitat shift, with four individuals occupying channel and forereef habitats by day and venturing up onto the shallow reef flats at night. One Galapagos shark showed the reverse pattern (arriving in the channel only at night), while the remaining individual did not show any obvious diel periodicity in movements (Fig. 7).

During September 2002, four giant trevally ranging in size from 100 to 146 cm FL were captured using hook and line (trolling and dunking from a boat) at Midway Atoll (Table 3). Three of the four giant trevally tagged at Midway were detected by the array of underwater receivers at Midway Atoll over periods ranging from 280 to 374 days (Table 3). Two of these fish had previously been tagged and released by the Midway sport fishery. Based on detections at receivers spread across the atoll, giant trevally were detected at receivers ranging from 5 to 9 km apart. The movements of these three fish overlapped, even though they were captured at different locations up to 9 km apart. The one receiver located on the outside edge of the atoll was lost (Fish Hole – Fig. 2b), but the four remaining receivers each detected at least two giant trevally on multiple occasions over a 12-month period (Fig. 8). The diel pattern of detections varied among the giant trevally, with one fish (U2792) showing a day-night habitat shift during 2002, whereas the other two lacked obvious diel periodicity (Fig. 8). There was also some seasonal variation in frequency of giant trevally detections, with fewest detections occurring during the winter months (Fig. 9).

## DISCUSSION

Acoustic monitoring proved to be an effective method for studying site fidelity and movement patterns of large marine fishes at French Frigate Shoals and Midway Atoll. This technology yielded tens of thousands of detections of transmitter-equipped animals, which provided new insight into both general patterns of behavior and distinct behavioral differences among individuals and among species of large fishes at these locations. For example, previous anecdotal observations of tiger sharks at French Frigate Shoals suggested that tiger sharks dramatically increase in abundance during summer and were perhaps only seasonal visitors to this atoll (Tricas et al., 1981; Lowe et al., 1996). However, acoustic monitoring data from 13 tagged tiger sharks indicated that at least 70% of these sharks exhibited some degree of year-round residence at FFS over a 3-year period. Although some tiger sharks were detected at islands within FFS during every month of the year, many were not detected for as long as 2-month intervals. While it is possible that these individuals could have traveled to neighboring atolls or shoals during these periods, it is also possible that they simply moved to other areas in or around the atoll where there was no receiver coverage. Some of the individuals tagged at FFS were detected by acoustic receivers at Midway and off the Kona coast (on the Island of Hawaii), indicating that individual tiger shark movements can encompass the entire Archipelago.

Even though tiger sharks were detected at FFS throughout the year, there was a strong seasonal trend in area use through the atoll, with tiger sharks spending more time

around East Island in the summer months, but more time around the northern islands (Tern, Trig, and Shark Islands) in winter months. The one tiger shark tagged at Midway Atoll (#019) in July 2001 was detected near the flats off Eastern Island and near the cargo pier only during summer months.

A total of 38,886 detections were recorded from all receivers placed near six islands at FFS. The estimated total acoustic detection area of all 10 acoustic receivers was approximately 0.031 km², which accounts for less than 0.004% of the shallow lagoon habitat at FFS. Considering the vast area of available habitat for tiger sharks at FFS and the small detection areas of acoustic receivers in these shallow reef areas, the high numbers of detections clearly indicate that tiger sharks regularly visit these islands, in response to concentration of important prey items at particular islands during summer months.

Compared to tiger sharks, there is a much smaller amount of data available for analysis of movement patterns of Galapagos sharks at FFS. Furthermore, the presence of these sharks at Trig Island varied within the diel cycle, within annual cycles, and among individual sharks. Although only four adult Galapagos sharks were caught and tagged at FFS, acoustic receiver data and visual observations by many researchers at FFS suggest that Galapagos sharks are most common at islands close to the outer reef of FFS (i.e., Tern, Trig, and Shark) and are not frequent visitors to the interior of the atoll. This contention is supported by previous studies which indicate that Galapagos sharks are typically found along outer reef drop-offs (DeCrosta et al., 1984; Wetherbee et al., 1996). Galapagos sharks were the most common species of large shark observed at Trig Island, possibly attracted by the recent increase in seasonal monk seal pupping at this site. Adult Galapagos sharks have been observed cruising very close to the shore (< 2 m) and occasionally preying on pre-weaned monk seal pups at this location (Baker and Johanos, 2004). Acoustic monitoring indicated high variability in Galapagos shark activity at Trig Island, but these data were primarily derived from only two individuals that each showed different patterns of activity around Trig. One shark was most commonly detected in the late afternoon during summer months, whereas the other was most commonly at Trig during early morning hours in winter. Clearly, more research is required to understand the behavior of adult Galapagos sharks at Trig Island, and to provide sufficient data for assessing the potential success of using shark culling to reduce seal predation. Nevertheless, it appears that Galapagos sharks do not exhibit the same island visitation patterns as tiger sharks.

The Galapagos sharks tagged at Midway exhibited different movement patterns from those tagged at FFS; however, this may be attributed to differences in size/age of sharks tracked. The lagoon and main channel at Midway contained large numbers of juvenile Galapagos sharks, which were not observed or caught at FFS. The juvenile Galapagos sharks at Midway tended to use the channel areas or forereef during the day, but would venture onto flats inside the atoll at night, and some of these small sharks moved at least 10 km between acoustic receivers. Considering the arbitrary positioning and limited number of acoustic receivers throughout the atoll, the number of detections and individual sharks detected suggest that these young Galapagos sharks move extensively throughout the lagoon habitat at Midway. The differences in Galapagos shark

movements and habitat use at FFS and Midway may be related to the different size of sharks. For example, in some locations Galapagos sharks use shallow lagoons as nursery grounds (Kato and Carvallo, 1967) and in the Main Hawaiian Islands Galapagos sharks segregate by size and sex, but do not appear to use lagoon nurseries (Wetherbee et al., 1996).

Three of the four giant trevally equipped with acoustic transmitters at Midway Atoll were detected by four acoustic receivers spread across the southern portion of the atoll. Only one of the three giant trevally detected at Midway showed any diel pattern of area use; however, all three were found to span at least 10 km between the most distant receivers. Interestingly, the one trevally that exhibited a diel pattern of habitat use (U2792) exhibited that behavior only for the first few months. Fish were typically detected on the flats by Eastern Island or Frigate Point at night, sometimes for many hours. These observations suggest high plasticity in behavior. Other fish have been shown to exhibit diel-habitat shifts, including bluefin trevally (*Caranx melampygus*) and juvenile giant trevally in the Main Hawaiian Islands (Holland et al., 1996; Wetherbee et al., 2004; Meyer and Honebrink, 2005). Two of the giant trevally detected at Midway were most common during summer and fall months, but decreased substantially in the winter months. It is unclear whether these fish left the atoll during winter or moved to locations at Midway that lacked receiver coverage. This sort of seasonal shift in habitat use has not been seen in younger size classes studied in the Main Hawaiian Islands (Wetherbee et al., 2004). Nevertheless, seasonal differences in water temperature between the Main Hawaiian Islands and Midway may explain these possible seasonal area use patterns observed among the few giant trevally monitored.

We demonstrate that acoustic monitoring can provide an effective method for assessing long-term site fidelity and behavior of large fishes in remote areas. Obviously, more detailed information about movement patterns and habitat use could have been obtained if there were a greater number of receivers spread throughout each atoll; however, the main focus of the studies at FFS and Midway was to examine shark and trevally affinity to islands that hold large numbers of semi-terrestrial prey. Extensive fishing, tag and recapture, and visual observations conducted continuously over many years would have been required to answer this question, resulting in a much higher cost and impact to the environment. While acoustic monitoring provides a far less labor-intensive method for measuring site fidelity and movement patterns of large fishes in remote areas, it still requires a certain degree of maintenance to ensure successful retrieval of data. Autonomous acoustic receivers must be periodically downloaded, and batteries must be replaced. Securing ground tackle also needs to be maintained annually, particularly in areas exposed to high surf. Although this maintenance does not take long and can be done by small crews, the remoteness of the NWHI makes regular array maintenance challenging, as was seen at Midway Atoll where we were unable to place personnel to regularly maintain receivers. This resulted in loss of data and a receiver. In addition, autonomous acoustic receivers have the capacity to record and store large amounts of data, which, over time, requires extensive database management.

With a moderate fishing effort, hundreds of large marine apex predators (fishes, sharks, seals, and turtles) could be tagged, and acoustic receivers could be placed

strategically around each of the major islands and shoals throughout the NWHI to assess long-term site fidelity, dispersal potential, and even species interactions. Receiver arrays can be maintained quickly and easily with moderate ship support. In fact, the newest form of autonomous acoustic receiver (VR3, Vemco Ltd.) now incorporates a tethered surface transmitter that can relay stored data to a satellite or via acoustic modem to a ship, eliminating the need to retrieve and manually download the receivers. Because of the logistical challenges of access to the NWHI, potential conflicts with endangered species, and difficulty in studying large marine fishes, acoustic monitoring coupled with satellite telemetry may provide the most cost-effective, environmentally sound means of studying the apex predators of the NWHI.

## ACKNOWLEDGEMENTS

Table 1. Summary of acoustic monitoring data for transmitter-equipped tiger and Galapagos sharks captured at French Frigate Shoals.

| Species | ID Tag Number | Length (cm) | | | Sex | Date Deployed | Date First Detected | Date Last Detected | Days Between Deployment & First Detection | Overall Detection Period (days) | Max. Distance Spanned (km) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | PCL | FL | TL | | | | | | | |
| *G. cuvier* | 002 | 255 | 284 | 330 | F | 25-Jun-00 | 30-Jun-00 | 16-Apr-03 | 5 | 1020 | 20 |
| *G. cuvier* | 001 | 294 | 320 | 389 | F | 27-Jun-00 | 18-Aug-00 | 27-Nov-02 | 52 | 831 | 12 |
| *G. cuvier* | 003 | 237 | 260 | 316 | F | 3-Jul-00 | 3-Jul-00 | 20-Dec-01 | 0 | 535 | 22 |
| *G. cuvier* | 004 | 127 | 138 | 178 | F | 10-Jul-00 | 6-Aug-00 | 10-Jan-04 | 27 | 1252 | 20 |
| *G. cuvier* | 005 | 320 | 354 | 392 | F | 11-Jul-00 | 11-Jul-00 | 19-Sep-02 | 0 | 989 | 1190 |
| *G. cuvier* | 007 | 295 | 318 | 372 | F | 11-Jul-00 | 22-Jul-00 | 28-Nov-03 | 11 | 1224 | 20 |
| *G. cuvier* | 008 | 302 | 333 | 364 | F | 12-Jul-00 | 12-Jul-00 | 26-Dec-02 | 0 | 897 | 1280 |
| *G. cuvier* | 009 | 301 | 328 | 392 | F | 19-Jun-01 | 25-Jun-01 | 16-Sep-03 | 6 | 813 | 18 |
| *G. cuvier* | 011 | 325 | 353 | 422 | F | 21-Jun-01 | 22-Jun-01 | 18-Nov-03 | 1 | 879 | 13 |
| *G. cuvier* | 001F | 280 | 303 | 342 | F | 30-Jun-01 | 30-Jun-01 | 28-Dec-01 | 0 | 181 | 22 |
| *G. cuvier* | 006F | 192 | 215 | 259 | F | 26-Oct-02 | 9-Nov-02 | 10-Jan-04 | 14 | 427 | 22 |
| *G. cuvier* | 305 | 306 | 334 | 394 | F | 28-Oct-02 | 17-Dec-02 | 22-Apr-03 | 50 | 126 | 20 |
| *G. cuvier* | 304 | 310 | 339 | 397 | F | 29-Oct-02 | 5-Nov-02 | 28-Nov-03 | 7 | 388 | 20 |
| *C. galapagensis* | 025 | 204 | 227 | 250 | F | 3-Jul-00 | 6-Aug-00 | 23-Oct-00 | 34 | 78 | 5 |
| *C. galapagensis* | 026 | 193 | 212 | 244 | M | 18-Jun-01 | 24-Jun-01 | 24-Jun-01 | 6 | 0 | - |
| *C. galapagensis* | 028 | 165 | 182 | 225 | F | 1-Jul-01 | 10-Jul-01 | 20-Oct-02 | 9 | 467 | 8 |
| *C. galapagensis* | 031 | 208 | 231 | 272 | F | 10-Jun-02 | 16-Jun-02 | 12-Feb-03 | 6 | 241 | 14 |

Table 2. Summary of acoustic monitoring data for transmitter-equipped Galapagos and tiger sharks captured at Midway Atoll.

| Species | ID Tag Number | Length (cm) | | | Sex | Date Deployed | Date First Detected | Date Last Detected | Days Between Deployment & First Detection | Overall Detection Period (days) | Max. Distance Spanned (km) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | PCL | FL | TL | | | | | | | |
| *G. cuvier* | 306 | 390 | 318 | 294 | M | 27-Jul-01 | 12-Aug-01 | 1-Sep-03 | 16 | 750 | 9 |
| *C. galapagensis* | 299 | 118 | 96 | 89 | M | 24-Jul-01 | 4-Aug-01 | 23-Aug-03 | 11 | 749 | 9 |
| *C. galapagensis* | 300 | 157 | 131 | 120 | F | 24-Jul-01 | 1-Aug-01 | 16-Apr-03 | 8 | 623 | 5 |
| *C. galapagensis* | 301 | 114 | 100 | 91 | M | 25-Jul-01 | 15-Nov-01 | 24-Jun-03 | 113 | 586 | 1 |
| *C. galapagensis* | 302 | 130 | 105 | 96 | F | 26-Jul-01 | 3-Aug-01 | 27-Sep-01 | 8 | 55 | 5 |
| *C. galapagensis* | 303 | 122 | 100 | 90 | M | 26-Jul-01 | 22-Aug-01 | 26-May-02 | 27 | 277 | 5 |
| *C. galapagensis* | 307 | 135 | 118 | 105 | F | 27-Jul-01 | 1-Aug-01 | 18-Oct-01 | 5 | 78 | 1 |

Table 3. Summary of acoustic monitoring data for four transmitter-equipped giant trevally (*Caranx ignobilis*) captured at Midway Atoll.

| Species | ID Tag Number | Fork Length (cm) | Date Deployed | Date First Detected | Date Last Detected | Days Between Deployment & First Detection | Overall Detection Period (days) | Max. Distance Spanned (km) |
|---|---|---|---|---|---|---|---|---|
| *C. ignobilis* | U2795 | 100 | 8-Sep-02 | 20-Sep-02 | 27-Jun-03 | 12 | 280 | 5 |
| *C. ignobilis* | U2793 | 116 | 8-Sep-02 | Not Detected | - | - | - | - |
| *C. ignobilis* | U2791[+] | 109 | 10-Sep-02 | 13-Sep-02 | 5-Sep-03 | 3 | 357 | 9 |
| *C. ignobilis* | U2792* | 146 | 10-Sep-02 | 11-Sep-02 | 20-Sep-03 | 1 | 374 | 9 |

*Recapture (original tag # 0148)
[+]Recapture (original tag # MAO 495)

**Figure 1** a. A 4 m tiger shark in tonic immobility along side a 5.2m Boston Whaler. La Perouse in the background. b. Field surgery on a 2.5 m tiger shark at Trig Island. c. A Vemco model V16 coded acoustic transmitter.

**Figure 2**. Surgical implantation of a V16 coded acoustic transmitter in an anaesthetized 1.3 m giant trevally.
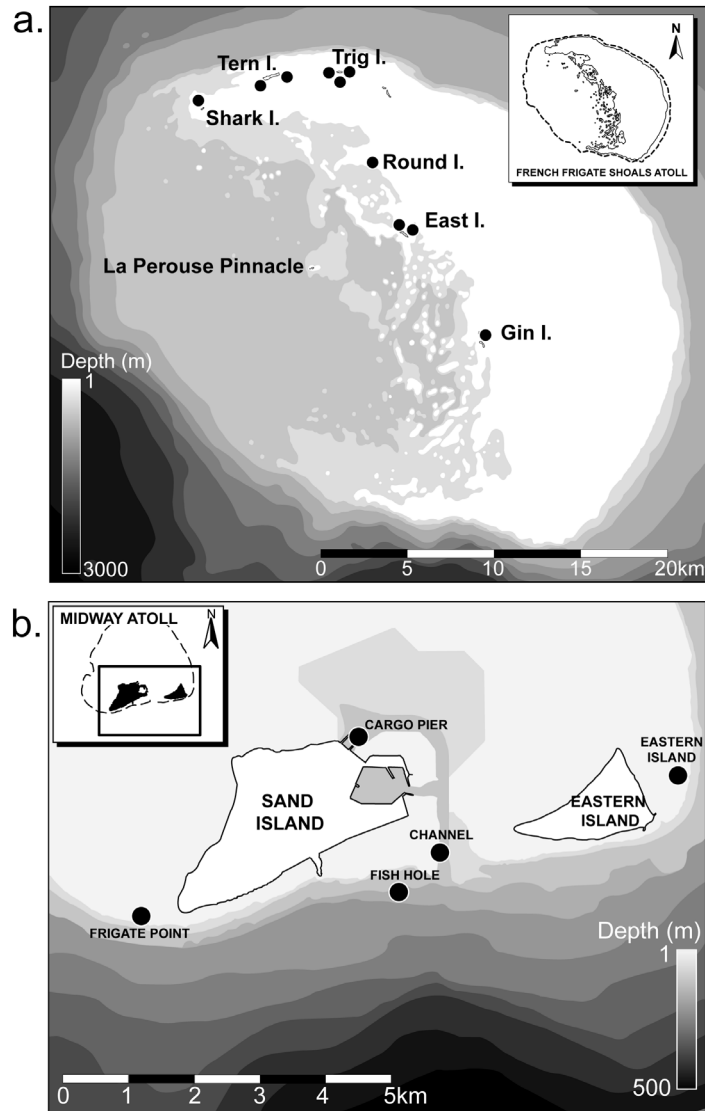
**Figure 3** a. Location of automated acoustic receivers (VR1, Vemco Ltd.) (solid circles) at French Frigate Shoals.  b. Locations of automated acoustic receivers (solid circles) at Midway Atoll.

**Figure 4**. Diver with a VR1 autonomous acoustic receiver anchored to the seafloor with sand screws.
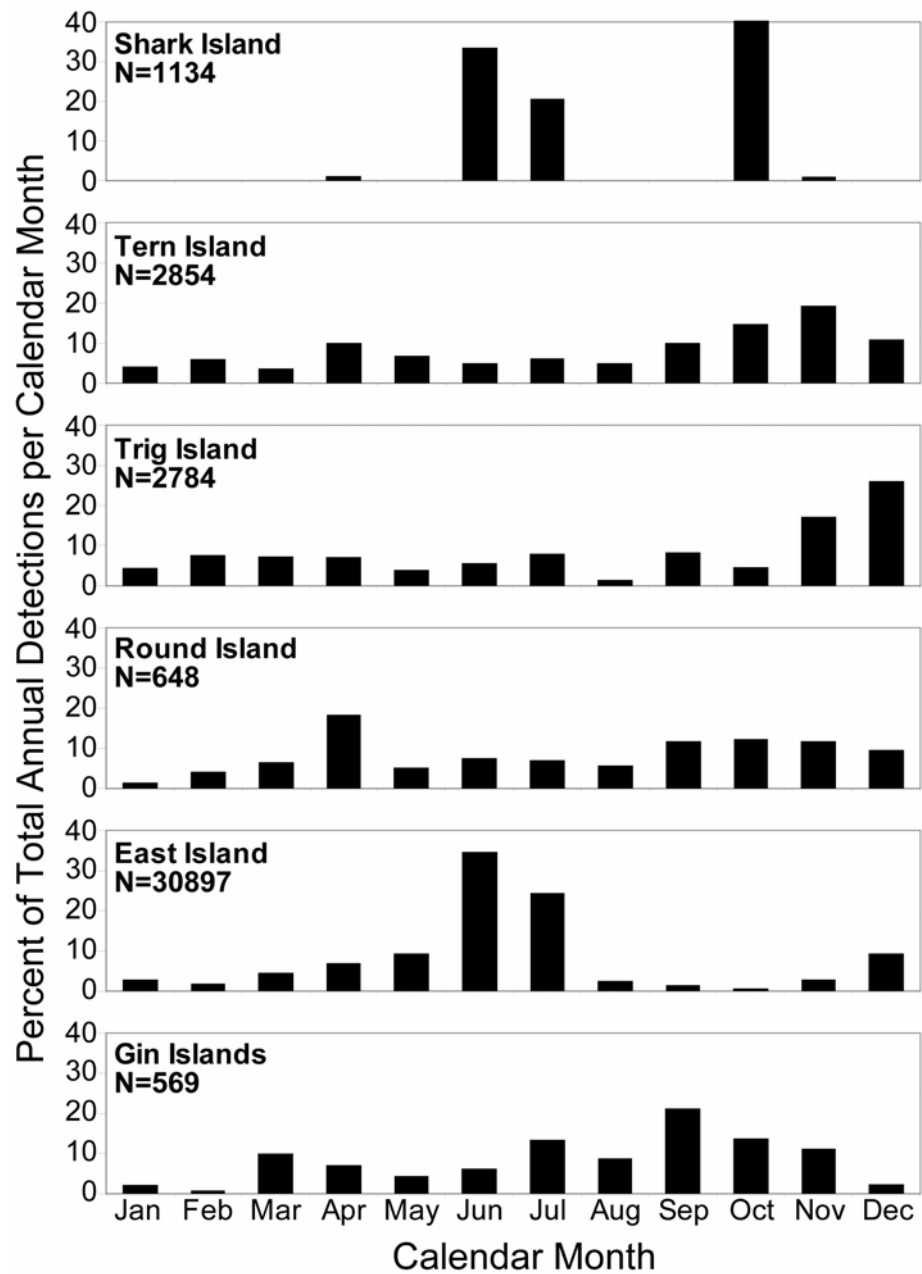
**Figure 5**. Percentage of all acoustic detections for all tiger sharks per month tagged at French Frigate Shoals at each island.
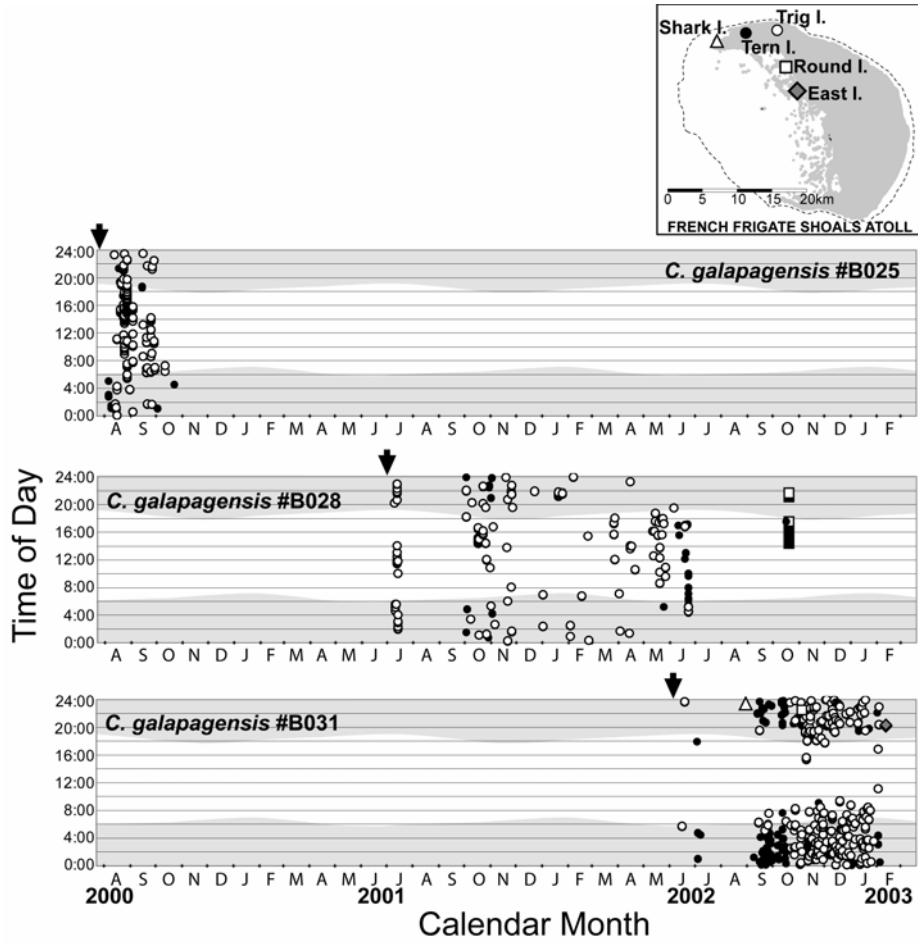
**Figure 6.** Diel detections of Galapagos sharks on receivers located at French Frigate Shoals (grey diamonds = East Island, open triangles = Shark Island, open squares = Round Island, and open circles = Trig Island) from July 2000 to February 2003. Black arrows at the top of the graph indicate the date when each shark was tagged.
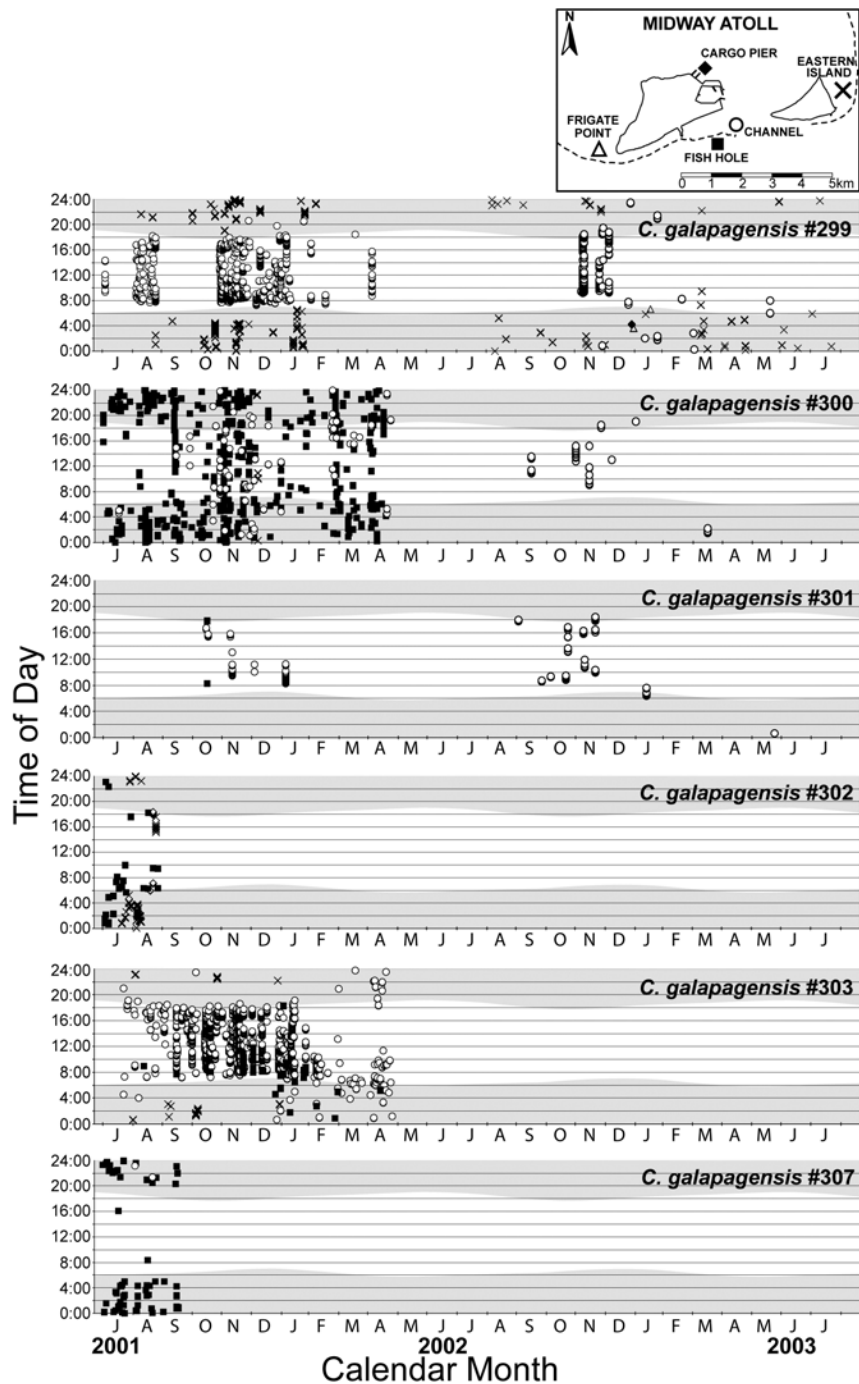
**Figure 7.** Diel detections of six Galapagos sharks on receivers located at Midway Atoll (solid diamonds = Cargo Pier, open triangles = Frigate Point, X = Eastern Island, and open circles = main channel) from July 2001 to September 2004.
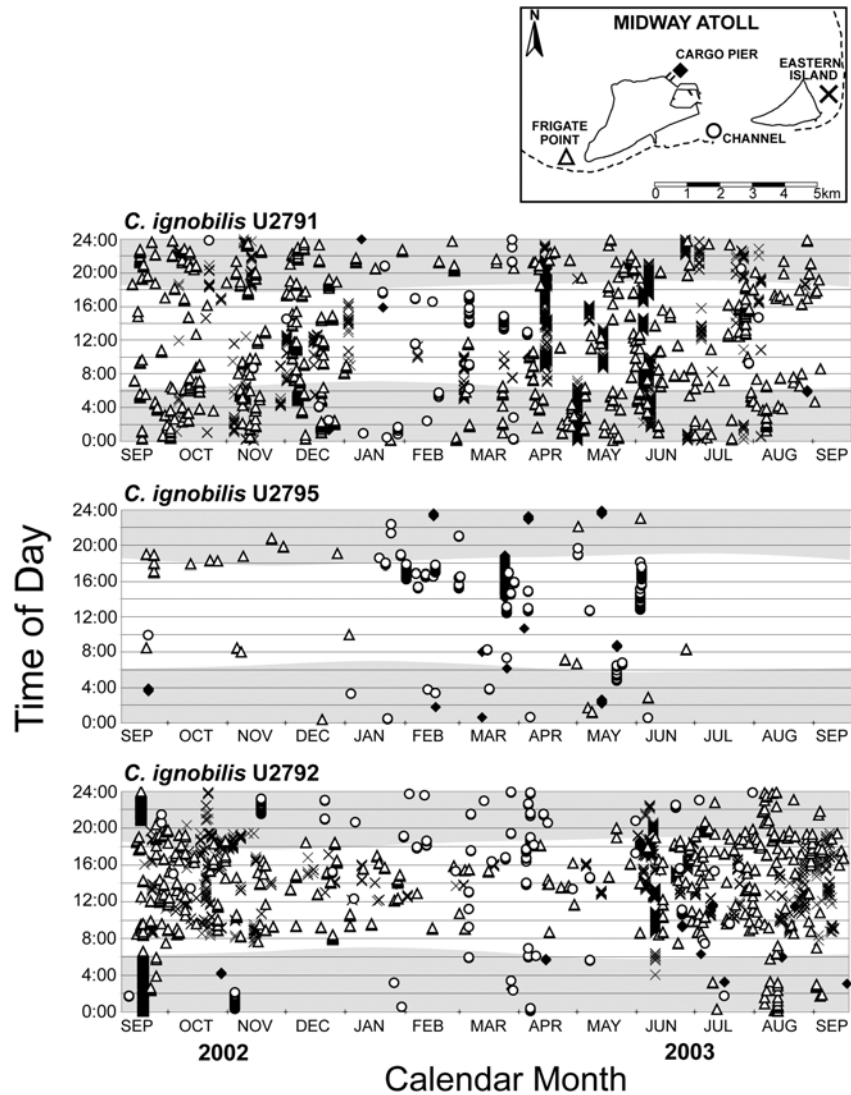
**Figure 8**. Diel detections of giant trevally on receivers located at Midway Atoll (solid diamonds = Cargo Pier, open triangles = Frigate Point, X = Eastern Island, and open circles = main channel) from September 2003 to September 2004. Shaded areas indicate nighttime.
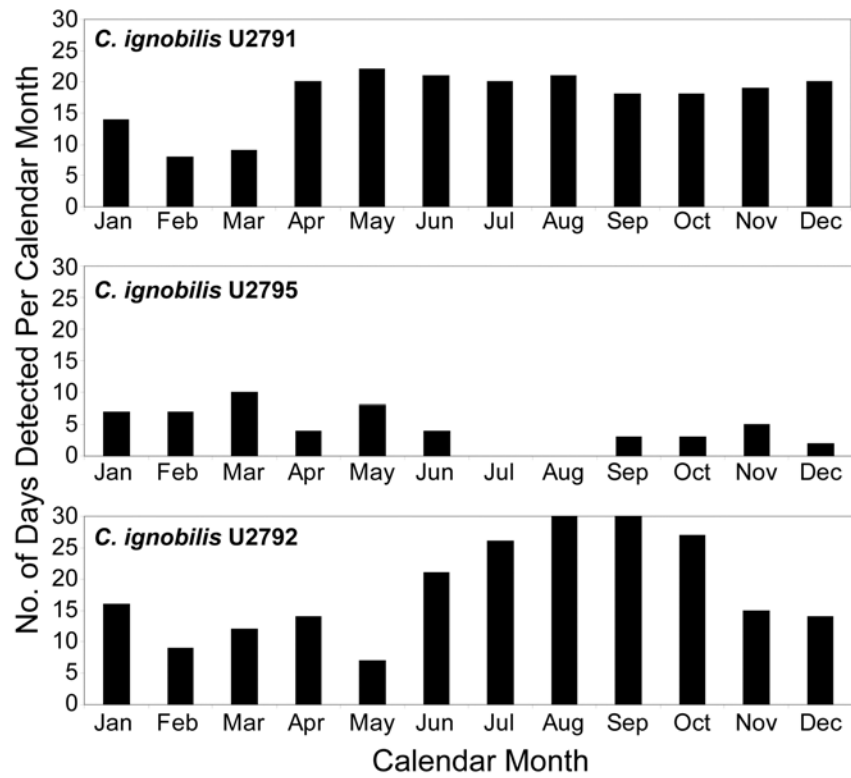
**Figure 9**. Seasonal variation in giant trevally detections at Midway Atoll, September 2002 to September 2003.

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# THE IMPACTS OF BOTTOMFISHING ON RAITA AND WEST ST. ROGATIEN BANKS IN THE NORTHWESTERN HAWAIIAN ISLANDS

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## ABSTRACT

The authors assessed the impacts of bottomfishing in the Raita and West St. Rogatien Bank Reserve Preservation Areas (RPAs) in the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve (NWHICRER). The executive order creating NWHICRER stipulates that bottomfishing will be allowed in these RPAs only if it is determined not to be having an adverse impact on their resources. In order to address that provision, known fishing sites on both banks were surveyed in 2001 using a submersible and a remotely operated vehicle (ROV). One site from each bank subsequently was selected where three submersible dives were conducted in both 2002 and 2003. During the dives, a standardized protocol was used to obtain data on the abundance and size of bottomfish targeted by fishermen, amount of fishing debris present at the sites, and the types and abundance of benthic invertebrates and other fish species that could be impacted by fishing activities. In 2002, comparative data also were obtained from dives in one other RPA ( Brooks Bank), two heavily fished sites in the Main Hawaiian Islands (MHI), and two sites within the Kahoolawe Island Reserve where bottomfishing has been prohibited for over 8 years. The impacts resulting from bycatch, lost fishing gear, and discarded trash are relatively low. The populations of one bottomfish species, onaga (*Etelis coruscans*), could be decreasing on Raita Bank, although previous estimates of maximum sustainable yield indicate the number being taken is sustainable.

## INTRODUCTION

The NWHICRER was created in 2001 by President Clinton's Executive Order (EO) 13178. Within the reserve, nine islets/atolls and six banks were designated as RPAs, each having its own additional layer of regulations regarding usage and access. Two of these RPAs, Raita Bank and the first bank west of St. Rogatien Bank (WSR Bank) have the specific condition that after 5 years, bottomfishing will be allowed to continue only if it is determined that it has no adverse impact on the resources of these banks. Commercial bottomfishing targets seven species of snappers (family Lutjanidae), one grouper (family Serranidae), and one jack (family Carangidae). All but one of these species are typically

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caught with hook and line at depths of 100 m or more. The exception, uku (*Aprion virescens*), is caught by surface trolling over the tops of the banks well above that depth.

In 2001, a 3-year study was initiated to address the bottomfishing provisions in the EO for Raita and WSR Banks. A comprehensive report on the findings from this study, along with recommendations regarding the continuation of bottomfishing in these two RPAs, was submitted to federal and state management agencies in August 2004. In this paper, we summarize the content of that report for a wider audience.

## MATERIALS AND METHODS

Potential bottomfishing impacts were classified into three categories: additions, removals, and alterations. "Addition" impacts included man-made materials found on the sites of which there were two types: a) lost fishing gear such as fishing lines, hooks, weights, and anchors; and b) trash such as beverage cans, bottles, plastics, metal objects, and cloth that may have been discarded by fishers or may have come from other sources. Removal impacts included reduced numbers of targeted bottomfish species as well as nontargeted or "bycatch" species that were caught, killed, and either kept or discarded. Alteration impacts were considered to be either direct or indirect. The former included damage caused by fishing gear to the substrate or benthic invertebrates, particularly attached cnidarians and sponges. Indirect alterations were considered to be changes in the community structure as a result of removals and or additions, (i.e., changes in predator, competitor, and prey abundances).

The locations of 15 potential study sites were obtained from commercial bottomfishers who were actively fishing these banks. Direction observations were made on each site with the use of the manned *Pisces IV* and *V* submersibles and unmanned *RCV-150 ROV* operated by the Hawaii Undersea Research Laboratory (HURL). Funding was provided for 6, 8-hour submersible dives per year and between 6 and 18, 2-hour ROV dives per year for a total of 3 years. The first set of dives in 2001 was for an initial survey of all 15 sites. One study site was subsequently selected on each bank where all 2002 and 2003 submersible dives were conducted.

During each submersible dive, counts of all fish, invertebrates, and fishing debris on the sites as well as size estimates for bottomfish species were obtained using two techniques: four 30-minute "contour" transects and two 30-minute bait stations. During transects, two observers made independent identifications and counts from each side of the submersible. The length of each transect varied as a result of current conditions and bottom topography, but on average covered a distance of 1 km. Bait stations were conducted in areas where targeted bottomfish species were seen during transects. At each station, approximately 4.5 kg of chopped squid and fish was released next to a 10-cm diameter spherical marker used as a size reference. After the bait and marker were deployed, the sub retreated to a distance of 5-10 meters and settled on the bottom with its lights out. Bottomfish and other predatory species attracted to the bait were recorded in ambient light on a ROS 20/20 Navigator wide-angle CCD camera. A 20-cm twin laser scale attached to the camera's pan and tilt provided additional size data during

the stations. After the dives, transect and bait station counts were extracted from the videotapes, the latter being the maximum number of fish caught on a single video frame and/or recorded by an observer at any one point in time. Bait station size measurements were extracted from video still captures using Scion Image software.

In 2002, sets of three submersible dives using the same data-collecting protocol were conducted on one other bottomfishing site in the NWHICRER (Brooks Bank), two sites on Penguin Bank (PB1 and PB2), which is a well-known bottomfishing area in the MHI, and two sites in the Kahoolawe Island Reserve (KIR 1 and KIR 2), where bottomfishing has been prohibited since 1993. These sites provided comparative data for interpreting the findings from the Raita and WSR dives.

Statistical comparisons of the 2002 and 2003 transect and bait station counts among sites were conducted according to the hypotheses shown in Table 1. Rankings (1 being the highest expected mean counts/transect) were based on presumed fishing activity at the different sites. For example, the two KIR sites were presumed to have the lowest fishing activity and therefore were expected to have the higher bottomfish counts (rank = 1), while the opposite was expected for the two Penguin Bank sites (rank = 3). Bycatch analyses were carried out only on bait station counts of nonbottomfish species. The assumption was that species attracted to the bait and recorded at the stations were also the most likely to be caught during commercial bottomfishing activities. Cnidarians and nonprey invertebrate (i.e., sponges, urchins, and seastars) counts also were hypothesized to be highest on the KIR sites and lowest on the PB1 and PB2 sites, because of their potential susceptibility to damage from fishing activities. Counts of potential prey and competitor species were hypothesized to be inversely related to bottomfish counts. Adult bottomfish targeted by fishers would have relatively few potential predators besides medium to large sharks. Predators of this size are observed infrequently from the submersible at bottomfish habitat depths, and therefore it was assumed that their response to bottomfish removals could not be evaluated.

Table 1: Expected (i.e., hypothesized) count rankings for each data category used in comparing 2002 transect and bait station data obtained from each site. Numbers and shadings are the expected ranks of mean counts for each category with 1 (dark shading) being the highest and 3 (no shading) being the lowest. Bottomfish and bycatch counts were used in evaluating removal impacts; fishing gear and trash counts were used in evaluating addition impacts; and counts of cnidarians, other invertebrates, potential competitor species, and potential prey species were used in evaluating alteration impacts. The last row shows the presumed fishing activity at each site. The expected rankings are also shown in Tables 3-5 for reference.

| Expected Count Rankings | Raita | WSR | KIR1 | KIR2 | PB1 | PB2 | Brooks |
|---|---|---|---|---|---|---|---|
| Bottomfish | 2 | 2 | 1 | 1 | 3 | 3 | 2 |
| Bycatch | 2 | 2 | 1 | 1 | 3 | 3 | 2 |
| Fishing Gear | 2 | 2 | 3 | 3 | 1 | 1 | 2 |
| Trash | 2 | 2 | 3 | 3 | 1 | 1 | 2 |
| Cnidarians | 2 | 2 | 1 | 1 | 3 | 3 | 2 |
| Other Inverts | 2 | 2 | 1 | 1 | 3 | 3 | 2 |
| Competitors | 2 | 2 | 3 | 3 | 1 | 1 | 2 |
| Prey | 2 | 2 | 3 | 3 | 1 | 1 | 2 |
| Presumed Fishing Activity | med | med | low | low | high | high | med |

Counts from transects were first extrapolated to a standard 1,000-m length, yielding a 2-hectare sampling area (20 by 1,000 m). These hypotheses were tested statistically using software based on the analytical methods described in Krebs (1999). First, the data from each site were fitted to a negative binomial distribution to derive an estimated mean, variance, and negative binomial exponent, k. Then the values for each site were used in both U-tests and T-tests to determine their approximate goodness of fit to this type of distribution. Different sites were tested for equality following the method of White and Eberhardt (1980). The results of these tests are presented as one of four models:

Model 1: the data from the tested sites have different means and different k values
Model 2: the data from the tested sites have different means but the same k values
Model 3: the data from the tested sites have the same means but different k values
Model 4: the data from the tested sites have the same means and the same k values

The analyses of the means were considered to be most relevant to the hypotheses above. Therefore, for the purpose of this report, only models 1 and 2 were considered indicative of a significant difference among the sites at $P = 0.05$.

Bait station size data on bottomfish species were normally distributed and analyzed by one-way analysis of variance (ANOVA) using Minitab 12.1 software. Similar to counts, average sizes were expected to be inversely related to the amount of fishing activity on the sites. It was hypothesized that the largest fish would be found on the KIR sites while the smallest fish would be found on the Penguin Bank sites. No statistical analysis was attempted on ROV transect records.

Commercial bottomfish and bycatch data from the Raita and "Rogatien" (combined WSR and St. Rogatien Banks) reporting grids were obtained for 2001-2003 by Robert Moffitt from the National Oceanic and Atmospheric Administration (NOAA) fisheries database and were used as a second means of evaluating removal impacts in these RPAs. Due to limitations imposed on the length of this paper, only the most relevant fishing data along with the submersible data obtained on bottomfish, fishing debris/trash, and cnidarians are presented here. For those interested, a full-length version of the original unpublished report from this study is available from the authors on request.

## RESULTS

In Table 2, we provide 2001-2003 bottomfish catch and bycatch data for the Raita and Rogatien grids. The values are the reported number of fish caught at each location by year. However, the listed locations may include a wider area than just the nominal bank, e.g., adjacent banks, pinnacles, and seamounts. On average, 2,017 bottomfish reportedly were removed from the Raita Bank area during each of the last 3 years. Onaga (*Etelis coruscans*) and uku accounted for 44% of the catch followed by hapuupuu (*Epinephelus quernus*), ehu (*Etelis carbunculus*), opakapaka (*Pristipomoides filamentosus*), gindai (*Pristipomoides zonatus*), butaguchi (*Pseudocaranx dentex*), and kalekale (*Pristipomoides sieboldii*). A reported 2,180 bottomfish were removed from the Rogatien area. Over half of the fish (51%) were opakapaka, followed by onaga, uku, ehu, butaguchi, kalekale, gindai, and hapuupuu. On average, 214 bycatch fish reportedly were

caught in the Raita area each year during 2001-2003, and 138 bycatch fish were caught in the Rogatien area. Of the six bycatch taxa, kahala (*Seriola dumerili*) was by far the most abundant species in the catch (93% and 88% for the two areas, respectively).

Table 2: Raita and St. Rogatien bottomfish catch and bycatch (# of fish 2001-2003 data).

| | Raita | | | | St Rogatien | | | |
| Species | 2001 | 2002 | 2003 | mean/yr | 2001 | 2002 | 2003 | mean/yr |
|---|---|---|---|---|---|---|---|---|
| *Pseudocaranx dentex* | 113 | 174 | 162 | **150** | 126 | 227 | 91 | **148** |
| *Etelis carbunculus* | 304 | 195 | 132 | **210** | 199 | 114 | 187 | **167** |
| *Pristipomoides zonatus* | 93 | 313 | 89 | **165** | 31 | 95 | 66 | **64** |
| *Epinephelus quernus* | 264 | 370 | 262 | **299** | 51 | 113 | 21 | **62** |
| *Pristipomoides sieboldii* | 82 | 203 | 119 | **135** | 85 | 156 | 133 | **125** |
| *Etelis coruscans* | 576 | 450 | 297 | **441** | 323 | 368 | 190 | **294** |
| *Pristipomoides filamentosus* | 173 | 259 | 99 | **177** | 1395 | 1089 | 839 | **1108** |
| *Aprion virescens* | 221 | 84 | 1016 | **440** | 214 | 61 | 362 | **212** |
| **Total Bottomfish** | **1826** | **2048** | **2176** | **2017** | **2424** | **2223** | **1889** | **2180** |
| Shark | 0 | 2 | 0 | **0.7** | 3 | 0 | 2 | **1.7** |
| *Galeocerdo cuvieri* | 0 | 1 | 0 | **0.3** | 0 | 0 | 0 | **0.0** |
| *Pontinus macrocephalus* | 8 | 3 | 2 | **4.3** | 0 | 6 | 4 | **3.3** |
| *Caranx ignobilis* | 9 | 17 | 0 | **8.7** | 36 | 0 | 0 | **12.0** |
| *Seriola dumerili* | 142 | 326 | 131 | **199.7** | 177 | 94 | 92 | **121.0** |
| Priacanthid | 1 | 0 | 0 | **0.3** | 0 | 0 | 0 | **0.0** |
| **Total Bycatch** | **160** | **349** | **133** | **214** | **216** | **100** | **98** | **138** |

In 2002 and 2003, all submersible dives were completed as planned which yielded 12 transects at each of the seven sites. With one exception (the KIR2 site, where five bait stations were conducted), all submersible bait stations were completed as planned which yielded six per site. A summary of the 2002 bottomfish, fishing/trash debris, and cnidarian transect count data is presented in Table 3. The first row of each section of the table shows the predicted ranking of the sites (different shadings) and whether they are expected to be significantly different (+ or -). The remaining rows provide the mean and standard error of counts, which were ranked and shaded for comparison to the predicted pattern, and indicate if the sites were significantly different at $P<0.05$. Data from sites where counts were either 0 or 1 for 12 transects, or where the variance was equal to or lower than the mean (failed the assumptions of a negative binomial distribution) could not be tested (nt).

Of the 10 bottomfish species observed during submersible dives, only onaga and ehu counts were significantly different among sites. PB1 had the highest mean onaga counts/hectare at 26.7, while Raita (0.6) and WSR (1.3) had the lowest. Raita had the second highest counts for hapuupuu. For bottomfish in general, the most number of counts were obtained from the Kahoolawe and Brooks sites while the least number of counts were obtained from Raita and PB2 sites. While a few counts were made on lehi (*Aphareus rutilans*), uku, yellowtail kale (*Pristipomoides auricilla*), and butaguchi, these species were not adequately sampled in this study, as a result of the transects being generally below their optimal depth. Between 2002 and 2003, there was a significant decrease in onaga, ehu, and kalekale counts at Raita Bank (Kelley and Moffitt, unpublished report). At WSR Bank however, unlike Raita, the difference was only significant for kalekale. In general, bottomfish counts at both banks decreased between 2002 and 2003.

Table 3: Comparison of bottomfish, fishing/trash debris, and cnidarian counts among all 2002 sites (counts/hectare, n = 12).

| Description | Raita Mean +/- SE | WSR Mean +/- SE | KIR1 Mean +/- SE | KIR2 Mean +/- SE | PB1 Mean +/- SE | PB2 Mean +/- SE | Brooks Mean +/- SE | P<0.05 |
|---|---|---|---|---|---|---|---|---|
| **Expected Count Rankings** | 2 | 2 | 1 | 1 | 3 | 3 | 2 | |
| **Bottomfish Counts** | | | | | | | | |
| Etelis coruscans | 0.6 +/- 0.25 | 1.3 +/- 0.71 | 11.7+/-7.90 | 2.4 +/- 0.90 | 26.7 +/- 25.40 | 2.3 +/- 1.41 | 2.8 +/- 1.62 | + |
| Etelis carbunculus | 5.2 +/- 1.84 | 3.8 +/- 1.28 | 8.4 +/- 3.91 | 4.9 +/- 1.65 | 2.6 +/- 0.89 | 7.5 +/- 2.52 | 1.0 +/- 0.31 | + |
| Epinephelus quernus | 1.0 +/- 0.36 | 0.7 +/- 0.33 | 0.1 +/- 0.13 | 0.3 +/- 0.21 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 1.3 +/- 0.86 | - |
| Pristipomoides filamentosus | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 2.2 +/- 1.48 | 0.8 +/- 0.43 | 0.1 +/- 0.08 | 0.0 +/- 0.04 | 3.2 +/- 3.12 | nt |
| Pristipomoides sieboldii | 0.2 +/- 0.11 | 5.4 +/- 4.29 | 1.0 +/- 0.97 | 15.9 +/- 15.80 | 5.2 +/- 4.95 | 0.9 +/- 0.66 | 11.0 +/- 4.26 | - |
| Pristipomoides zonatus | 0.9 +/- 0.34 | 0.9 +/- 0.58 | 0.8 +/- 0.40 | 2.4 +/- 0.99 | 0.5 +/- 0.20 | 0.7 +/- 0.32 | 3.5 +/- 1.55 | - |
| Pseudocaranx dentex | 0.0 +/- 0.00 | 0.1 +/- 0.09 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 1.2 +/- 1.17 | nt |
| Aphareus rutilans | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.1 +/- 0.10 | 0.4 +/- 0.30 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.04 | nt |
| Pristipomoides auricilla | 0.0 +/- 0.00 | 0.1 +/- 0.08 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.1 +/- 0.07 | 0.0 +/- 0.00 | nt |
| Aprion virescens | 0.0 +/- 0.00 | 0.1 +/- 0.06 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | nt |
| **Fishing/Trash Debris Counts** | | | | | | | | |
| anchors | 0.0 +/- 0.00 | 0.0 +/- 0.03 | 0.2 +/- 0.10 | 0.1 +/- 0.07 | 0.0 +/- 0.20 | 0.2 +/- 0.07 | 0.2 +/- 0.11 | - |
| anchor chains | 0.0 +/- 0.00 | 0.0 +/- 0.03 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.04 | 0.0 +/- 0.04 | 0.0 +/- 0.00 | nt |
| anchor lines | 0.0 +/- 0.04 | 0.2 +/- 0.07 | 0.3 +/- 0.13 | 0.2 +/- 0.12 | 0.2 +/- 0.12 | 0.4 +/- 0.10 | 0.0 +/- 0.00 | - |
| fishing weights | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.1 +/- 0.06 | 0.0 +/- 0.00 | 0.0 +/- 0.04 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | nt |
| fishing lines | 0.1 +/- 0.05 | 0.3 +/- 0.13 | 0.4 +/- 0.26 | 0.1 +/- 0.07 | 1.6 +/- 0.39 | 0.7 +/- 0.22 | 0.3 +/- 0.15 | + |
| traps and lines | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | nt |
| netting | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | nt |
| **Total Fishing Debris Counts** | 0.1 +/- 0.06 | 0.6 +/- 0.17 | 0.9 +/- 0.40 | 0.4 +/- 0.14 | 2.3 +/- 0.58 | 1.3 +/- 0.30 | 0.6 +/- 0.16 | + |
| wood/paper debris | 0.0 +/- 0.04 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | nt |
| metal debris | 0.0 +/- 0.00 | 0.2 +/- 0.07 | 0.3 +/- 0.13 | 0.7 +/- 0.24 | 0.0 +/- 0.04 | 0.1 +/- 0.09 | 0.2 +/- 0.13 | - |
| plastic/rubber debris | 0.0 +/- 0.04 | 0.1 +/- 0.08 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.04 | nt |
| cloth debris | 0.0 +/- 0.00 | 0.0 +/- 0.04 | 0.1 +/- 0.00 | 0.7 +/- 0.22 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | nt |
| ceramic/stone/glass debris | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.1 +/- 0.10 | 0.0 +/- 0.04 | 0.0 +/- 0.04 | 0.1 +/- 0.12 | 0.1 +/- 0.05 | nt |
| **Total Trash Counts** | 0.1 +/- 0.06 | 0.3 +/- 0.17 | 0.5 +/- 0.16 | 1.4 +/- 0.37 | 0.1 +/- 0.05 | 0.2 +/- 0.14 | 0.3 +/- 0.17 | + |
| **Cnidarian Counts** | | | | | | | | |
| Actinarians | 1.6 +/- 0.48 | 0.9 +/- 0.35 | 2.4 +/- 1.15 | 37.8 +/- 32.30 | 2.9 +/- 1.98 | 4 +/- 1.62 | 1.7 +/- 1.00 | + |
| Alcyonaceans | 3.8 +/- 3.39 | 5.7 +/- 4.75 | 14.1 +/- 6.25 | 0.6 +/- 0.24 | 7.3 +/- 4.63 | 0.8 +/- 0.40 | 0.5 +/- 0.52 | + |
| Antipatharians | 24.3 +/- 14.10 | 28.7 +/- 8.81 | 22.4 +/- 6.54 | 16.3 +/- 7.08 | 71.1 +/- 43.90 | 1.7 +/- 1.00 | 127.6 +/- 52.30 | + |
| Gorgonians | 7.4 +/- 2.68 | 0.2 +/- 0.10 | 1190.2 +/- 516.00 | 262.7 +/- 174.00 | 483.3 +/- 341.00 | 19.1 +/- 9.89 | 19.0 +/- 13.90 | + |
| Pennatulaceans | 2.4 +/- 1.24 | 0.2 +/- 0.13 | 4.6 +/- 2.52 | 165.4 +/- 81.60 | 0.1 +/- 0.07 | 0.2 +/- 0.12 | 1.9 +/- 1.18 | + |
| Scleractinians | 0.2 +/- 0.12 | 0.2 +/- 0.18 | 1116.1 +/- 630.00 | 242.1 +/- 185.00 | 32.3 +/- 27.40 | 3.2 +/- 1.43 | 0.2 +/- 0.17 | + |
| Unidentified | 1.2 +/- 1.11 | 0.0 +/- 0.04 | 0.0 +/- 0.00 | 23.3 +/- 22.80 | 0.0 +/- 0.05 | 0.0 +/- 0.04 | 2.6 +/- 2.45 | + |
| **Total Cnidarians** | 40.9 +/- 13.90 | 36.1 +/- 11.10 | 2349.7 +/- 665.00 | 748.3 +/- 232.00 | 597.1 +/- 381.00 | 28.9 +/- 9.71 | 153.5 +/- 50.10 | + |

As expected, the total amount of fishing debris was significantly higher on PB1 and PB2 in comparison to other sites. However, Raita had the lowest level of all seven sites including KIR1 and KIR2, while WSR and Brooks had intermediate levels as expected. Fishing lines, rather than anchors, anchor chains, or fishing weights, were the major type of lost gear. Overall, trash counts were low with KIR1 and KIR2 topping the list at 0.5 and 1.4 items/hectare, respectively. Metal and cloth debris resulting from past military activities off Kahoolawe accounted for the majority of items seen. Raita and PB1 had the lowest levels of trash counts, both of which had 0.1 items/hectare. Neither fishing debris nor trash appeared to be significant problems on any of the seven sites in 2002; also there was no change in the amount of fishing debris or trash on Raita between 2002 and 2003 (Kelley and Moffitt, unpublished report). Bottomfishing debris *per se* was rarely encountered and did not significantly increase on either bank.

With respect to alteration impacts, 64 different cnidarians were counted which were grouped into seven categories: Actinarian-like (anemones, corallimorpharians, and ceriantharians), Alcyonacean-like (soft corals and tubularid hydrozoans), Antipatharians (black corals and "bushy" hydrozoans), Gorgonians (gorgonians and zoantharians that grow on gorgonians), Pennatulaceans (sea pens), Scleractinians (hard corals), and unidentified cnidarians that could not be assigned to one of the other six groups. Significant differences among sites were present in all seven categories as well as the total numbers of cnidarians. Of particular interest were the low counts at Raita, WSR, and PB2 (28-41/hectare) in comparison to the other sites (153-2,350/hectare). KIR1 and KIR2 had the highest total cnidarian counts due to high numbers of gorgonians (263-1,190/hectare) and scleractinians (242-1,116/hectare). Antipatharians and alcyonaceans were the only two groups on Raita and WSR with moderate numbers in comparison to the other sites.

Tables 4a and 4b summarize the bottomfish and bycatch bait station counts from each site. Mirroring the results from transects, Raita and WSR generally had the lowest mean number of bottomfish per station. Raita hapuupuu and WSR kalekale were the two exceptions, although neither was significantly higher than other sites. Similar to transect data, the PB1 and KIR1 sites had the highest onaga counts, followed by Brooks. Between 2002 and 2003, mean onaga bait station counts decreased on both Raita and WSR, although the difference on the latter was not significant. Consistent with commercial catch data, kahala were the predominant "bycatch" species observed at bait stations. Two *Seriola* species were observed at a number of the stations (*S. dumerili* and *S. rivoliana*), which were not always easy to differentiate. Therefore, the data on these species were combined in Table 4b as *Seriola sp.*

Bait station size data are presented in Table 5. Size data from the Brooks site were not available for the preparation of this report. With the exception of one extremely large individual at PB2 (FL = 99 cm), Raita Bank had the largest sized onaga (mean = 65.3 cm FL, n = 30), ehu (mean = 44.5 cm FL, n = 16) and hapuupuu (77.7 cm FL, n = 19). In contrast, WSR had the smallest onaga (mean = 49.3 cm FL, n = 39) as well as the smallest ehu (34.3 cm FL, n = 8) of the six sites shown. Gindai were the only other species of which measurements were made at more than two sites. WSR had the second largest individuals (mean = 36.3 cm FL, n = 8) after PB1 (mean = 36.8 cm FL, n = 10). In general, size measurements did not follow the expected pattern among sites. Furthermore, 2003 Raita and WSR size data did not follow the expected pattern either.

Table 4a: Comparison of bottomfish bait station counts among all 2002 sites (counts/station, n = 6 except KIR2, n = 5)

| DESCRIPTION | Raita Mean +/- SE | WSR Mean +/- SE | KIR1 Mean +/- SE | KIR2 Mean +/- SE | PB1 Mean +/- SE | PB2 Mean +/- SE | Brooks Mean +/- SE | P<0.05 |
|---|---|---|---|---|---|---|---|---|
| **Expected Count Rankings** | 2 | 2 | 1 | 1 | 3 | 3 | 2 | |
| **Bottomfish Counts** | | | | | | | | |
| *Etelis coruscans* | 3.0 +/- 0.82 | 3.8 +/- 2.87 | 14.7 +/- 5.73 | 5.6 +/- 3.11 | 17.5 +/- 3.71 | 0.5 +/- 0.50 | 10.5 +/- 4.82 | + |
| *Etelis carbunculus* | 1.8 +/- 1.33 | 1.0 +/- 0.82 | 4.5 +/- 1.65 | 3.4 +/- 1.60 | 4.0 +/- 1.24 | 4.0 +/- 1.18 | 0.5 +/- 0.34 | - |
| *Epinephelus quernus* | 2.3 +/- 1.05 | 1.7 +/- 0.92 | 0.0 +/- 0.00 | 0.2 +/- 0.2 | 0.2 +/- 0.17 | 0.0 +/- 0.00 | 2.7 +/- 0.72 | + |
| *Pristipomoides filamentosus* | 0.0 +/- 0.00 | 0.3 +/- 0.21 | 0.2 +/- 0.17 | 7.6 +/- 5.75 | 0.0 +/- 0.00 | 0.5 +/- 0.34 | 2.8 +/- 1.49 | + |
| *Pristipomoides sieboldii* | 0.0 +/- 0.00 | 8.5 +/- 8.50 | 0.0 +/- 0.00 | 6.2 +/- 5.95 | 3.3 +/- 3.3 | 3.8 +/- 3.64 | 0.0 +/- 0.00 | - |
| *Pristipomoides zonatus* | 0.0 +/- 0.00 | 1.0 +/- 0.52 | 0.2 +/- 0.17 | 3.0 +/- 0.84 | 1.2 +/- 0.40 | 2.2 +/- 0.83 | 0.5 +/- 0.34 | + |
| *Pseudocaranx dentex* | 0.3 +/- 0.33 | 0.2 +/- 0.17 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 4.7 +/- 2.95 | - |
| *Aphareus rutilans* | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.3 +/- 0.33 | 2.8 +/- 1.96 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | nt |
| *Pristipomoides auricilla* | 0.0 +/- 0.00 | 1.2 +/- 1.17 | 0.0 +/- 0.00 | 0.6 +/- 0.6 | 2.8 +/- 2.83 | 1.7 +/- 1.17 | 0.0 +/- 0.00 | |
| *Aprion virescens* | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | nt |

Table 4b: Comparison of bycatch bait station counts among all 2002 sites (counts/station, n = 6 except KIR2, n = 5)

| DESCRIPTION | Raita Mean +/- SE | WSR Mean +/- SE | KIR1 Mean +/- SE | KIR2 Mean +/- SE | PB1 Mean +/- SE | PB2 Mean +/- SE | Brooks Mean +/- SE | P<0.05 |
|---|---|---|---|---|---|---|---|---|
| **Expected Count Rankings** | 2 | 2 | 3 | 3 | 1 | 1 | 2 | |
| **Bycatch Counts** | | | | | | | | |
| *Bodianus vulpinus* | 0.5 +/- 0.50 | 0.8 +/- 0.54 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.2 +/- 0.17 | - |
| *Carcharhinus sp* | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.5 +/- 0.34 | nt |
| *Gymnothorax sp* | 1.2 +/- 0.31 | 1.0 +/- 0.45 | 0.7 +/- 0.21 | 0.8 +/- 0.37 | 1.8 +/- 0.40 | 1.2 +/- 0.17 | 0.0 +/- 0.00 | - |
| *Randallichthys filamentosus* | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 1.0 +/- 0.63 | 0.3 +/- 0.21 | 0.7 +/- 0.33 | nt |
| *Seriola sp* | 3.3 +/- 1.00 | 3.7 +/- 1.12 | 0.5 +/- 0.22 | 1.8 +/- 0.80 | 2.0 +/- 0.45 | 1.7 +/- 1.00 | 10.7 +/- 3.60 | + |
| *Dasyatis sp* | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.8 +/- 0.31 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | nt |
| *Polylepion russelli* | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.3 +/- 0.33 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | nt |
| *Taractichthys steindachneri* | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.3 +/- 0.33 | 0.0 +/- 0.00 | nt |
| *Conger oligoporus* | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.3 +/- 0.33 | 0.0 +/- 0.00 | nt |
| *Squalus mitsukurii* | 0.7 +/- 0.70 | 0.2 +/- 0.17 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.0 +/- 0.00 | 0.2 +/- 0.17 | 0.0 +/- 0.00 | nt |

Table 5: Comparison of bottomfish bait station size measurements (fork lengths in centimeters) among 2002 sites (Brooks not included)

| | Raita | | WSR | | KIR1 | | KIR2 | | PB1 | | PB2 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Expected Rankings** | 2 | | 2 | | 1 | | 1 | | 3 | | 3 | | |
| **Bottomfish species** | N | Mean +/- SE | N | Mean +/- SE | N | Mean +/- SE | N | Mean +/- SE | N | Mean +/- SE | N | Mean +/- SE | P |
| *Etelis coruscans* | 30 | 65.3 +/- 3.51 | 39 | 49.3 +/- 1.42 | 49 | 59.7 +/- 1.60 | 51 | 52.3 +/- 1.17 | 69 | 53.6 +/- 1.40 | 1 | 99.1 | 0.00 |
| *Etelis carbunculus* | 16 | 44.5 +/- 2.69 | 8 | 34.3 +/- 4.80 | 31 | 36.3 +/- 1.50 | 28 | 37.8 +/- 1.83 | 26 | 38.9 +/- 1.37 | 40 | 35.3 +/- 0.84 | 0.01 |
| *Epinephelus quernus* | 19 | 77.7 +/- 4.70 | 9 | 62.5 +/- 5.11 | - | - | 2 | 37.8 +/- 2.16 | 3 | 58.9 +/- 1.42 | - | - | 0.02 |
| *Pristipomoides filamentosus* | - | - | 5 | 48.8 +/- 4.11 | - | - | 97 | 48.3 +/- 1.12 | - | - | - | - | 0.90 |
| *Pristipomoides sieboldii* | - | - | 28 | 33.8 +/- 0.56 | - | - | 28 | 37.6 +/- 1.68 | - | - | 11 | 30.2 +/- 1.07 | 0.00 |
| *Pristipomoides zonatus* | - | - | 8 | 36.3 +/- 2.54 | - | - | 35 | 35.1 +/- 0.91 | 10 | 36.8 +/- 1.63 | 12 | 32.0 +/- 1.42 | 0.17 |
| *Aphareus rutilans* | - | - | - | - | 2 | 63.2 +/- 27.4 | 8 | 56.4 +/- 2.16 | - | - | - | - | - |

**DISCUSSION**

All types of fishing methods lead to removal impacts. Methods are considered selective when they yield a high percentage of target versus bycatch species in the catch. Different methods also have varying potential for addition and alteration impacts. Bottom trawling is the subject of the largest number of reports on fishing impacts over the last 3 years (Rester, 2003). Bottom trawling generally causes substantial removal impacts with low selectivity (high levels of bycatch); can cause dramatic alterations to the benthic habitat and community (particularly cnidarians and other sessile benthic invertebrates); and when lost can contribute heavily to the addition of fishing debris. Trap fishing is more selective than trawling, but can produce moderate levels of addition and alteration impacts. In contrast, hook-and-line methods (including trolling, longline, and handline fishing) are considered to be "low impact" (Morgan and Chuenpagdee, 2003). Longline fishing has been shown to alter prey and competitor populations in pelagic ecosystems (Ward and Myers, in press); however, trolling and handline fishing are relatively selective and are not considered to have major impacts. Bottomfishing (a form of handline fishing) and trolling are the only types of fishing permitted on Raita and WSR Banks.

Commercial catch data from 2001-2003 indicated that on average, over 2,000 bottomfish are being removed from each of the Raita and St. Rogatien reporting grids per year. The estimated maximum sustainable yields (MSY) are reported as 16.9 and 11.7 mt, respectively (WPRFMC, 1986). If the mean fish weight is assumed to be 4.5 kg, the take on these banks is just below MSY. Unfortunately, due to poor spatial resolution of the reporting grids, it is not known exactly how many fish are removed annually from each of the two RPAs. This is a particular problem for the St. Rogatien grid data which includes both the WSR as well as the larger St. Rogatien Bank. Above the 100-fathom contour, the calculated areas of Raita, WSR and St. Rogatien are 570, 54, and 484 km$^2$, respectively. The combined area of the latter two is 538 km$^2$, or approximately the same as Raita, which may be why the catches from these two grids are similar. However, the extent of suitable bottomfish habitat on each of the banks has not been determined.

Fishing undoubtedly has a significant effect on the abundance and mean fish size of targeted species from these and other areas throughout the Hawaiian Archipelago. Perhaps the more important question is whether the sustainability of the populations on these banks is being impacted by this activity. As Table 2 shows, landings of onaga and opakapaka generally decreased while landings of uku generally increased during the 3-year study period. Both changes were most likely due to a shift in fishing effort. Either an increase in uku catchability (previously reported several times for the NWHI fishery) or a decrease in onaga and opakapaka catchability could have been the cause of this pattern. These data are difficult, if not impossible, to interpret without knowing the effort expended targeting each species during that period.

In 2002, the number of onaga counted from the submersible at both Raita and WSR were significantly lower than at the other five study sites (Kelley and Moffitt, unpublished report). Comparison between the 2002 and 2003 data also supports the possibility that onaga abundance is decreasing at the two sites as well. Opakapaka observations were too low to be statistically tested, but it should be noted that they

followed the same pattern. Comparison of bait station size measurements in our study shows that the onaga mean size at the WSR site is similar to or lower than most of the MHI sites. It is, however, presumptuous to assume that abundance and size estimates obtained at one site on each bank are reflective of what is occurring on each bank as a whole. The data cannot be considered conclusive but rather only indicate the possibility of a problem with onaga populations in these two RFAs. Furthermore, the problem does not appear to extend to populations of other bottomfish species. Hapuupuu counts at Raita were second highest only to Brooks, with the other species falling between the heavily and no-fished sites as expected. Raita onaga were larger, not smaller than MHI onaga in contrast to what was observed on WSR. The WSR pattern was not true for all species nor was it true for the period from 2002 to 2003, when sizes actually increased at both banks (Kelley and Moffitt, unpublished report).

Bycatch from bottomfishing potentially is being understated on commercial catch reports, as has been suggested for other types of fisheries (Morgan and Chuenpagdee, 2003). The data from bait stations combined with fishing surveys (Kelley, unpub.; Moffitt, unpub.) identify 41 potential bycatch species, most of which are rarely caught. Of these, kahala are by far the most common and usually are thrown back alive, as are dogfish, *Squalus mitsukurii*. Hogos (*Pontinus macrocephalus*) are occasionally caught on deeper drops and are kept to be sold or eaten. Bycatch impacts are probably not significant on either Raita or WSR Banks.

Counts of debris from bottomfishing on Raita and WSR were the lowest of all seven sites. This is probably because the number of boats permitted to fish the banks is low, with only four or five operating during the study period. Second, these are more experienced commercial fishers, who are much less likely to lose gear than recreational or part-time fishers. For probably the same reasons, significant amounts of trash also were not observed on either bank. This type of impact was not found to be significant on either bank.

Cnidarians, particularly fan-like gorgonians, are considered to be the highest risk organisms for alteration impacts, since they are attached to the bottom and present a relatively large surface area that could be entangled with fishing line. In contrast to what was expected, Raita and WSR cnidarian densities were significantly lower than those observed on other study sites as well as at other sites surveyed by submersible and ROV on the banks. With averages of less than 50 cnidarians per hectare, bottomfishing gear contacting these animals must be occurring at a very low frequency. Although not presented here, three other groups of benthic invertebrates, sponges, urchins, and seastars, were examined that could also be at moderate to low risk. However, Raita and WSR urchin and sponge counts were significantly lower, while seastar counts were approximately the same as those on other sites (Kelley and Moffitt, unpub. report).

In conclusion, bottomfishing in the WSR and Raita RPAs may be reducing the populations of onaga, particularly on Raita; however, the data are not conclusive. Bottomfishing is a form of handline fishing, which is considered to have low collateral impact in comparison to other types of fishing. The data obtained in this study are consistent with that position. The number of fishers working in the WSR and Raita RPAs is low, as is the amount of gear and trash they appear to be leaving. The substrate

on each of the banks has been described by submersible pilots as a "barren, lifeless wasteland" (Kerby, pers. comm.) in comparison to the many other dives they have made during their careers. The tops are primarily covered with rhodoliths while the slopes are relatively featureless carbonate rock and sediment. Reef-building corals are not found at bottomfishing depths, only other types of cnidarians whose abundance is also low. Sponge, urchin, and seastar abundances are relatively low. In general, there appears to be very little damage that bottomfishing could do on either Raita or W. St. Rogatien. However, these findings do not apply to all of the banks in NWHICRER where fishing activity has been and is taking place. For example, Brooks was found to have a relatively extensive bed of black coral, *Antipathes ulex*, within bottomfishing depths (Kelley and Moffitt, unpub.). Whether other banks in NWHICRER also have extensive coral beds or other resources vulnerable to bottomfishing impacts is presently unknown.

## ACKNOWLEDGEMENTS

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# MEGA- TO MICRO-SCALE CLASSIFICATION AND DESCRIPTION OF BOTTOMFISH ESSENTIAL FISH HABITAT ON FOUR BANKS IN THE NORTHWESTERN HAWAIIAN ISLANDS

BY

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## ABSTRACT

We coupled multibeam sonar data with submersible and remotely operated vehicle (ROV) observations to classify and describe bottomfish essential fish habitat (EFH) on four banks in the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve (NWHICRER). From 2001 to 2003, a total of 22 *Pisces IV* and *V* dives along with 37 *RCV-150 ROV* dives were conducted on Raita Bank, W. St. Rogatien Bank, Brooks Bank, and Bank 66 to evaluate the impacts of bottomfishing on these banks. In the process of addressing that issue, extensive data were collected on the biological communities and substrate characteristics within the EFH depth range of 100 to 400 meters. Multibeam mapping was conducted between dives from the submersible support ship "*KOK*" as well as during a separate cruise on the RV *Kilo Moana*. All four banks had relatively flat featureless tops (i.e., <5 % slopes) which extended down to a depth of 120 m. ROV dives revealed that the area between 100-120 m was characterized by sediment interspersed with rhodoliths and carbonate outcrops. At this depth on Raita, W. St. Rogatien, and Brooks Bank, the slope increased to 25-60 degrees, which continued down to 300-400 m. The substrate on these slopes was carbonate bedrock interspersed with flats and channels. Ten sponge, 64 cnidarian, 1 ctenophore, 49 echinoderm, 15 mollusk, 30 crustacean, 3 tunicate, and 152 fish species were observed during the dives. A distinct transition occurred between shallow-water and deep-water fish families within this depth range that may be temperature related.

## INTRODUCTION

The term EFH was defined by Congress as "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity" (16 U.S.C. 1802(10). According to the EFH website maintained by the National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS), "waters" in the definition refers to the "aquatic areas and their associated physical, chemical, and biological properties that are used by fish." "Substrate" refers to "sediment, hard bottom, structures underlying the waters, and associated biological communities," and "spawning,

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breeding, feeding, or growth to maturity" encompasses the full life cycle of the fish. EFH is therefore a term that blends together the more basic concepts of "habitat", which have traditionally been used to describe just the physical aspects of an environment, with "ecosystem", which has been used to describe the biological communities and their interactions, and the physical properties of an environment. The concept of EFH was created in an attempt to advance the application of ecosystem-based approaches to fishery management (Park, 2002). To develop an EFH definition for a managed fish species, the task is to describe not only substrate and hydrological features but also the other living organisms (e.g., fish, invertebrates, and algae) living in association with that species.

Hawaiian bottomfish are a group of federally managed species, most of which are commercially valuable deep-slope snappers. The NMFS is presently engaged in refining its EFH definition for this fishery, which for years has been simply the 100-400 m depth zone around each island and bank within the Hawaiian Archipelago. Studies on benthic habitats and their biological communities are typically approached by coupling seafloor mapping with direct observations and/or benthic sampling (Greene et al., 1999). The bottomfish EFH depth range precludes optical mapping techniques and SCUBA, requiring instead the use of acoustic mapping techniques coupled with manned and/or unmanned deepwater vehicles. The costs associated with these types of operations have prevented examination of all but a few specific sites. Furthermore, multibeam mapping and direct observations have been carried out opportunistically and usually in conjunction with other mission priorities. Even so, valuable data have been obtained for use in creating a more accurate and specific EFH definition for this fishery. In this paper we initiate the development of a mega- to micro-scale classification and description of bottomfish EFH by providing a summary of acoustic mapping data and submersible/ ROV observations obtained on bottomfish habitats in the Northwestern Hawaiian Islands (NWHI).

## MATERIALS AND METHODS

During September-November, 2001-2003, three cruises were conducted in NWHICRER on the Hawaii Undersea Research Laboratory's (HURL) submersible support ship, *Kaimikai-o-Kanaloa* (*KOK*). These cruises had two tasks: a) to map the 100-fathom contour around Raita Bank, W. St. Rogatien Bank, Brooks Bank, and Bank 66 to obtain a more accurate position for each bank, and b) to obtain *in situ* observations of bottomfish fishing sites for use in evaluating the impacts of bottomfishing on the banks. The first task was carried out with the *KOK*'s SeaBeam 210 multibeam sonar mapping system while the second was carried out with HURL's manned and unmanned deepwater vehicles.

Multibeam Sonar Data

Mega- (1-10 km) and meso-scale (10 to 1000 m) features of the bottomfish EFH on the four banks were revealed from multibeam sonar data obtained in conjunction

with submersible operations. The SeaBeam multibeam system on board the submersible support ship *KOK* was used to map the 100-fathom contour around Raita and W. St. Rogatien banks between submersible and ROV dives. During this process, a large portion of the bottomfish EFH was covered. These data, which include only bathymetry, were processed using the freeware multibeam sonar processing and plotting packages MB-System (Caress and Chayes, 1996) and the generic Mapping Tools [GMT] (Wessel and Smith, 1991). Manual and/or automatic bathymetric "ping" editing was carried out on the data to reduce outliers, followed by gridding of the swath data collected in various years. The optimum grid cell size was used for the target water depth, usually 10-20 meters, along with running a median filter of minimum width over the grids to further reduce noise while maintaining maximum resolution. The data were converted into ASCII grids and subsequently imported into ArcGIS where they were layered over digitized NOAA nautical charts. The charts provided a visual reference for understanding the multibeam coverage on each bank.

*In Situ* Submersible and ROV Data

*In situ* data within the 100-400 m depth range were obtained during 22 manned *Pisces IV* and *V* submersible dives and 37 unmanned *RCV-150 ROV* dives conducted on the four banks. All vehicles were deployed from the *KOK*. Each 8-hour submersible dive was conducted during the day between 0830-1630 hrs while each ROV dive was conducted at night between 1900-0200 hrs. During submersible dives, temperature, dissolved oxygen (DO), and salinity data were obtained from Seabird CTDs mounted on the vehicles. Macro- and micro-scale geological observations and biological data were obtained during 30-min transects (four per dive) designed to obtain quantitative data on potential bottomfishing impacts (see Kelley et al., submitted for this volume). Transects were conducted at different depths (i.e., T1: 190-210 m, T2: 240-260 m, T3: 290-310 m, and T4: 340-360 m) during which substrate observations as well as counts of fish and invertebrates were made. These data were recorded on the audio tracks of the *Pisces* digital video camera systems along with the submersible's GPS positions at 10-minute intervals. The average length of each transect was 1 km and the average visual range from each side of the sub was 10 m. Each transect therefore covered an area of approximately 2 hectares while each dive covered approximately 8 hectares.

The ROV was typically deployed to conduct 1.6-3.2 kilometer transects over selected survey sites. Two trained observers were present in the ROV control room and tasked with making substrate observations and identifications of fish and invertebrates encountered. The video along with the audio remarks from the observers were recorded throughout the dives on mini-DV video cassettes. After the dives, observer counts from the submersible transects were extracted from the videotapes. However, ROV transect videos were processed only by following HURL's standard ROV video-logging protocol that identifies species encountered during the dives with only rough quantification.

Light, an additional physical factor, changes considerably within the bottomfish EFH depth range. Since we are unaware of any actual light intensity measurements being made on these banks, theoretical values were derived from Wetzel's (2001)

attenuation equation:  $I_z = I_0 e^{-kz}$ , where

$I_z$ = irradiance at depth z

$I_0$ = irradiance just below surface (i.e., z = 0)

e = natural logarithm

k = extinction coefficient (0.033 for clear seawater)

NWHICRER waters are known to be extremely clear, and therefore it was assumed that the k value used in this equation would be appropriate.

Bottomfish EFH Classification and Description

Sonar data coupled with substrate observations made from the submersibles and ROV were used to describe the geological aspects of the bottomfish EFH around the banks according to the mega- to micro-scale classification scheme designed by Greene et al. (1999) for deep-water benthic habitats. Hydrological data were analyzed for each 100 m interval. Biological data (i.e., algae, invertebrate, and fish observations) were grouped into taxonomic categories and by abundance.

## RESULTS

Multibeam Sonar Data

The multibeam sonar coverage of the EFH around each bank is shown in Figure 1 between black lines. Multibeam data outside of the 100-400 m depth range from a 2002 Kilo Moana mapping cruise, as well as single-beam sonar data obtained on the top of Raita Bank (courtesy of J. Miller), were included in the Raita and W. St. Rogatien images (see Miller et al, 2004). No EFH boundaries are shown for Bank 66, which is located entirely within the 100-400 m depth range. For simplification, each map provides a slope analysis whereby green represents lower and red represents higher slope values. The tops of the banks were generally flat with slope values below 5°. With the exception of Bank 66, all were above 100-m depth. The "break" occurred at approximately 120 m where slope values increased rapidly to over 25°, and in some locations off Raita, over 60°. Steep slopes continued down to varying depths, however, in general, not below the lower 400-m boundary of the bottomfish EFH. Furthermore, the steepest slopes on Raita, W. St. Rogatien, and Brooks were found on the southwest sides of the banks while the lowest slope values were found on the northeast sides. The top of Bank 66 came up to approximately 120 m with the break generally beginning at 170 m. Slope values below the break to a depth of 250-270 m were for the most part between 10-20°. At that point, the slope flattened out to less than 5°, similar to the top.

The multibeam data did not reveal any particularly surprising features on the banks. All four had a relatively homogenous structure consisting of a flat top with a moderately steep slope in the bottomfish EFH that generally flattened out before reaching a depth of 400 m. The one exception was the presence of several small pinnacles found

within the northern boundary of the EFH off Raita. These features extended up from the seafloor approximately 40-60 m and it is likely that more will be found when the mapping of the EFH in this area is completed.

Submersible Data

The number of submersible and ROV dives conducted on each bank within the 100- to 400-m depth range are summarized in Table 1. Since more than one dive took place on some sites, the number of sites examined on each bank also is provided. Data from submersible, ROV, or both vehicles, were obtained during a total of 59 dives on 28 different sites.

Observations made during the dives revealed that the substrate within the EFH on all banks consisted of carbonate bedrock interspersed with sediment deposits. The latter were mostly composed of carbonate sand and pebbles with smaller amounts of gravel and cobbles. Not surprisingly, bedrock was predominant just below the break where the slope was the steepest, whereas sediment was predominant above the break as well as deeper, near the lower boundary of the EFH where the slope was flatter (Fig. 2). Low amplitude sediment waves were present even where the sand layer was relatively thin. In these cases, the underlying bedrock was clearly visible in the troughs.

Exposed carbonate bedrock clearly had different levels of complexity (i.e., rugosity + porosity). Bottomfish, as well as many other fish species observed, were typically found in association with high complexity bedrock rather than low complexity bedrock or sediment. Furthermore, porosity (i.e., the number of holes in the rock as the term is used here) was clearly a more important factor than rugosity, presumably because it offered more effective shelter against predators.

A summary of the CTD data obtained within the bottomfish EFH on the banks as well as the calculated theoretical light intensity values are presented in Table 2. Due to technical problems, temperature and salinity measurements were only available from 15 of the 16 submersible dives conducted in 2001 and 2002. Furthermore, only the DO measurements from 9 of the 10 submersible dives in 2002 were considered useable. Within the 100-400 m EFH depth range, both salinity and DO remained relatively constant at all sites, varying between 34-35 ppt and 5-6 ml/l, respectively. In contrast, temperature ranged from a high of 23°C at 100 m to a low of 10°C at 400 m, while the theoretical irradiance values ranged between a low of 0 to a high of 4,098 klux (4% of the light intensity just below the surface).

A summary of the biological organisms observed within the EFH depth range on these four banks is presented in Table 3. Of the invertebrates, a total of 64 cnidarian, 49 echinoderm, 30 crustacean, 15 mollusk, 10 sponge, 3 tunicate, and 1 ctenophore species were recorded during the dives. Examples of these are provided in Figure 3. Anemones (11 species), seastars (22 species), gastropods (10 species), and crabs (11 species) were the most diverse groups of cnidarians, echinoderms, mollusks, and crustaceans, respectively. Most urchins, seastars, and crustaceans were identified to species; however, many of the sponges and cnidarians were not, due to the difficulty in making accurate identifications of these organisms without close inspection of specimens. Clearly different

types were noted, such as small white pennatulids vs. large orange ones, which were assumed to be different species. Small branching hydrozoans were not routinely recorded because in most cases, they could not be distinguished from small dead antipatharians. Furthermore, the seven different species of algae observed during the dives were not identified past major division. Those observed appeared to be primarily non-attached fragments which had originated from the tops of the banks and were subsequently carried down slope. Therefore, these were not considered to be part of the natural biota within the bottomfish EFH and were not carefully recorded, although that assumption should be more thoroughly investigated. Furthermore, the importance of algae to the bottomfish EFH may be understated in this study, because locations at or near the 100-m upper boundary where naturally growing algae occur were underrepresented.

One hundred and fifty-two different fish species were observed within the EFH on the banks representing fifty-nine families (Table 3). Of these, serranids (groupers) were the most specious (12) followed by lutjanids (snappers, 9), labrids (wrasses, 9), scorpaenids (scorpionfish, 7) and morids (cods, 7). Twenty-one families had only one representative and included a berycid (alfonsin), a mullid (goatfish), an apogonid (cardinal fish), an ammodytid (sandlance), and an argentinid (deep-sea smelt).

Two clear patterns were evident from the fish identifications and count data. First, a diurnal-nocturnal shift in the fish communities on the banks was detected within the EFH depth range. The majority of the families shown in Table 3 appeared to be diurnal; however, there were a number of families that were only observed during ROV surveys at night. Most notable among these were the morids, carapids (pearlfish), myctophids (lantern fish), trachichthyids (slimeheads), and nettastomatids (duck-billed eels). Furthermore, most of the congrid (conger eels) observations were made at night as well. Three types of behaviors appeared to be responsible for this pattern. Morids and the congrid, *Conger oligoporus,* appeared to remain in the EFH during the day, hiding in holes in the rocks until night when they presumably emerged to feed. In contrast, other congrids, such as *Ariosoma marginatus*, also hid during the day but by digging burrows in the sediment instead. The nettastomatid, *Saurenchelys stylurus,* was enigmatic since these fish never were observed during the day and only observed on sediment substrates at night. Unlike the burrowing congrids, this species was not observed digging in response to the approach of the ROV, and, furthermore, it has a delicate caudal fin that does not appear to be well adapted for creating burrows. Third, it is well known that many myctophids undergo a daily vertical (i.e., from further down the slope) and/or lateral (i.e., from further offshore) migration at night. It is believed that these fish most likely leave the bottomfish EFH, or that portion close to the substrate, during the day and return each night.

The second pattern was a shift in the families observed between the upper and lower boundaries of the EFH, clearly indicating this depth range is the major transition zone between shallow and deep-water fish species. The depth ranges observed on the banks for 39 of the 59 families are shown in Figure 4. A complete change takes place between 100 and 400 meters with the upper end of the EFH dominated by shallow-water families such as acanthurids (surgeonfish), chaetodontids (butterflyfish), pomacentrids (damselfish), priacanthids (big-eyes), while the lower end was dominated by deep-water families such as epigonids (deepwater cardinal fishes), chlorophthalmids (green-eyes),

bembrids (deep-water flat-heads), symphysanodontids (no common name), and others. While this pattern is not surprising given the changes in both water temperature and light, it is certainly worth noting in any update of the bottomfish EFH definition. Similarly, invertebrate communities showed a considerable change between 100 and 400 m, although not with such a clear pattern at the family level.

## DISCUSSION

EFH definitions are designed to guide management decisions on the protection and sustainable exploitation of fishery resources and therefore need to be as complete and specific as possible. Similar to many other fisheries in the U.S., the EFH for the Hawaiian bottomfish fishery has been defined in general terms due to the lack of available information on their ecology (Park, 2002) and therefore does not provide the value it was intended to provide. This situation is changing, however, with several recent studies generating multibeam sonar data and *in situ* observations useful for creating a more specific definition. In the Main Hawaiian Islands (MHI), a bottomfish habitat geographic information system (GIS) that incorporates multibeam bathymetry and sidescan data with over 5,000 fishing survey records was submitted this past year to state and federal fishery management agencies (Kelley, unpublished). Additional ship days have been scheduled for 2005-2006 to complete the mapping of the entire MHI 100-400 m EFH depth zone. Recent submersible dives have been conducted on bottomfish grounds off the islands of Oahu, Molokai, and Kahoolawe (Kelley et al., unpublished report; Moffitt et al., unpublished) which provided macro- and micro-scale geological and biological data. In the NWHI, multibeam mapping and submersible/ROV dives have also been conducted on four banks, the data from which are summarized in this paper. In short, a more extensive archipelago-wide description of the EFH is forthcoming which will include multibeam and *in situ* data from both the NWHI and MHI.

With respect to the larger picture, this paper presents only a brief look at the EFH- relevant information obtained on a deep-water fishery during a study examining the impacts of fishing activities in the NWHI. Many studies are being conducted elsewhere, which are also accumulating large amounts of EFH-relevant data for other fisheries (see Benaka, 1999). However, a widely accepted data framework for creating EFH definitions has not been developed, and consequently these efforts are not being conducted in a coordinated manner. GIS is being commonly used to visualize habitat types and boundaries and may provide the means by which the process can be standardized. All of the various types of data summarized in this paper, including multibeam bathymetry, substrate observations, water quality parameters, and the various species present at different times of the day and at different depths, can be converted into GIS layers. One can imagine many other types of data layers, such as current vectors, catch data, and life stage distributions, which would be useful toward achieving more accurate and functional definitions. A consensus needs to be attained as to which layers to include and how each type of data are collected and coded. Once this occurs, the concept of EFH truly can begin to achieve its intended goal of ecosystem-based fishery management.

Table 1: Number of submersible and ROV dives conducted on each bank.

| Bank | Sub Dives | ROV Dives | Total Dives | # Sites |
|---|---|---|---|---|
| Raita | 10 | 14 | **24** | **9** |
| W. St. Rogatien | 8 | 15 | **23** | **12** |
| Brooks | 3 | 5 | **8** | **3** |
| Bank 66 | 1 | 3 | **4** | **4** |
| **Total** | **22** | **37** | **59** | **28** |

Table 2: Summary of CTD data and calculated light intensity.

| Depth Range (m) | Salinity (ppt) | DO (ml/l) | Temp (°C) | Light (klux) |
|---|---|---|---|---|
| 100-200 | 34-35 | 5-6 | 15-23 | 38-4098 |
| 200-300 | 34-35 | 5-6 | 12-21 | 1-151 |
| 300-400 | 34-35 | 5-6 | 10-17 | 0-6 |
| **100-400** | **34-35** | **5-6** | **10-23** | **0-4098** |

**Figure 1**: Multibeam sonar coverage of the 100-400 m EFH (area between the black lines) around a) Raita Bank, b) W. St. Rogatien Bank, c) Brooks Bank and, d) Bank 66.
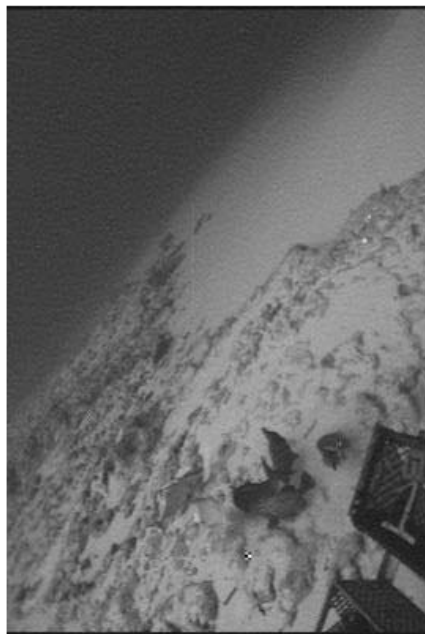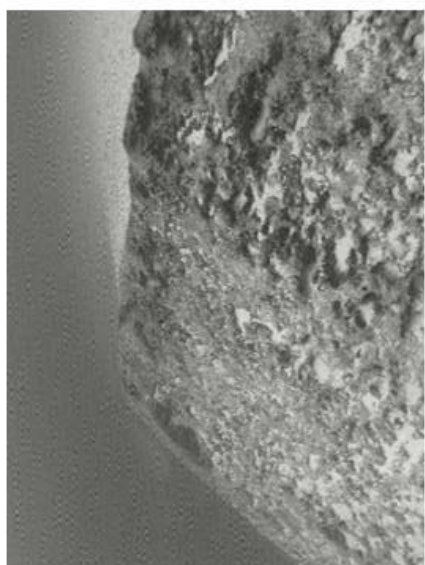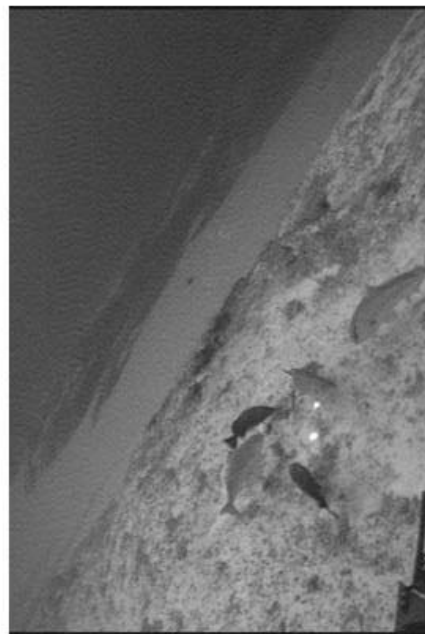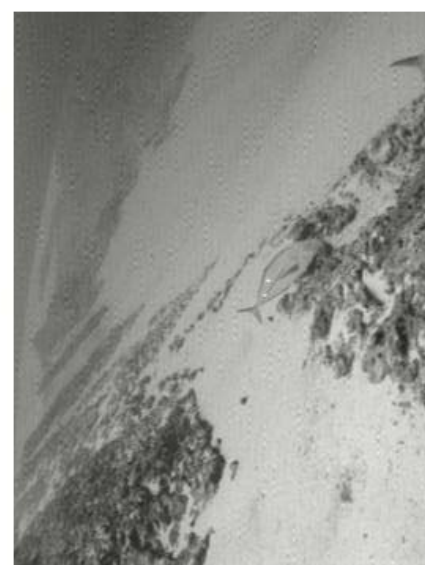
**Figure 2**: Low-light camera images of the break (a) and further down the slope (b,c,d) at Raita and W. St. Rogatien Banks.
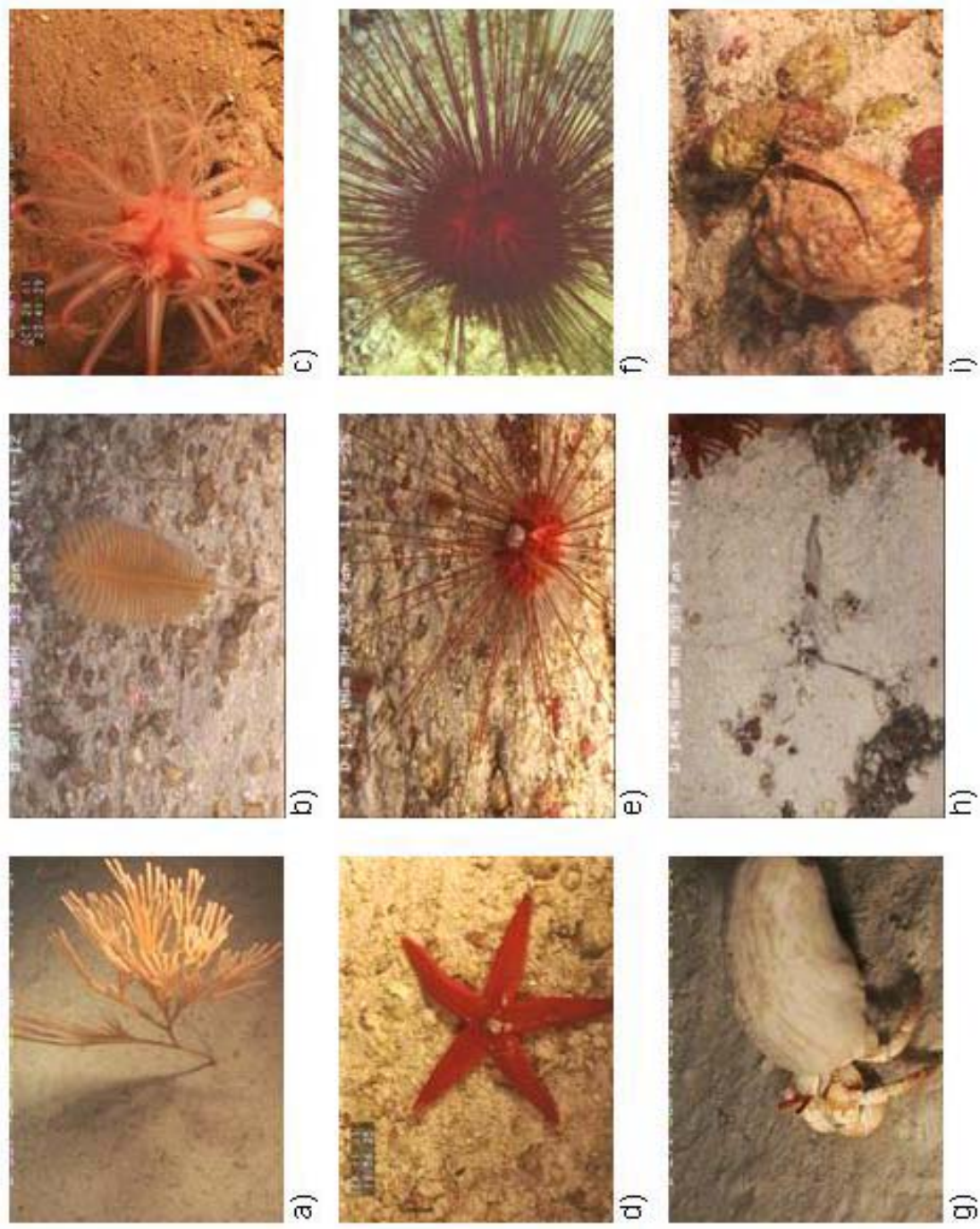
**Figure 3**: Examples of invertebrates recorded during the dives (a:*Fanellia eurytheia*, b:*Pennatula perci*, c:*Anthomastus sp*, d: *Ctenophoraster hawaiiensis*, e:*Diadema savignyi*, f:*Diadema sp*, g:*Dardanus sp*, h:*Plesionika sp*, i: *Calappa pokipoki*).
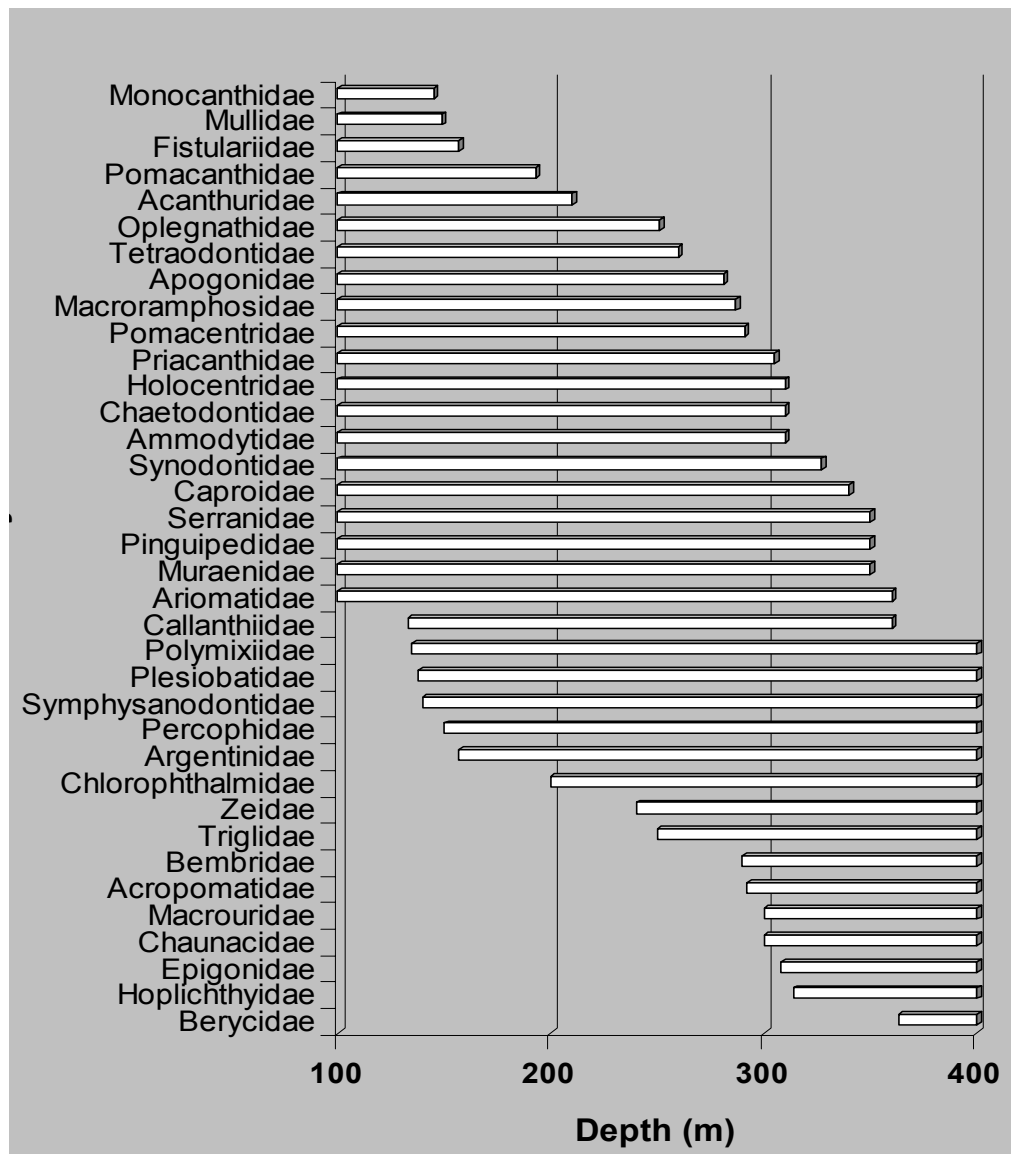
**Figure 4**: Depth ranges for 39 of the 59 fish families recorded during the dives.

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# HISTORICAL AND PRESENT STATUS OF THE PEARL OYSTER, *PINCTADA MARGARITIFERA*, AT PEARL AND HERMES ATOLL, NORTHWESTERN HAWAIIAN ISLANDS

BY

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## ABSTRACT

Populations of the black-lipped pearl oyster, *Pinctada margaritifera*, at Pearl and Hermes Atoll in the Northwestern Hawaiian Islands were first reported in 1928 and heavily harvested over the next 2 years. Approximately 150,000 pearl oysters were either exported or killed during the exploitation. An expedition in 1930 to assess post-harvest population status found 480 *P. margaritifera* and determined the population to be severely depleted. Limited surveys in 1994 and 2000 found only a few pearl oysters and led to the conclusion that the population was still depleted. In 2003, the National Oceanic and Atmospheric Administration (NOAA)-led multi-agency marine debris removal team spent several months conducting surveys at Pearl and Hermes Atoll that included quantitative observations of *Pinctada margaritifera*. Data were collected on location, size, depth, habitat, and orientation of individual pearl oysters on the reef. Analyses of the 1930 and 2003 data sets revealed similar size-frequency distributions of the *P. margaritifera* population. The population has a spatial distribution within the Atoll similar to the 1930 post-harvest distribution, and some sustained level of reproduction. Density and depth distribution comparisons from the two survey periods suggest that pearl oysters are significantly more abundant in the shallow waters where they were harvested during the fishery but at a similar density overall as they were during the 1930 survey. Although no estimates of absolute population size are available for any time period, the large number of oysters harvested prior to the 1930 survey, together with estimates of oyster density in 1930 and 2003, suggest that the population may never have recovered to its pre-exploitation level.

## INTRODUCTION

The pearl oyster, like other shellfish and many other marine animals (e.g., abalone; Tegner et al., 1996), has a long history of exploitation throughout the world.

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Records from the pearl industries in India and Venezuela document the discovery, harvest, and eventual over-exploitation of these populations (Arunachlam, 1952; Romero et al., 1999). Pearl oysters have been prone to exploitation due to the considerable value of the pearls and the nacre, or "mother of pearl", of the shell, and because of the animal's sessile nature and tendency to occur in sufficient densities at shallow depths for relatively easy collection.

The first documented discovery of *Pinctada margaritifera* at Pearl and Hermes Atoll in the Northwestern Hawaiian Islands (NWHI) (Fig. 1) was in May 1928 by Captain William B. Anderson of the Lanikai Fishing Company (Amerson et al., 1974). For the next 2 years, the pearl oysters were heavily harvested for their nacre. This shiny portion of the shell was exported to the U.S. mainland where it was used primarily to make buttons. Although documents concerning the harvest are wanting, conservative estimates are that the shells of approximately 100,000 oysters were exported (Galtsoff, 1933). It is estimated that about 50,000 more oysters were killed and discarded, some due to their poor shell quality and others in the search for pearls (Galtsoff, 1933). After the extent of the harvest was realized by the Hawaii Territorial government, an expedition was undertaken to assess the population and a temporary ban on harvesting was put in place. This six-week expedition, led by P. Galtsoff in the summer of 1930, utilized several Filipino divers and produced a lengthy report including data on pearl oyster size, weight, location (Fig. 2, modified from Galtsoff (1933)) and survey effort. Galtsoff (1933) found 480 *P. margaritifera* and pronounced the population too depleted to sustain further harvesting. At this time the Territory of Hawaii made the taking of pearl oysters illegal without permission, and a resurvey was suggested in five years to assess the recovery of the population. Subsequently the industry collapsed, coinciding with replacement of pearl shell with plastic for button making and the advent of commercial pearl oyster farms. Due to the lack of interest in further fishing of *P. margaritifera* in Hawaii, the suggested 5-year resurvey at Pearl and Hermes was not conducted; however, the species has remained under state protection since that time.
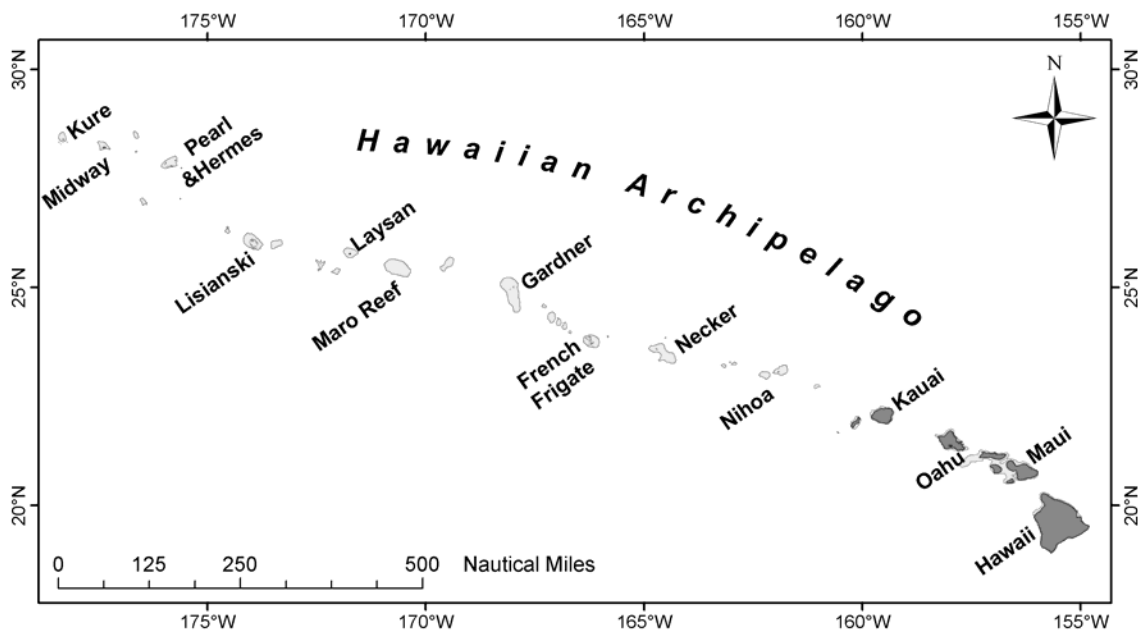


**Figure 1**. Map of the Hawaiian Archipelago.
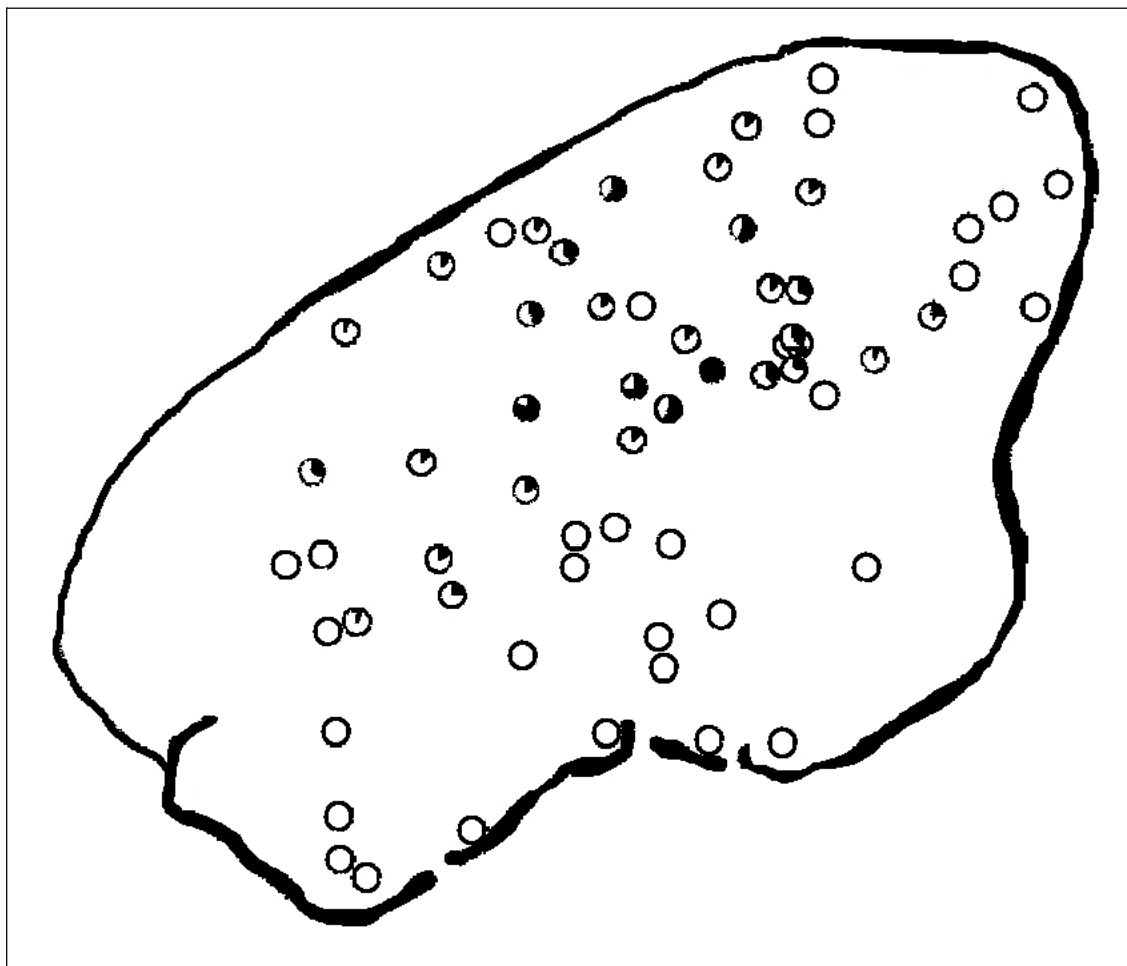
**Figure 2**. (From Galtsoff, 1933). Pearl oyster survey sites at Pearl and Hermes Atoll from the 1930 survey. The single black circle represents the highest relative abundance found (33 oysters / diver hour) and is represented as 100 percent. Other circles indicate the proportional relative abundance found at other sites in the 1930 survey. White circles are sites at which no oysters were found.

There have been three recent surveys at Pearl and Hermes which included documentation of pearl oyster presence: (1) by the U.S. National Marine Fisheries Service (NMFS) in 1993 (Moffitt, 1994); (2) the 2000 NWHI Reef Assessment and Monitoring Program (NOWRAMP) expedition (Maragos and Gulko, 2002); and (3) the 2002 NOWRAMP expedition (Basch, unpublished data). Each of these surveys reported only a few pearl oyster sightings, suggesting that the population did not rebound from the harvesting event and remained severely depleted. However, researchers had insufficient data to determine an accurate status of the pearl oyster population. The 1993 NMFS effort was a two-day survey of the general areas which had the highest pearl oyster densities in Galtsoff's (1933) survey. The densities at the three sites assessed in 1993 were found to be lower than in 1930 (Moffitt, 1994). One problem with the 1993 survey is that the methods used to determine the locations of survey sites in 1930 were not sufficiently accurate. They were comprised of calculations using triangulation of distant markers

and dead reckoning; moreover, these methods were made less accurate by the scientists' inability to navigate straight lines through the shallow, reticulated reef. Consequently, it is not possible to locate the 1930 sites with enough accuracy to make site-by-site comparisons over time, particularly considering the patchy distribution characteristic of pearl oysters.

The 2000 and 2002 NOWRAMP cruises were not specifically focused on surveying for pearl oysters. The relatively small areas surveyed were selected to record detailed information on the fish, algae, corals, and other invertebrate species present. Pearl oysters were also recorded on some of these transects. A report documenting the results of the 2000 cruise states that only a few oysters were found, and they were smaller than those taken in 1930 (Maragos and Gulko, 2002). The transects were purposely located on varying habitat types and many were not in preferred pearl oyster habitat. The few observations made on the status of the pearl oyster and the constraints of the surveys limit the usefulness of these surveys for determining the status of the population.

The purposes of this study were to: (1) accurately document the recent status of the pearl oyster population at Pearl and Hermes by means of a systematic, quantitative, and broad-scale survey of the *P. margaritifera* population at the Atoll, and (2) make initial comparisons between historical and recent survey results.

## MATERIALS AND METHODS

Data Collection

As part of an ongoing NOAA-led multi-agency effort to remove derelict fishing gear and other marine debris from the coral reef ecosystems of the NWHI, divers from NOAA's Coral Reef Ecosystem Division (CRED) have methodically and systematically surveyed large areas of the shallow water reef habitats at Pearl and Hermes Atoll (Donohue et al., 2001). Since 2003, the survey protocols have included extensive pearl oyster observations. Divers surveyed reefs using snorkel gear while swimming or being towed along patch or reticulated reefs. Areas surveyed were recorded using a Garmin Geographic Positioning System (GPS) 12 (NAD84) in a small boat closely following diver tracks. For each pearl oyster observed, latitude, longitude, size, and depth were recorded. Maximum shell length and width were measured. Length was measured as the maximum dorsal ventral measurement (DVM), and width was recorded as the measurement of the shell perpendicular to the length. For a small number (approximately 10 percent) of the oysters no measurements, depths, or locations were recorded. Since identification of juvenile recruits to species requires more time and greater taxonomic skills than were available, and usually requires observation in the laboratory, juvenile oysters (<1.5 cm)were not included in the data analysis.

For a subset of observations, additional data were collected, when time allowed, on habitat (substratum, dominant biotic cover category), and orientation of individual oysters on the reef. For 40% percent of observations substrate was documented, and for 59% percent orientation was recorded. Habitat was characterized by percent cover of the

substratum types in the 1 m$^2$ area centered on an oyster. The substrate categories were recorded as algae, sand, coral, and coral cement. The algae category consisted of macro-algae only, which were not identified to species. The coral cement category encompassed coral rubble and dead coral either exposed or with associated turf or coralline algae. Orientation, the angle between the plane of the oyster's shell and the substrate it was attached to, was classified as horizontal, vertical or diagonal.

Data Analysis

Field data were transcribed daily to an Excel worksheet containing all parameters for each oyster. The GPS tracklines and waypoints were imported into ESRI Arcview© 3.2 Geographic Information System (GIS) software, where they were used to map both the reefs surveyed and the point location of oysters on those reefs (Fig. 3). The total area of the reef surveyed during 2003 was determined by creating polygons in ArcView which delineated the reef contours of areas where divers swam. These polygons were created using an Ikonis satellite image of the atoll (Fig. 4). The areas of all polygons were added to obtain total reef area surveyed.

Several manipulations of Galtsoff's (1933) observations were performed to enable comparison of his and our survey results. Galtsoff (1933) reported survey effort in diver minutes. He reported that the divers covered a reef at the speed of 42.7 ft/min (0.01 km/min), and that in order to cover the entire breadth of the reef the divers swam a zigzag pattern with a width of 60 to 100 ft. Galtsoff reported survey effort only for areas where oysters were found. In order to compensate for the rest of the survey area effort, we assumed that the average effort for a site with no oysters reported was approximately the same as for the sites where oysters were observed. There were 32 sites with oysters and 32 without, so the total minutes were doubled for a best approximation of survey effort. To estimate the distance surveyed from effort we multiplied the survey rate (0.01 km/min) by total minutes (4,562 min) for a result of 58.9 km. We multiplied this distance by the associated width (60 to 100 ft, or 0.01 to 0.03 km) to estimate the survey area covered, with a result of 1.1 km$^2$ to 1.8 km$^2$.

**RESULTS**

A total of 1,057 pearl oysters were found at Pearl and Hermes Atoll during the 2003 summer survey. The pearl oysters were distributed primarily throughout the inner lagoon area (Fig. 2) with the exception of ten observations where individuals were found on the sand flats or outer fringing reefs. The lagoon habitat was surveyed by swimming only; we did not factor in the towed-diver survey areas in our density estimates as they were largely performed over sand and on habitat unsuitable for pearl oysters. This facilitated comparisons with Galtsoff's (1933) results as observers in the 1930 survey intentionally avoided the sand flats. Area computations using GIS resulted in a total lagoon survey area of 5.9 km$^2$. With an observed total of 1,047 pearl oysters in this area, we calculated an average density of 177 pearl oysters/km$^2$ in the lagoon area surveyed.
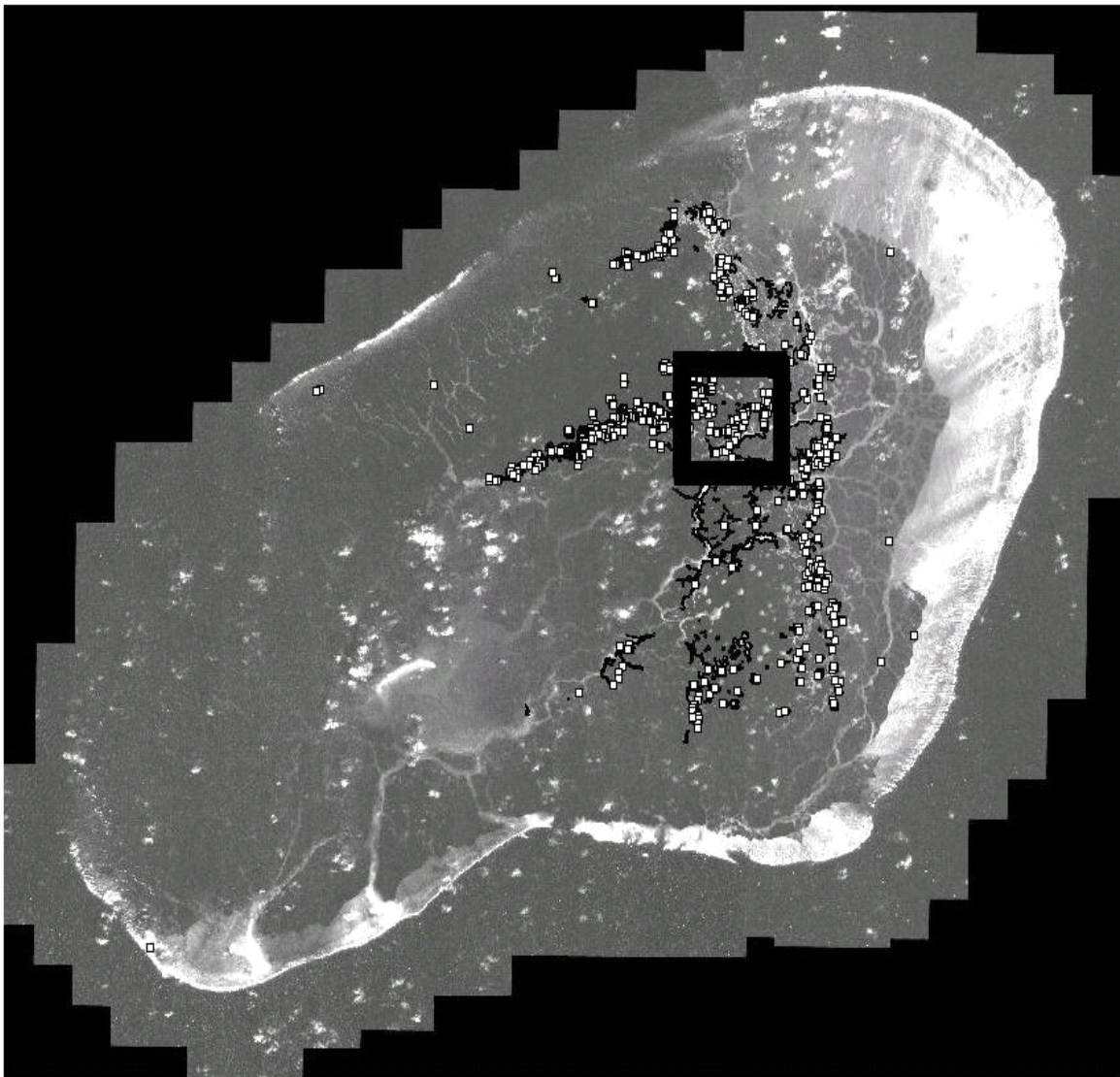
**Figure 3**. Distribution map of 2003 pearl oyster sightings, Pearl and Hermes Atoll. Areas surveyed by swimming are displayed as black lines, and oysters are represented as white squares. Only the survey areas and oysters in the inner lagoon were used in the density calculations. The black box represents the area portrayed in Figure 4.

This density estimate assumes that all oysters present were observed by the divers, when in reality some oysters were missed. Therefore, this is not an estimate of absolute oyster density, but a density estimate that can be compared to the 1930 survey, assuming that in each study there was the same probability that an oyster present in the surveyed area was observed by the divers. Pearl oysters were found at depths ranging from 0.31 m to 6.1 m with a mean of 1.36 m and standard deviation (sd) of 0.87 m (Fig. 5).

The average shell length of pearl oysters measured was 20.2 cm (sd = 4.76 cm, n = 963). Shell length ranged from 1.5-33.0 cm. Pearl oysters smaller than 1.5 cm were excluded from analysis since oysters of that size could not be accurately identified
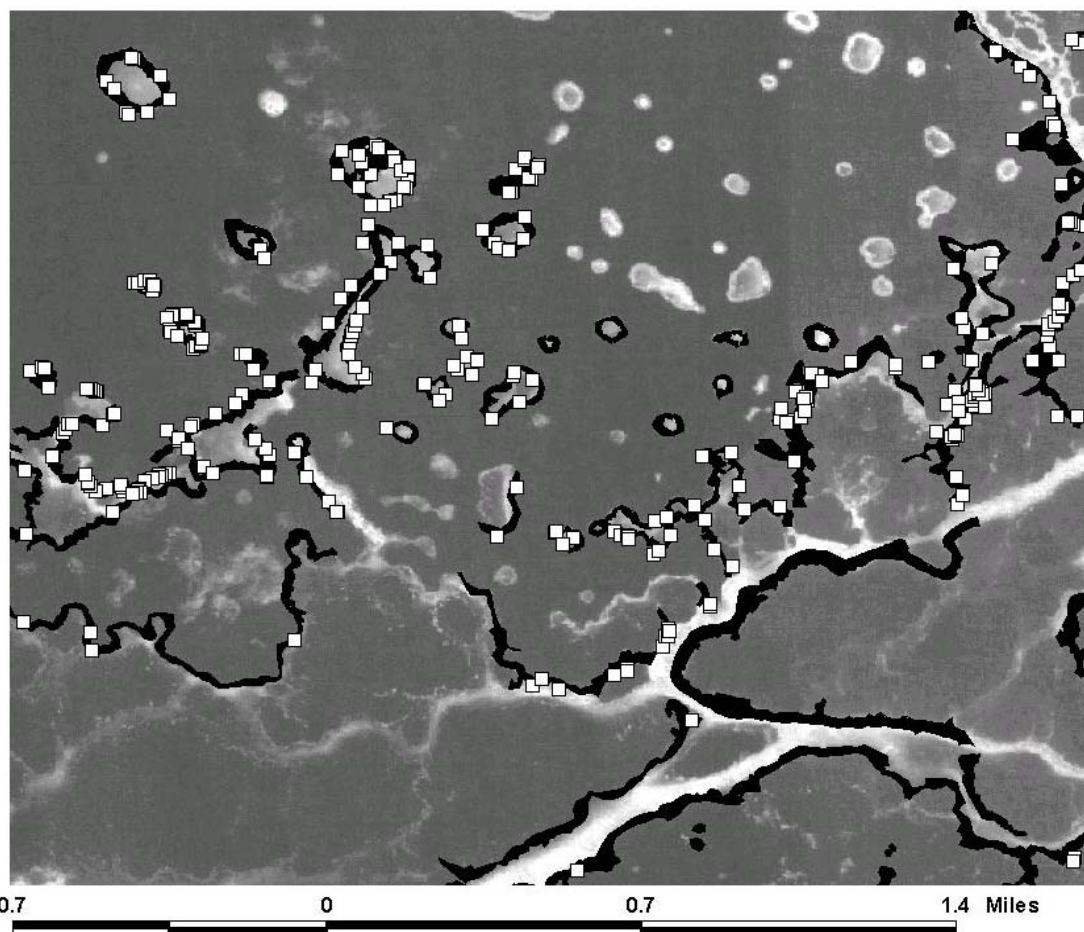
**Figure 4**. An enlargement of a section of the lagoon at Pearl and Hermes Atoll (Area portrayed is outlined by the black box in Figure 3). The black areas are the polygons created in Arcview 3.2 to delineate the surveyed reef area at Pearl and Hermes during 2003. Pearl oysters are represented by white squares.

to species in the field. The *P. margaritifera* size frequency distribution (Fig. 6) has a single mode. However, immature oyster recruits, or spat (shell length <5 cm), were excluded from the size-frequency data set. The mean shell length of 20.2 cm found in 2003 is remarkably similar to the mean shell length of 20.23 cm for the 164 adult pearl oysters measured by Galtsoff (1933), although the distributions have different shapes (Fig. 6). For 419 (40% of total surveyed) pearl oysters observed, data were recorded on substratum type. Within the lagoon, the typical substratum composition consisted of: sand 11% (sd =24.8), coral 13% (sd = 17.3), algae 28% (sd = 32.1), and coral cement 48% (sd = 34.6). The oysters were found in various orientations. In the subset of oysters for which orientation data were collected (n = 624), most were horizontal (53%). Of the remaining oysters, 32% were vertical, and 15% were diagonal.
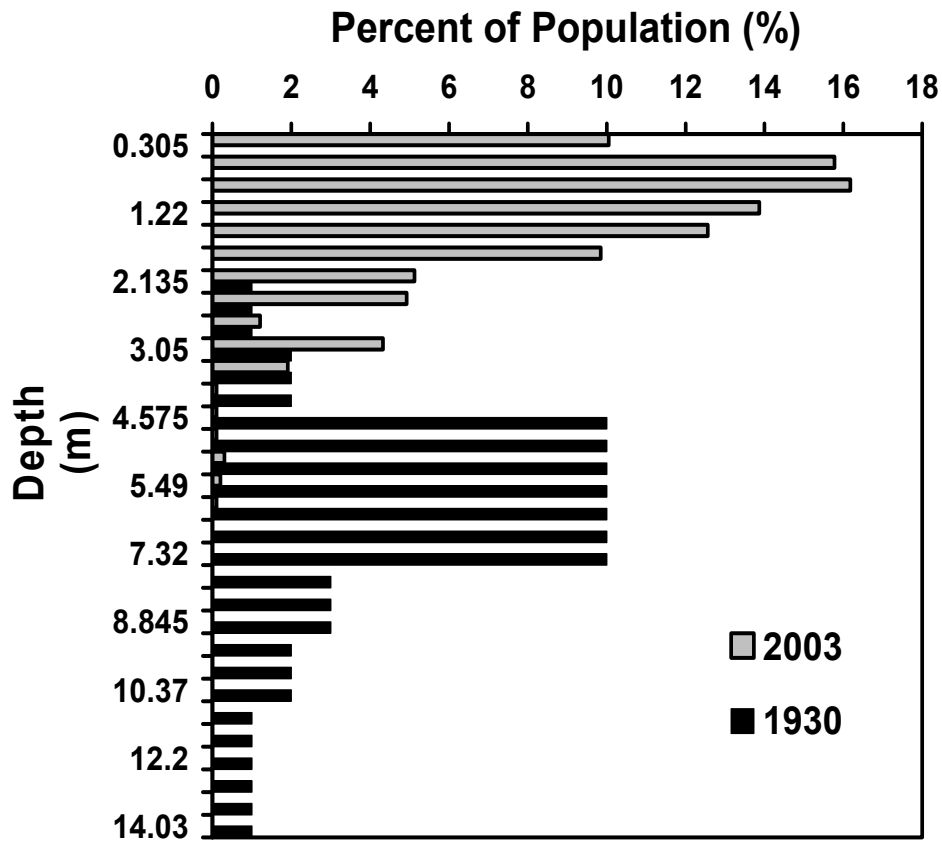
**Figure 5**. Depth range frequency distribution for pearl oyster surveys in 1930 and 2003. Percent values for the 1930 data set are estimates based on the given mean depth range and minimum and maximum depths from Galtsoff (1933).
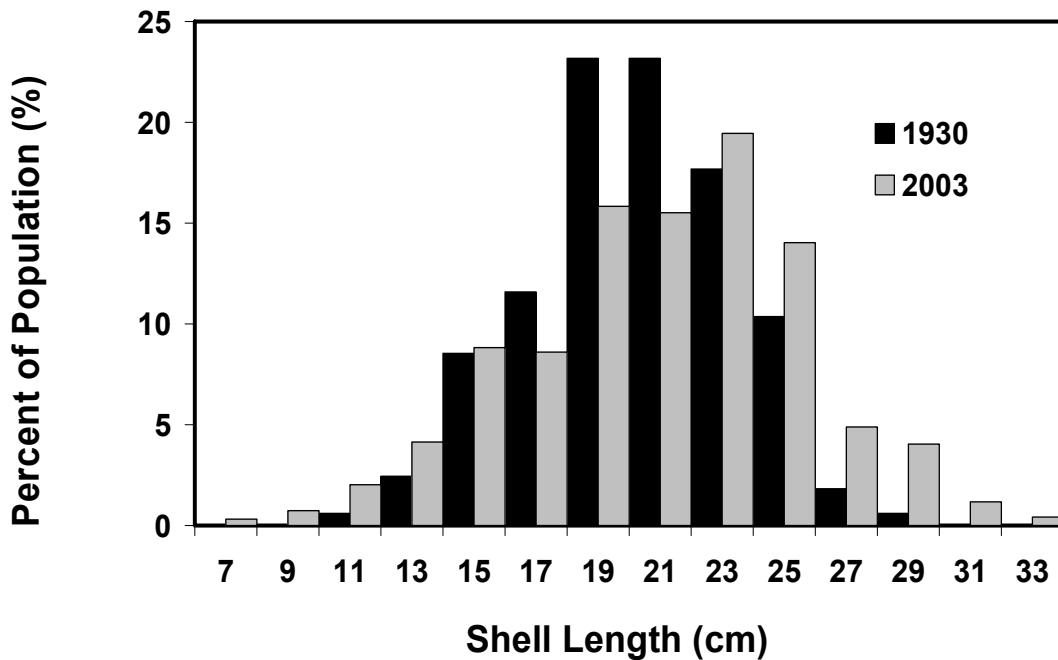


**Figure 6**. Size-frequency distribution of the pearl oyster population at Pearl and Hermes Atoll, Northwestern Hawaiian Islands in 1930 (N =197) and 2003 (N =963).

## DISCUSSION

In distribution maps (Figs. 3 and 4) we indicate that pearl oysters are widespread throughout the Atoll lagoon. When comparing our results with Galtsoff's (1933) post-harvest data, we considered whether changes in the population occurred since that time. By visually comparing the maps from the 1930 and 2003 surveys (Figs. 2 and 3), a general idea of the difference in spatial distribution can be obtained. Although the locations from the 1930 map (Galtsoff, 1933) are only roughly estimated, no oysters were recorded in 1930 for the reefs in the southeast and south ends of the islands. When those areas were surveyed in 2003, relatively high levels of pearl oysters were observed on almost all reefs. It is likely there has been new recruitment and population expansion into this region since the 1930 survey. Moreover, reefs in the south central and north central lagoon, where some oysters were seen in 1930, were not surveyed in 2003; some oysters may be present in these areas.

Determining whether *Pinctada margaritifera* populations have recovered to pre-harvest levels is complicated by the fact that there are no estimates of pre-harvest population density, and no estimates of absolute oyster abundance at Pearl and Hermes for any time period. Comparisons between early and recent post-harvest data sets are facilitated by the fact that Galtsoff (1933) did report numbers of oysters found and the survey effort, which can be used to estimate oyster density in the 1930 survey. After converting Galtsoff's (1933) reported effort into survey area, we determined an average density of 209 to 349 pearl oysters/km$^2$ during his surveys. In our 2003 survey, we estimated an average density within the lagoon areas of 177 pearl oysters/km$^2$, lower but of the same order of magnitude as the density found in 1930, and presumably lower than the density just prior to exploitation. Given the lack of data between the two surveys, changes in pearl oyster abundance during the intervening 73 years cannot be determined. However, if abundance has not reached pre-exploitation levels, it is useful to ask why. One explanation for this would be that adult pearl oyster densities were reduced by exploitation below a threshold where Allee effects (or inverse density dependence) came into play (Levitan, 1995). *Pinctada margaritifera* is a broadcast spawner with planktonic larvae (Pouvreau et al. 2000); consequently, reduced adult densities could have imposed a direct bottleneck on fertilization success, and subsequent embryonic, larval, and recruitment success (Pouvreau et al., 2000). With a lowered adult density there would be less likelihood that female gametes would become fertilized in the water column, as has been shown for octocorals, sea urchins, abalone, and other sessile or sedentary benthic marine invertebrates (Levitan, 1995; Tegner et al., 1996; Coma and Lasker, 1997). Subsequently, if a larva was produced and dispersed proximate to a suitable settlement site, the likelihood that it would encounter a settlement cue associated with an adult shell also would be more remote. In other words, Allee effects would be further enforced given that pearl oyster larvae tend to settle gregariously on the shells of adult oysters (Pascal and Zampatti, 1995; Zhao et al., 2002).

Comparison of the pearl oyster population depth distribution between the 1930 and 2003 surveys shows some intriguing differences (Fig. 5). In 1930, oysters were reported as ranging from 2.5 to 15.0 m, and were most abundant from 4.4 to 8.3 m.

Galtsoff (1933) also reports that, according to Captain Anderson, when the oysters were first discovered they were very abundant in water depths of 1 to 3 m. In our 2003 survey, we found oysters from 0.3 to 6.0 m depth, but animals were most abundant in the 0.5 to 2.2 m range (determined using the mean of 1.36 m $\pm$ 0.87 m sd). In Figure 5, we illustrate the difference in the depth ranges between the two studies. The absence of any oysters in waters shallower than 2.5 m in 1930 is evidence of the heavy harvesting effort at these shallow depths in the immediately preceding years. Seventy-three years later, we found oysters to be very abundant at these shallow depths, suggesting that the remaining population contributed to a reseeding of shallow areas of the reef. What remains elusive at this time is an explanation for the apparent scarcity of oysters at deeper depths in our survey. The most likely explanation is that oysters still occur in higher abundance at these greater depths but that our sampling did not detect them.  Since the lagoon surveys were performed by snorkeling, the divers spent most of their time at or near the surface while surveying. Oysters which may have been on the deeper reef slopes may have been missed because of their smaller size in relation to other search images (since the primary mission was to locate generally larger marine debris) and the greater distance with depth from the divers.  We have no reason to believe that the lagoonal reefs have changed in a way that would impose biological limits to the depth range of the oysters.

Alternatively, though less likely, pearl oysters may recruit preferentially to shallower depths and may be less abundant in deeper areas due to this preference in combination with (1) reduced adult densities at depth sustained over the post-harvest period and (2) Allee effects. A directed survey for pearl oysters at Pearl and Hermes conducted along multiple-depth contours would help determine the distribution and other population parameters of oysters at deeper depths.

The present study indicates that the *Pinctada margaritifera* population at Pearl and Hermes Atoll is reproducing at some level, as indicated by individuals of a broad range of size classes, including recruits. The mean shell length of the 963 pearl oysters measured in the 2003 survey was 20.2 cm. The oysters were found predominantly on coral cement and macro-algae dominated habitat. This observation contrasts with Galtsoff's (1933) report that most oysters were found "confined exclusively to those sections where the bottom is covered with corals." Initially, we thought that the difference between surveys in composition of oyster-occupied habitat might be attributed to differences in the depth range, but examination of the data showed similar coral percent cover at all depths.

The shell orientation of the oysters was measured in our survey because our initial observations of orientation were inconsistent with a comment in Galtsoff's (1933) report. Galtsoff (1933) noted that oysters were found in a vertical or slightly inclined position, while we commonly observed oysters in a horizontal position. Our results indicate that only about 1/3 of oysters were oriented vertically, and $\geq$ 1/2 were horizontal. These differences in orientation may be a residual artifact of harvesting, or may reflect depth-related differences in the nature of near-boundary layer water movements which the animals may respond to by orienting themselves, either to minimize drag due to sheer forces, or to optimize filter-feeding efficiency in different flow regimes.

We report the first systematic, quantitative survey for pearl oysters throughout

the lagoon at Pearl and Hermes Atoll since Galtsoff's 1930 post-harvest expedition. By comparing the estimated densities of post-harvest and present populations, it would appear that the abundance of oysters in 2003 is similar to the population size in 1930. Given the lack of data during the intervening 73 years, we cannot determine whether the population ever recovered to its pre-exploitation abundance, but all available observations suggest it has remained at a reduced level. However, because we found the majority of pearl oysters at depths where the historical exploitation was focused, we conclude that the pearl oyster population has increased in density at shallower depths since the 1930 survey. In addition, it seems likely that the oyster density in deeper waters may be comparable to historical densities, if not higher. Depth-stratified surveys of pearl oysters at Pearl and Hermes are needed for a more thorough understanding of current population status; these additional surveys likely would yield a higher present population density.

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# OCEANOGRAPHY AND MAPPING
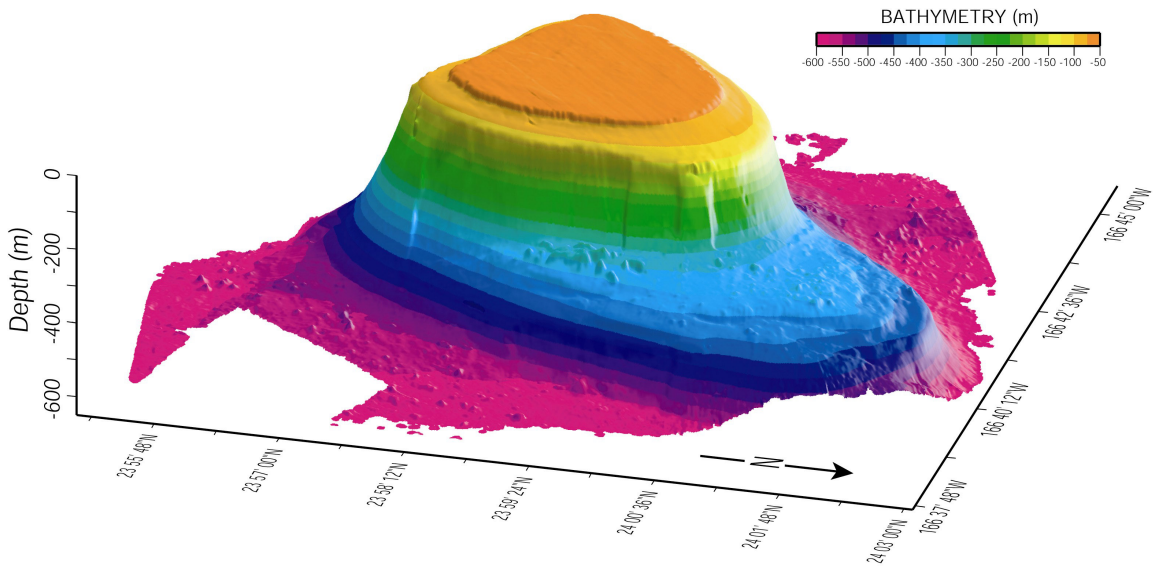
# TEN YEARS OF SHIPBOARD ADCP MEASUREMENTS ALONG THE NORTHWESTERN HAWAIIAN ISLANDS

BY

JUNE FIRING[1,2], AND RUSSELL E. BRAINARD[2]

## ABSTRACT

Ten years of shipboard acoustic Doppler current profiler data, resulting in 105 transects along the Hawaiian Ridge, have been analyzed to describe the spatial and temporal variability of the mean currents and vertical shear structure in the vicinity of the Northwestern Hawaiian Islands. The analysis spans the period October 1990 through November 2000, with data being most sparse during the boreal winter months. The current field is dominated by mesoscale variability; only in a few locations is the mean statistically significant. The mean shows the North Hawaiian Ridge Current flowing westward south of Kauai and Nihoa. The average from March to July shows the eastward Subtropical Countercurrent, from Maro Reef to Necker Island. Information on ocean current structure is critical to better understand biological connectivity among the Northwestern Hawaiian Islands as well as between the Main Hawaiian Islands and the Northwestern Hawaiian Islands.

## INTRODUCTION

The Hawaiian Archipelago is one of the most geographically and oceanographically isolated island groups in the world, extending northwest from the Island of Hawaii at 19° N latitude, 155° W longitude to Kure Atoll at 28° N latitude, 178° W longitude. The Archipelago includes the inhabited Main Hawaiian Islands (MHI) to the southeast comprised of high volcanic islands, and the uninhabited Northwestern Hawaiian Islands (NWHI) to the northwest, consisting of low coral islands and atolls, a few basaltic pinnacles, and submerged banks (Fig. 1). With the designation of the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve (NWHI-CRER) by Executive Orders in 2000 and 2001, the Reserve is now the nation's largest marine protected area (MPA), and second globally only to Australia's Great Barrier Reef Marine Park. With this designation, there has been considerable attention to improving the management and conservation of the region using science-based ecosystem principles.

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Understanding the many complex biological and biophysical interactions of ecosystem science is challenging, and much of the recent focus for conservation ecologists and marine resource managers has been centered on the connectivity of the region. Managers are trying to identify 'best places' to locate no-take MPAs to effectively preserve the biodiversity and abundance of natural resources Archipelago-wide. The biological linkages of reef fish and other biota between and among islands and atolls of the NWHI and the MHI are poorly known. Recent surveys indicate that shallow-water reef fish populations in the NWHI are relatively pristine and those in the MHI, especially apex predators, are presently overexploited (Friedlander and DeMartini, 2002). Among many important factors influencing this connectivity, ocean circulation is among the least known.

The oceanographic isolation of the Hawaiian Archipelago has resulted in the highest percentages of endemic marine organisms in the insular tropical Pacific (Jurik et al., 1998; Randall, 1995, 1998; Randall and Earle, 2000; Allen, 2002; DeMartini and Friedlander, 2004). Researchers found a gradient of increasing endemism of reef fishes to the northwest along the Archipelago, with highest endemism by species, numbers, and biomass at the three northernmost atolls, Pearl and Hermes, Midway, and Kure, and reefs surrounding Lisianski Island-Neva Shoal (DeMartini and Friedlander, 2004). Other recent evidence suggests the central portion of the NWHI, from French Frigate Shoals to Lisianski Island, may be a 'gateway' of genetic diversity for the Archipelago (B. Bowen, pers. comm.). Rivera et al. (2004) found the highest nucleotide and gene diversity of the Hawaiian grouper, *Epinephelus querus*, within the Archipelago at Gardner Pinnacles. Ongoing genetic work on tube snails (A. Faucci, pers. comm.) and spinner dolphins (K. Andrews, pers. comm.) suggests diversity peaks in this same central portion of the NWHI. The highest species diversity of scleractinian corals in the Archipelago is found in this region (Maragos et al., 2004). Several species of the coral *Acropora*, a group absent in MHI and most of NWHI, are abundant in the mid-Archipelago (Maragos et al., 2004). The cone shell *Turbo articulatus* has only been reported within the Archipelago at French Frigate Shoals (S. Godwin, unpublished data). *E. querus*, *Acropora*, and *T. articulatus* are all common at Johnston Atoll, the closest shallow reef ecosystem to the Archipelago, situated several hundred km southwest (Heemstra & Randall, 1993). The relative proximity of these two atolls, along with the similarity in marine species composition, has led to hypotheses of an oceanographic connection between Johnston and the midsection of the NWHI (Grigg, 1981), which then serves as a stepping-stone for colonization of the rest of the Archipelago.

The ocean circulation in the vicinity of the NWHI has not been described in great detail, but the large-scale aspects are well known. Lying within the North Pacific Subtropical gyre, near a ridge of maximum dynamic height, is the transition between the eastward and westward upper ocean geostrophic flow (Kobashi and Kawamura, 2002). Lumpkin (1998) analyzed paths of World Ocean Circulation Experiment (WOCE) drifters moving through the region of the Hawaiian Archipelago, and found few passing north of 25° N. Lumpkin showed drifters moving toward the north around 160° W, with others moving to the lee side of the ridge, returning to the west in circular flows. Dynamic topography shows a highly variable eastward flowing Subtropical Counter

Current (STCC) roughly between 24° N and 27° N from 130° E to 160° W. The flow becomes more unstable in late fall to winter due to strong vertical velocity shear between the eastward flowing STCC and the underlying westward flow of the North Equatorial Current. To date, there have not been reports of direct observations of the STCC across the NWHI (Kobashi and Kawamura, 2002).

To better understand connectivity, biogeography, and endemism, we examine the spatial and temporal variability of mean currents and vertical shear structure in the vicinity of the NWHI using upper-ocean velocity measurements from 10 years of shipboard acoustic Doppler current profiler (ADCP) transects along the Hawaiian Ridge. This general description of measurements collected by the Pacific Islands Fisheries Science Center on repeated cruises of the NOAA Ship *Townsend Cromwell* is used to examine the structure of long-term mean currents and shear to determine potential transport of larvae among the islands and atolls of the NWHI, and between the NWHI and MHI. We address the question of whether the NWHI are more likely to be a source or a sink of larvae for the MHI, and examine the mean currents for observational evidence of the eastward flowing STCC.

## METHODS

Data Collection

From October 1990 to November 2000, shipboard ADCP data were collected on repeated cruises of the NOAA Ship *Townsend Cromwell*, resulting in 105 north or south sections along all or part of the NWHI from Honolulu to Kure Atoll. The hull-mounted RD Instruments narrow-band (150 kHz) ADCP transmitted sound pulses along four beams and measured the Doppler-shifted frequency of the backscattered sound to estimate the velocity of the scatters, such as plankton, small fish, and detritus, relative to the ship. Water velocity over ground is computed by removing the ship's velocity based on Transit satellite fixes for the early cruises and GPS positions after 1993 (Firing, 1991). To improve accuracy of velocity estimates, an Ashtech 3DF GPS provided ship's heading during the later years. Velocity profile data were ensemble-averaged over 5 minutes with an 8-m vertical resolution over the depth range of 20 to 300 m, with data often being inconsistent below 200 m due to limited scatterers in the water column or excessive air bubbles under the ship during heavy sea conditions. Figure 2 shows the temporal distribution of the 105 ADCP transects along the NWHI over the period from October 1990 to November 2000. The number of sections per year ranged from 1 in 1991 to 16 in 1997. From 1993 thru 2000, each year had at least eight sections along the NWHI. Seasonally, June through October had the highest density of observations, and the months of November and December had the lowest. All months, except December, had at least three sections along the NWHI.

Data Analysis

Data were processed using the Common Oceanographic Data Access System (CODAS) processing suite developed at the University of Hawaii (Firing, 1991). For statistical analysis, individual ADCP velocity sections were gridded using a coordinate system aligned with the ridge (Fig. 3); with 0.25° by 0.25° grid spacing (~25 km). From Honolulu to Kure Atoll, there are 88 along-ridge boxes by 10 across-ridge boxes. Only boxes with data from 15 or more sections are used for producing mean velocity vector maps, with the exception of the seasonal analysis of the Subtropical Counter Current. The mean, standard deviation, and standard error of the means were computed for current velocity and root mean square (rms) vertical shear of velocity. With one exception (noted in the caption), spatial maps are based on velocities depth-averaged from 28 to 148 m. Vertical sections of velocity and rms vertical shear of velocity along the ridge axis were computed by averaging in the across-ridge dimension.

**RESULTS**

Synoptic Sections

Before proceeding with the statistical analysis, it is useful to see the character of the individual sections. The northbound/southbound pair of sections from a single cruise in May and June 1997 illustrates the typical magnitude of the synoptic currents (0.2-0.5 ms$^{-1}$), and their spatial and temporal variability (Fig. 4). Although the southern ends of the sections were occupied less than two weeks apart, the measured currents look very different. This anticipates a major conclusion of the statistical analysis to follow: the long-term mean currents are weak relative to the variability, so there is generally little resemblance between any synoptic section and the long-term mean. Indeed, it is difficult to arrive at a statistically significant mean in much of the region.

Spatial Distribution of Depth-Averaged Velocity

Spatial distributions of depth-averaged mean horizontal velocity vectors along the entire Archipelago from Honolulu to Kure Atoll are shown in Figure. 5. In order to more closely examine mean currents, standard errors, and standard deviations, the NWHI is subdivided into three regions: a southern region from Oahu to Necker (157° W to 165° W; Fig. 6), a mid-region from Necker to Raita Bank (164° W to- 170° W; Fig. 7), and a northern region from Maro Reef to Kure Atoll (170° W to- 180° W; Fig. 8).

The mean currents in the southern region show moderately strong mean westward velocities (~0.15 ms$^{-1}$) south of Kauai and Niihau and in most of the region from Kauai to an area west of Nihoa Island (Fig. 6). This mean westward current most likely reflects the westward extension of the North Hawaiian Ridge Current (NHRC; Firing, 1996; Qiu et al., 1997), and suggests that the NHRC crosses the Hawaiian Ridge in the large region between Oahu and Nihoa. The westward extent of the NHRC in these observations

appears to be near 164° W, just southwest of Necker Island. For most of this southern region, the mean velocities generally exceed the standard errors (Fig. 6a), but are much smaller than the standard deviations (Fig. 6b), indicating that the variability is greater than the mean for most locations. For this southern region, there was not an obvious seasonal cycle.

The mean currents in the mid-Archipelago region, between Necker Island and Raita Bank, showed a strong seasonal cycle with moderate eastward flow (~0.10 ms$^{-1}$) during March through July (Fig. 7a) and weaker northward flow during August through February (Fig. 7b). The eastward flow is consistent with the intermittent presence of the STCC in the late spring/early summer months described by Kobashi and Kawamura (2002); these observations provide the first direct evidence of the STCC impinging on the mid portion of the NWHI. During the fall/winter season, when the STCC is not recognizable, there is a moderately strong mean northward current between Gardner Pinnacles and Raita Bank (Fig. 7b).

The mean currents in the northern region of the NWHI, between Maro Reef and Kure Atoll, are based on fewer sections than are available in the central and southern region. Mean currents in this region are highly variable with eastward flow near Laysan Island and south of Maro Reef (Fig. 8). There appears to be coherent mean flow to the southwest between Pearl and Hermes and Kure Atolls and to the northeast between Pearl and Hermes and Pioneer Bank. Interestingly, there also appears to be an anti-cyclonic circulation around Lisianski Island/Neva Shoals, though this could be an artifact of spatial and temporal averaging of sparse data. Though the data here are too sparse to resolve a mean seasonal cycle, it is important to note that the transition zone chlorophyll front (TZCF) migrates south to intersect this region during some winters (Bograd et al., 2004).

## Variation of Velocity with Depth

The previous section showed results of depth-averaged velocity vectors. In this section, we focus on the mean vertical structure of velocity along the Archipelago, where velocities are averaged in the across-ridge dimension (Figs. 9, 10). Beginning with the mean over all seasons (Fig. 9), the moderate westward flow of the NHRC is observed in the Kauai Channel between Oahu (158° W) and Kauai (160° W) and between Kauai and Nihoa (162° W) and south of the bank to the west of Nihoa at 163° W. For most of this region between 159° W and 163° W, the westward NHRC extends over the depths of the measurements from 20 m to 250 m, with maximum velocities observed south of Nihoa Island at depths between 100 and 200 m. From French Frigate Shoals westward, there are several regions of moderate eastward mean velocity in the upper 50 – 80 m that probably indicate the presence of the STCC. The strongest eastward mean velocities (~0.10 ms$^{-1}$) are observed in the regions between Southeast Brooks Bank (167° W) and the area west of Gardner Pinnacles (169° W) and between Lisianski Island (174° W) and Pearl and Hermes Atoll (176° W). Weaker mean eastward surface velocities are noted between Maro Reef (171° W) and 173° W. The meridional component of the mean flow tends to alternate from north to south through various channels in the Hawaiian Ridge.

Flow is moderately strong to the south just east of Maro Reef (possibly between Maro Reef and Raita Bank) and moderate to the north in the deep channel between West St. Rogatien Bank and Gardner Pinnacles; in both cases these meridional currents extend throughout the measurement depths.

Dividing the year into summer (March through July) and winter (August through February) seasons, we find that the summertime mean zonal velocity (Fig. 10a) is similar to the overall mean (Fig. 9), except for the greater strength and extent of eastward flow (STCC) across the broad region between Necker Island (164° W) and Pearl and Hermes Atoll (172° W). A stronger and broader eastward flow in the summer season is also seen from Laysan (172° W) to Pearl and Hermes Reef across the channel at 176° W. The winter mean zonal velocity (Fig. 10b) shows intensified westward flows in the Kauai Channel and between 173° W and 174° W (just east of Lisianski Island). A surprising feature of the depth structure, the subsurface maximum of the westward flow from 161° W to 163° W, is evident in both seasons (Fig 10).

Variation of RMS Shear with Depth

Root mean square (rms) vertical shear of velocity is maximal at the base of the presumed mixed layer (Fig. 11). The depth of maximum shear gradually shoals from ~50-60 m in the southern region (Oahu to Necker) to ~20-30 m in the northern region (Maro Reef to Kure Atoll). More notable, however, is that rms shear is relatively small for the entire region from the Kauai Channel (159° W) to Necker Island (164° W) and relatively large from French Frigate Shoals (166° W) to Kure Atoll (178° W). The most noteworthy seasonal differences of rms shear are that summertime maxima are stronger and shallower than during the winter season.

**DISCUSSION**

Although the currents along the NWHI are dominated by mesoscale variability, there are many features in the mean or seasonal components of the flow described here which have important influences on larval dispersion and recruitment in the Hawaiian Archipelago. These ADCP observations provide the first observational evidence describing the spatial and vertical extent and magnitude of both the NHRC and the STCC within the NWHI. Concerning the NHRC, the mean flow is westward from the MHI toward the NWHI, crossing the Hawaiian Ridge between Oahu and Nihoa. Observations here also show that the NHRC in this region extends from near the surface to at least 200 m with relatively little rms shear. While the high variability of the NHRC certainly allows for the possibility of direct larval transport toward the MHI, the mean currents indicate that direct recruitment is more likely from the MHI to the NWHI. That said, it is recognized that indirect paths of larval transport are clearly possible. In fact, recent Surface Velocity Program (SVP) drifter observations have confirmed some transport from the NWHI to the MHI (Firing et al., 2004). Nevertheless, these long-term mean observations suggest that the NWHI alone are not likely a suitable refuge to replenish resources in the MHI.

Concerning the STCC, the ADCP observations reported here provide evidence for mean eastward flow to the mid-Archipelago region roughly between Lisianski Island and Necker Island during March to July. These findings are consistent with oceanographic observations based on dynamic topography that indicate the likely presence of a seasonal STCC impinging on the NWHI in this same region (Kobashi and Kawamura, 2002). Furthermore, these observations of the STCC are consistent with biological and genetic observations showing higher diversity in this part of the NWHI (Maragos et al., 2004; Rivera et al., 2004). The observed eastward velocities during the summer months have maxima near the surface layer (20-60 m) with significant rms shear across this layer and decreasing eastward velocity with depth. Generally, these eastward surface currents oppose the presumed northward Ekman drift driven by the prevailing northeast trade winds. While eastward currents appear to increase northwestward of Brooks Bank (167° W), northeast trade winds decrease northwestward along the Archipelago (Brainard et al., 2004).

These observations show predominantly southwestward mean currents in the vicinity of the three northern atolls of the NWHI, Kure, Midway, and Pearl and Hermes, and eastward surface currents to the southeast of Pearl and Hermes Atoll. This pattern of the mean currents suggests that these northern atolls might be more oceanographically isolated than the other islands and atolls to the southeast, which is consistent with increased endemism in this northwestern portion of the Archipelago (DeMartini and Friedlander, 2004).

While there is an obvious need for more detailed information on the circulation in the NWHI to better understand larval dynamics, these observations of the mean currents provide useful insights for resource managers to more effectively manage and conserve the resources of the region. Measurements on finer space and time scales are needed to increase our understanding of larval retention, dispersion, and recruitment in the Hawaiian Archipelago.

**Figure 1.** Map of NWHI. Shaded bathymetry from Smith and Sandwell (1997).
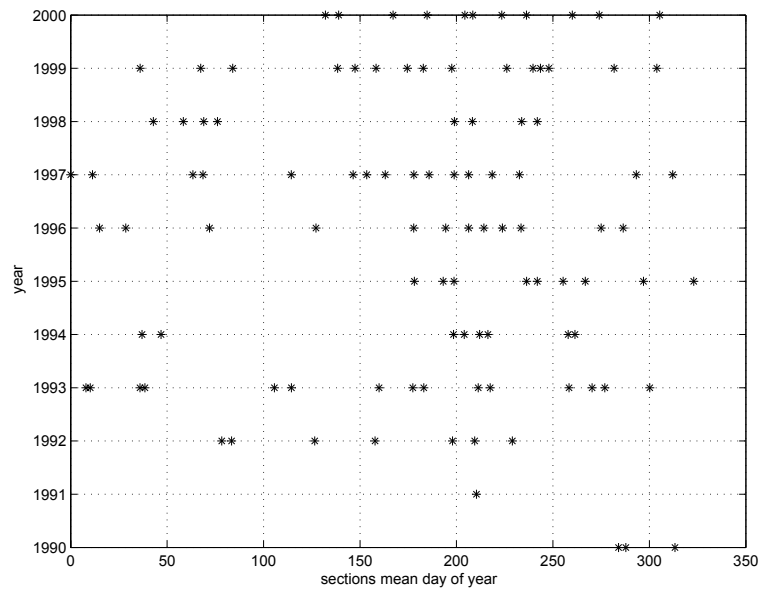


**Figure 2.** Temporal distributions of research cruises of the NOAA ship *Townsend Cromwell* along the NWHI from October 1990 to November 2000 showing mean day of year of each cruise for the 105 ADCP transects used for this analysis.
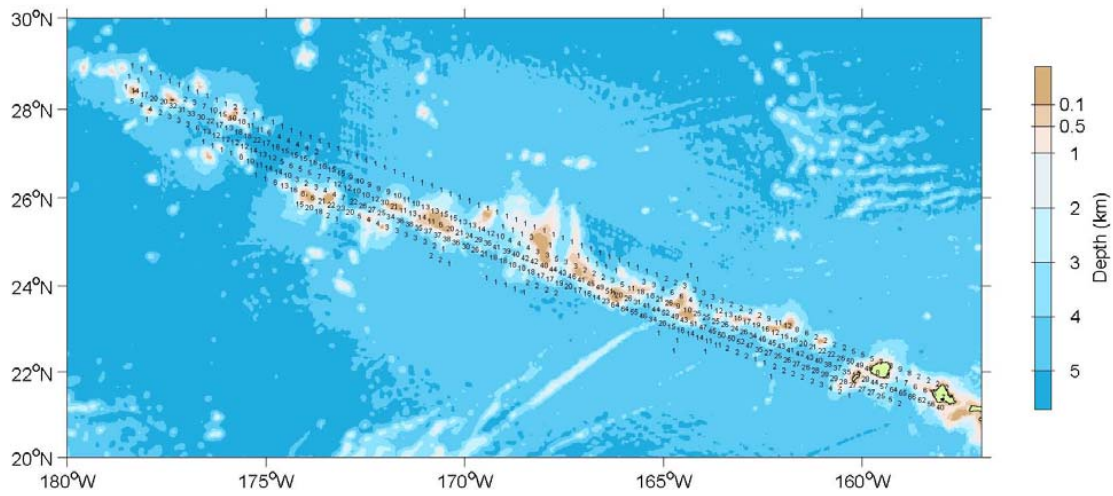
**Figure 3.** Spatial distribution of gridded 0.25° by 0.25° rotated boxes showing number of cruise sections within each grid box over the period from October 1990 to November 2000.
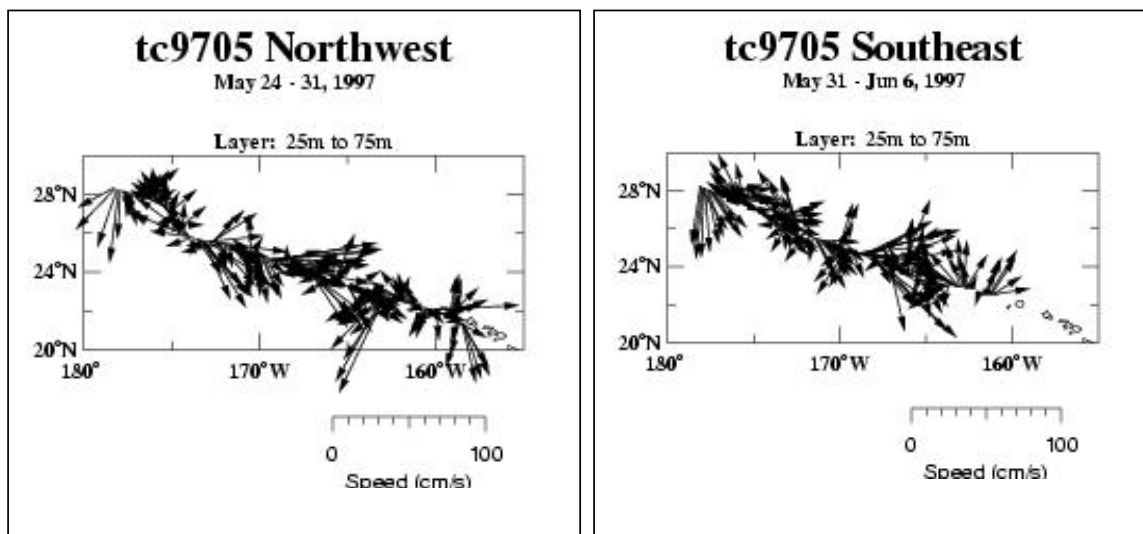


**Figure 4**. Depth-averaged (25-75 m) velocity vectors from the northwestward leg of cruise TC-9705, May 24-31, 1997 (left panel), and from the southeastward leg, May 31- – June 6 (right).
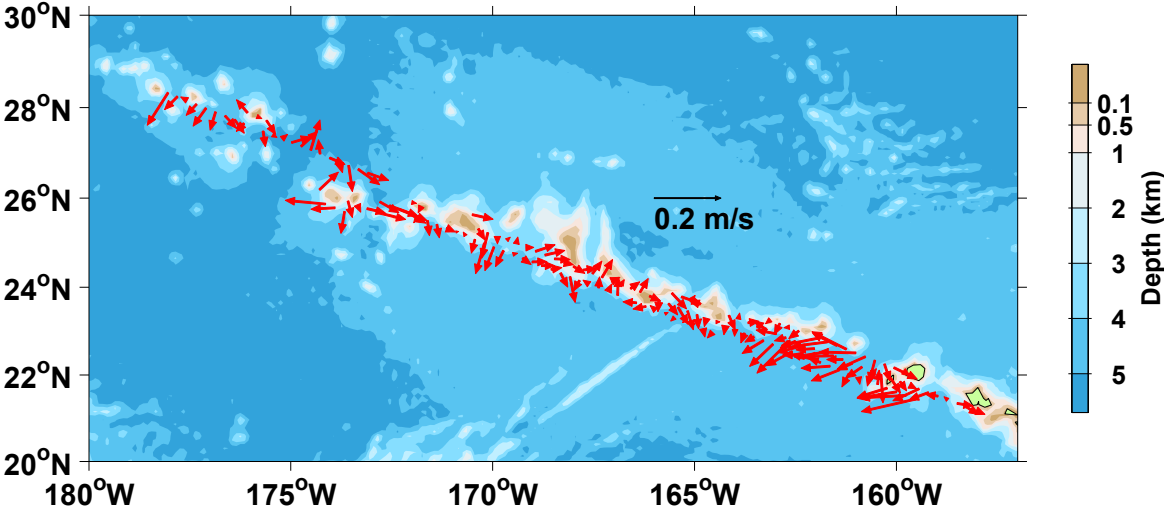
**Figure 5.** Mean velocity vectors, depth-averaged from 28-148 m, for all grid boxes with 15 or more sections along the Hawaiian Archipelago from Honolulu to Kure Atoll.
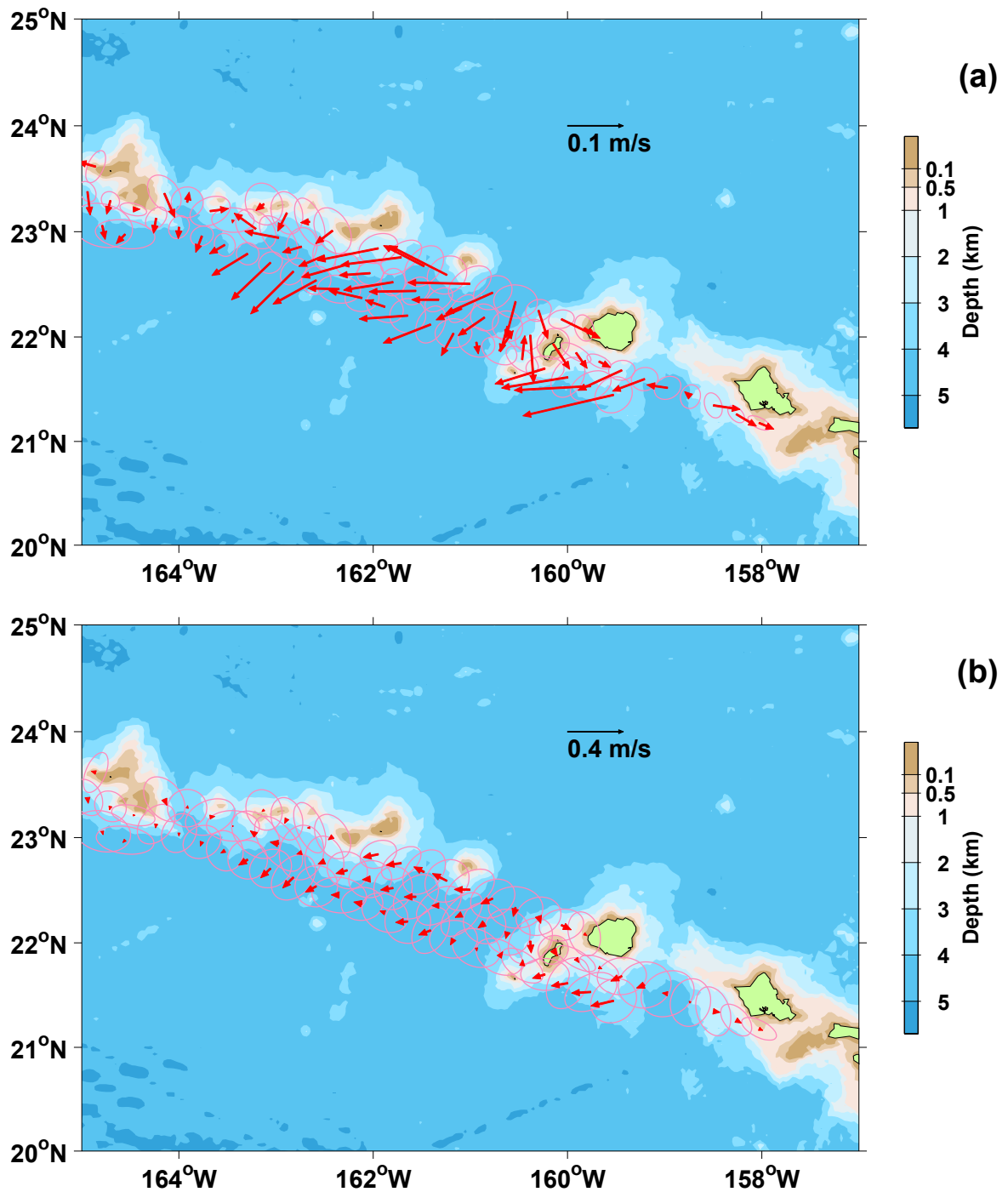
**Figure 6.** Long-term mean current vectors in the southern region from Oahu (158° W) to Necker Island (164.5° W). The dominant westward current south of Kauai and Nihoa may come from the North Hawaiian Ridge Current. In the top panel, the ellipses show standard errors of the mean; vectors which extend beyond the ellipses are considered significant. In the lower panel, the ellipses show the standard deviations; the variability everywhere exceeds the long-term mean.
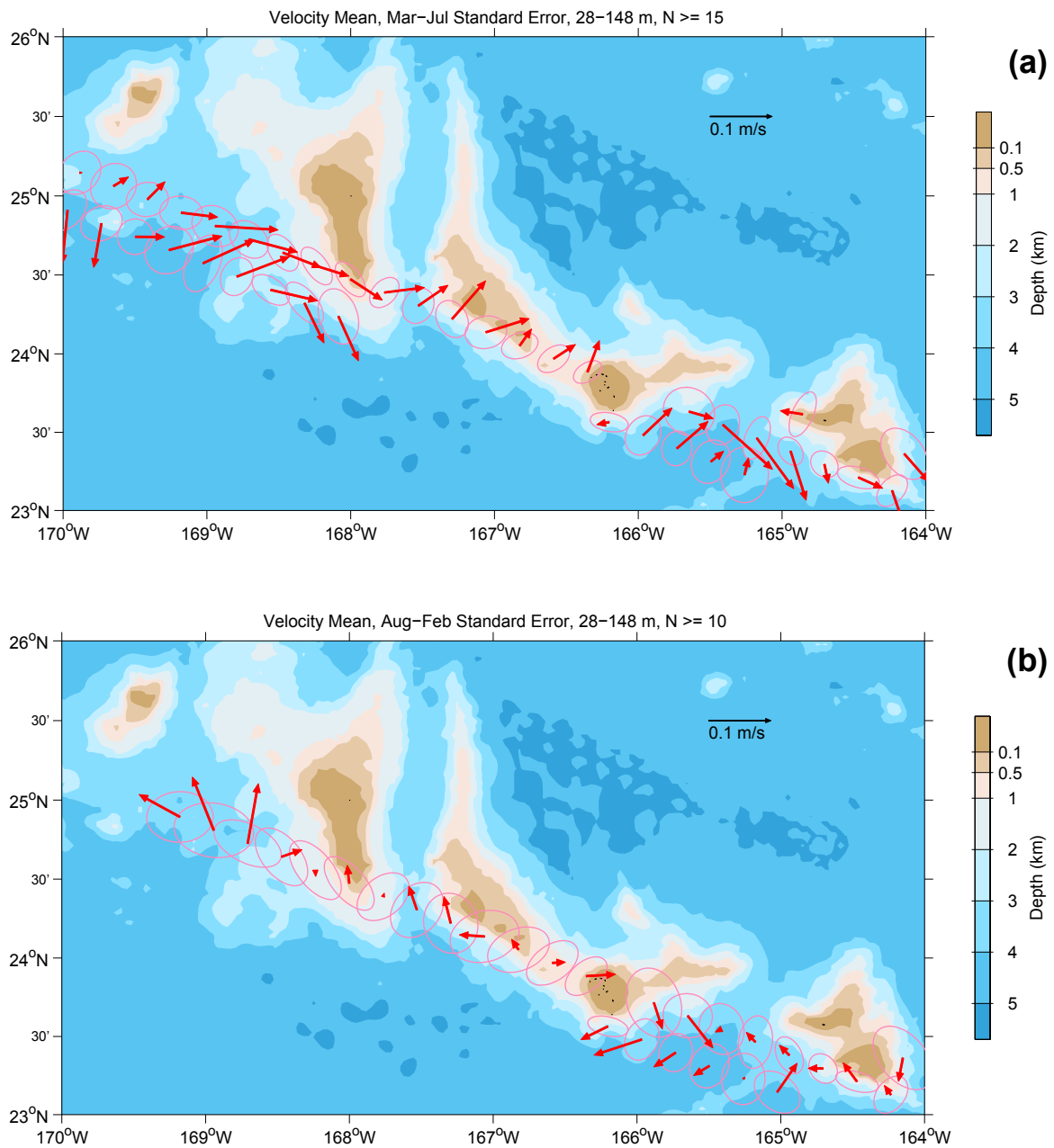
**Figure 7.** Long-term mean current vectors and standard error ellipses in the middle region of the NWHI from Necker Island (164.5° W) to Raita Bank (169° W) during the period March through July (top panel), and August through February (bottom panel). The dominant eastward current during March through July is the Subtropical Counter Current; it is not observed in the August-February average.
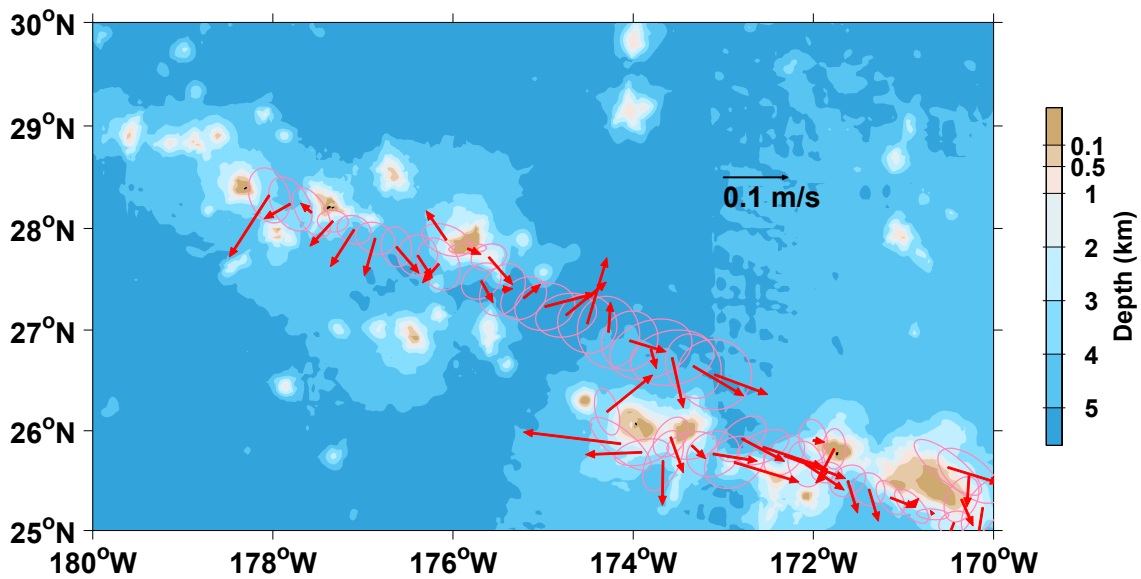
**Figure 8.** Long-term mean current vectors and standard error ellipses in the northern region of the NWHI, from Maro Reef (170.5° W) to Kure Atoll (178° W) for grid boxes having at least 15 cruise sections. Unlike all previous figures, the vertical averaging interval for this region is 28-100 m.
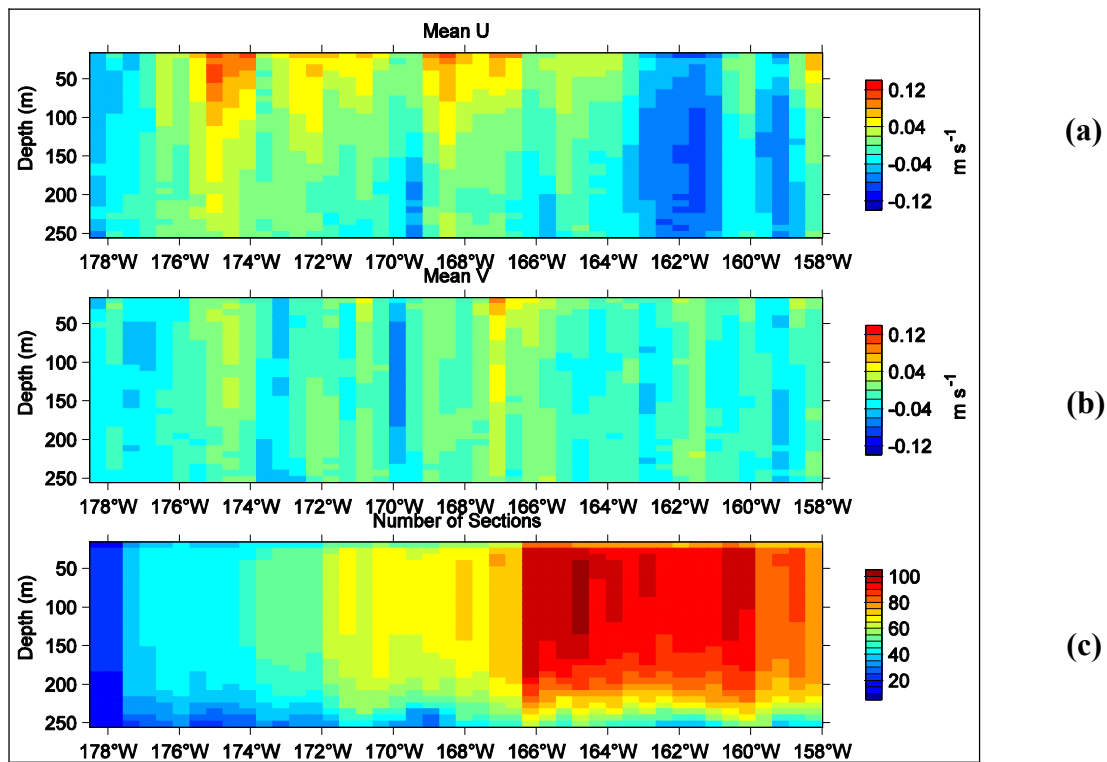


**Figure 9.** Long-term mean a) zonal and b) meridional velocity along the rotated-longitude on the axis of the NWHI between Honolulu and Kure Atoll during all seasons. Velocities are averaged across rotated-latitude sections. c) Number of cruise sections used for each velocity calculation.
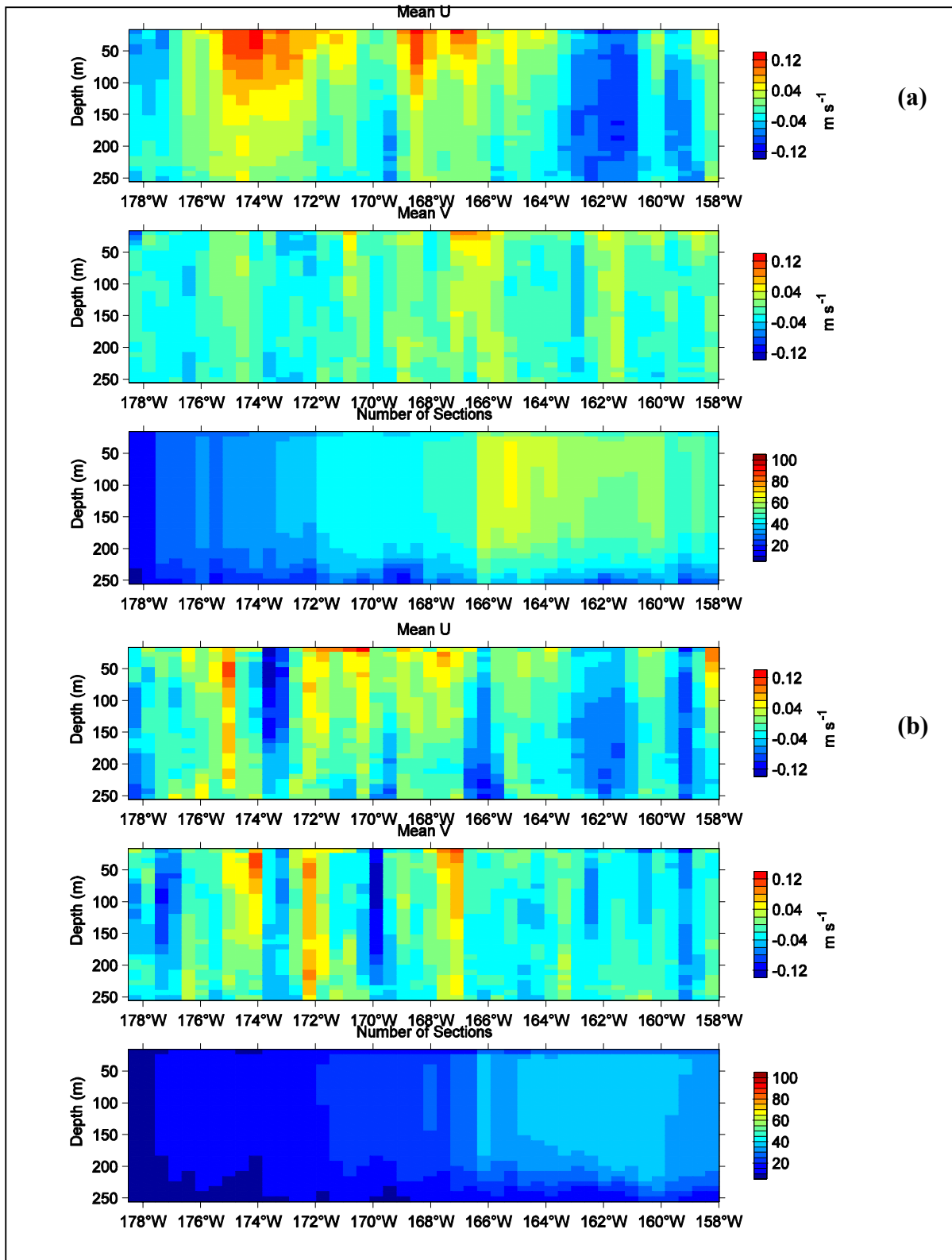
**Figure 10.** Long-term mean zonal and meridional velocities and number of sections for a) summer months (March – July) and b) winter months (August – February).
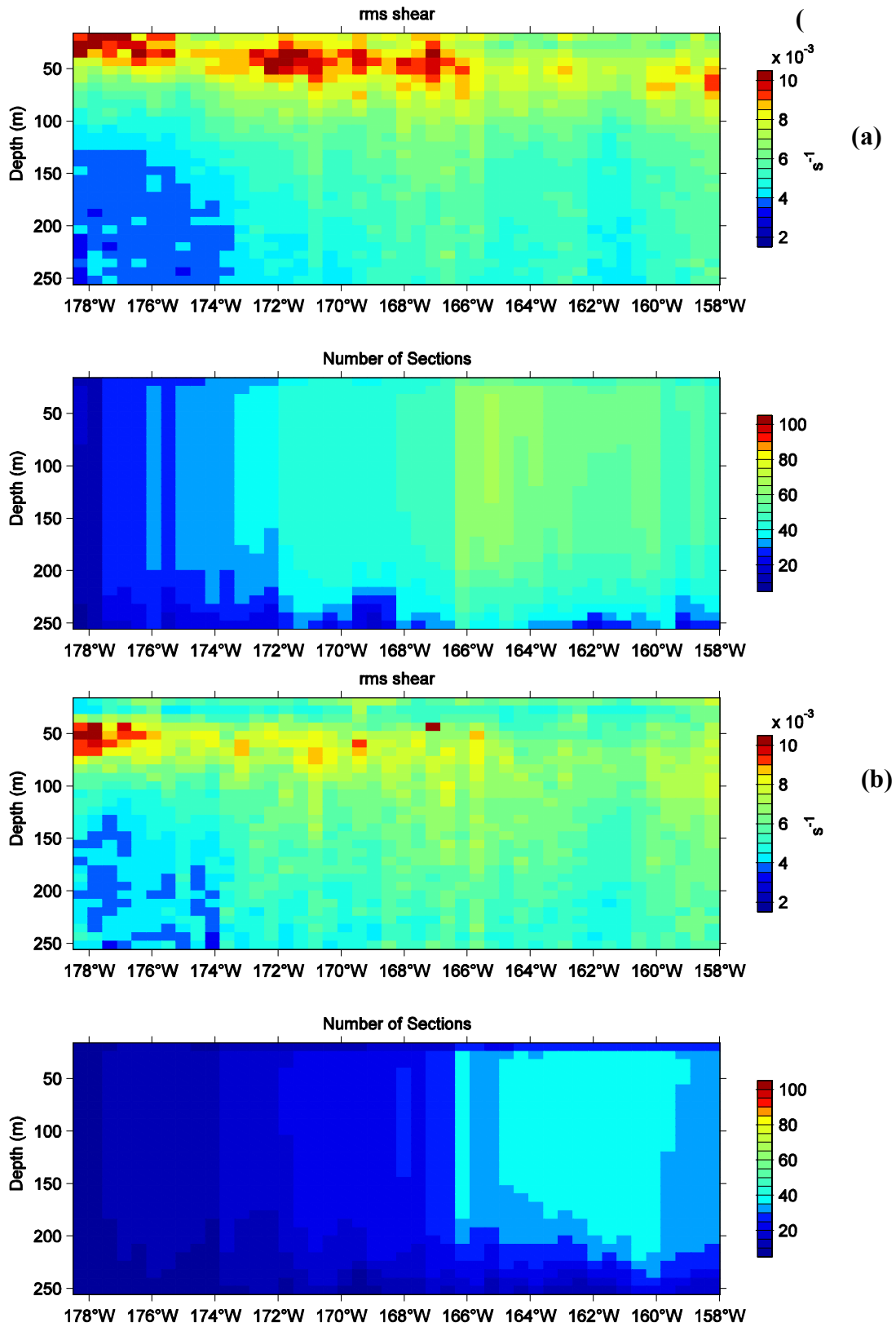
**Figure 11**. Long-term mean rms vertical shear of velocity and number of sections for a) summer months (March – July) and b) winter months (August – February).

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# SIMULATED SEASONAL AND INTERANNUAL VARIABILITY IN LARVAL TRANSPORT AND OCEANOGRAPHY IN THE NORTHWESTERN HAWAIIAN ISLANDS USING SATELLITE REMOTELY SENSED DATA AND COMPUTER MODELING

BY

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## ABSTRACT

Larval transport and oceanographic conditions experienced by pelagic larvae in the Northwestern Hawaiian Islands were simulated using an individual-based approach to track daily movements in a Lagrangian modeling framework. These advection-diffusion models were configured with 1°x1° resolution, monthly geostrophic currents estimated from satellite altimetry. Larval dispersal was simulated for each month of the year from 1993-2002 for 3-, 6-, and 12-month larval durations. Four release locations were evaluated: Midway Island, Maro Reef, Necker Island, and Oahu. Larval retention was evaluated by tabulating successfully simulated settlement, which was scored based on larval proximity to release sites after completion of the pelagic duration. Sea surface temperature and chlorophyll concentration at each daily larval location were tabulated utilizing similar resolution, satellite remotely sensed data products (NOAA Pathfinder AVHRR SST and SeaWiFS ocean color), and these *in situ* values were integrated over the entire larval duration for each larval track. These oceanographic variables are of critical importance in the early life history because of their hypothesized relationships to larval growth and feeding success, both critical determinants of larval survival and successful recruitment. The sea surface temperature and chlorophyll histories experienced by successfully settling larvae display strong seasonal and interannual patterns, which were decomposed using generalized additive models (GAMs). These patterns may be useful towards understanding episodic recruitment events, as well as for posing hypotheses towards understanding the mechanisms underlying spawning seasonality. These transport dynamics and oceanographic patterns have general implications for a variety of vertebrate and invertebrate metapopulations in the Northwestern Hawaiian Islands and their effective management.

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## INTRODUCTION

Temporal patterns of reproduction are a widespread phenomenon in both plant and animal ecology. Organisms can maximize their fitness by propagating at times which are optimal for maximum reproductive output and/or enhanced survival of their young. It is commonly thought that the latter is of more importance for highly fecund aquatic species which broadcast their abundant young into the pelagic environment (Johannes, 1978; Thresher, 1984). Several scales of temporal variability may be of importance in the timing of reproduction. Diel patterns, such as spawning near dawn or dusk, may be important to minimize predation on both the spawning individuals and their pelagic propagules (e.g., Doherty, 1983). Lunar patterns, such as spawning near spring tides (full and new moon) may be related to key variables which change consistently on a monthly scale such as tidal currents and moonlight illumination (e.g., May et al., 1979). Seasonal patterns, such as spring or summer spawning, may be related to key variables which change consistently on an annual scale such as currents, plankton blooms, and temperature (Johannes, 1981). Seasonality in spawning has been well documented in a variety of Hawaiian fish and invertebrate species (e.g., Itano, 2000; Lobel, 1989; Randall, 1961; Reese, 1968; Walsh, 1987). Various hypotheses have been put forth to explain such seasonality. Johannes (1978) has argued that predatory losses on pelagic propagules have been a driving selective force for spawning seasonality. More recent views of pelagic larval transport have emphasized the importance of retention with the view that many marine populations are more closed than open (Cowen, 2002; Cowen et al., 2003; Jones et al., 1999; Kingsford et al., 2002; Leis, 2002; Mora and Sale, 2002; Robertson, 2001; Sponaugle et al., 2002; Swearer et al., 1999). While predation and retention issues may be important, the predominately oligotrophic pelagic environment has led some to suggest that larval food supply is the single most important factor governing the numbers of marine fish (Cushing, 1972). Reese (1968) suggested that the different spawning seasons used by ecologically similar species of hermit crabs were a mechanism to reduce competition for pelagic larval food, and that there would be selective advantage to offsetting reproductive periods if larval food supply were a limiting factor. Larval food supply involves spatial and temporal patchiness, and the species composition of the phytoplankton and microzooplankton is critically important (Lasker, 1975). In addition to starvation issues, variability in food supply has been shown to be an important determinant of larval growth and subsequent survival (e.g., Booth and Alquezar, 2002). Faster growth has been hypothesized to favor survival by reducing cumulative predatory mortality (e.g., Anderson, 1988). Leis and Carson-Ewart (1999) suggest that larger size is an important factor for evading predation during the settlement process, citing fin erection behavior and importance of speed when fleeing predators, based on field experiments with coral trout larvae. It is possible that small size may be an advantage for remaining undetected during settlement; however, the advantages of being larger in the plankton probably outweigh the disadvantages, considering the gauntlet of size-based pelagic predators (reviewed by Purcell and Arai, 2001; Zaret, 1980). Additionally, larvae which grow faster may retain a size and survivorship advantage during the critical first few weeks post-settlement on the reef (Bergenius et al., 2002; Booth and Hixon

1999; Sponaugle and Pinkard, 2004). While size is most directly a function of age, both food and ambient temperature have been shown to have a strong positive effect on larval growth (e.g., Buckley et al., 2004). Clearly, in addition to physical retention, there is a suite of other considerations critical in the early life history survival of insular species. These important ecological considerations can be synthesized within a computer simulation using available tools and data products.

Earlier works have used advection-diffusion models to examine larval transport and retention (e.g., Griffin et al., 2001; Hill, 1991; Polovina et al., 1999; Siegel et al., 2003). Few such applications have integrated the oceanographic conditions experienced by individual larvae directly into the model. With the availability of remotely sensed data products, it is logical to incorporate these environmental fields into the computer simulation framework, particularly with individual-based modeling approaches (e.g., Mullon et al., 2002). Sea surface temperature (SST) and chlorophyll-a concentration are widely available from a variety of satellite sensors, and both of these variables may have important linkages to the ecology of early life history stages, as described above for growth and mortality. The goals of this paper are to examine, via computer simulation and use of remotely sensed environmental data, the seasonal and interannual components of larval retention, transport, growth, and survival in selected regions of the Hawaiian Archipelago.

## MATERIALS AND METHODS

Simulated larval releases were stratified by year ($n$=10: 1993-2002), month ($n$=12: January-December), locations spanning the Hawaiian Archipelago ($n$=4: Midway, Maro, Necker, and Oahu, see Fig. 1), and larval duration ($n$=3: 3, 6, and 12 months) to yield a total of 1,440 model treatments. These larval durations were chosen to bracket the known durations of several commercially important species of lobster and deep-water bottomfish. Five thousand simulated larvae were released for each model treatment for a total of 7.2 million individuals. Each individual was tracked daily for the entire larval duration in Lagrangian fashion using the following equations:

$$x_{t+\Delta t} = x_t + \left[ u_{(x_t, y_t, t)} \Delta t + \varepsilon \sqrt{D \Delta t} \right] / \cos(y_t)$$

$$y_{t+\Delta t} = y_t + \left[ v_{(x_t, y_t, t)} \Delta t + \varepsilon \sqrt{D \Delta t} \right]$$

where $x$ represents longitude, $y$ represents latitude, $t$ represents time in days, $u$ represents the East/West component of the current speed, $v$ represents the North/South component of the current speed, $\cos(y_t)$ adjusts distance by latitude to account for the spherical coordinate system, and $D$ is the diffusivity coefficient (500 m$^2$/sec following Polovina et al., 1999). The currents utilized in this study were monthly 1° latitude/longitude resolution geostrophic flow fields calculated from satellite altimetry obtained from CNES/AVISO/SSALTO (CLS Space Oceanography Division, France). Integrated SST and chlorophyll-a histories encountered daily by individual larvae were tabulated daily

using interpolations from monthly 1° latitude/longitude resolution data grids. SST data were obtained from the MCSST (NOAA Pathfinder AVHRR satellites) product from NASA/JPL. Chlorophyll-a data was obtained from the Sea-viewing Wide Field-of-View Sensor (SeaWiFS) instrument on board the Seastar satellite. Integration was performed by averaging the daily SST or chlorophyll-a interpolations over the entire pelagic duration. Additionally, only averages from the subset of larvae scored as successfully being retained by the source site following completion of the entire pelagic duration were tabulated to each treatment. A 140-km radius for scoring larval retention was used, similar to Polovina et al. (1999). This is an arbitrary threshold utilized as a compromise to achieve some larval settlement at this level of propagule sample size ($n$=5,000). Since settlement success was evaluated in a relative manner (e.g., comparing between years, months, sites, pelagic durations), this exact dimension is not critical. For each of the 1,440 treatments, the following were tabulated: the number of larvae scored as retained, the number of larvae scored as settling at Oahu, the number of larvae scored as not settling at any of the four sites, the average SST encountered by this subset of retained larvae, and the average chlorophyll-a encountered by this subset of retained larvae. SST was available for the entire temporal duration of this analysis; however, chlorophyll-a data were available only from 1997 onwards. The advection-diffusion model was written in the open-source software XBASIC (http://www.xbasic.org) and run on an Intel P4 Windows XP system. Generalized Additive Models (GAMs) were used to identify relationships between a suite of response variables (retention, SST history, or chlorophyll-a history) and a suite of predictor variables (year, month, location, and pelagic duration). GAM is a relatively new analytical technique (Hastie and Tibshirani, 1990) which is useful when the predictor variables have unknown *a priori* and possibly nonlinear effects upon the response variable. GAM analysis was carried out using the analytical software package S-Plus v. 6.1.2r2 on an Intel P4 workstation using Redhat LINUX 7.3 OS. Six GAM analyses were performed as outlined in Table 1, with each utilizing a different suite of predictor variables as described. The graphical output in the form of smoothing splines and comparative categorical effects serve as the primary basis for interpretation, using standard error terms to indicate statistical significance. The GAM plots indicate the modeled relationships between the suite of predictor variables and the response variable, and the cumulative (hence additive) sum across each predictor function scaled by an intercept results in the predicted value for the response variable. Higher values along the y-axis indicate a higher contribution towards the predicted value for the response variable, and vice-versa.

## RESULTS

Retention varied from a low of 0/5,000 (scored for 39 different treatments) to a high of 3,908/5,000 (scored for October, 1993, Midway, 3-month release). Retention was strongly related to year and larval duration, and had weak relationships to month and site (Figs. 2A-2D). Larval settlement at Oahu was strongly dependent on spawning site (Fig. 3). The Oahu settlement GAMs were run separately for the spatial effect and other

variables due to the numerous zeros in the data for sites farther from Oahu. For example, 85% of the Midway runs yielded 0 larval settlement to Oahu, and the small amount of successful settlement was accomplished only at the longest larval duration (Table 2). This lack of data contrast in other sites effectively weighted the GAM primarily towards the Oahu site, leading to difficult interpretation. Hence, the GAM was run separately for each site (Figs. 4-7), with the last GAM being a simple retention analysis for Oahu only. Strong yearly effects were observed in all sites, with weak monthly effects, and duration only becoming important at Necker and Oahu. Oahu settlement was favored by a longer larval duration from Necker (Fig. 6C, the closest site to Oahu), and by a shorter larval duration from Oahu itself (Fig. 7C).

Larval nonsettlement was cursorily examined in this analysis. Considering that there are abundant other sites available for larval settlement, this result should be treated with caution. However, by examining the larvae that did not settle at any of the four sites, some useful hypotheses can be posed for further analyses. The data suggest that yearly and monthly effects may be relatively weak and that perhaps there is a spatial component involved with Oahu exhibiting higher rates of larval loss (Fig. 8C). As expected, a longer larval duration is positively correlated to larval non-settlement (Fig. 8D).

SST and chlorophyll-a histories had strong yearly, monthly, and site relationships (Figs. 9-14), with the expected deterioration of a seasonal effect at a 12-month larval duration (Figs. 11B, 14B). For a 3-month larval duration, SST history was optimized by a July-August spawning, peaking in late July/early August (Fig. 9B). For a 6-month larval duration, the optimal spawning with respect to SST history is offset accordingly to May-July, peaking in June (Fig. 10B).


## DISCUSSION

Larval retention and loss were found to depend primarily on larval duration. The negative relationship between retention and larval duration is intuitive, in that a longer larval duration implies a greater chance of long-distance transport with subsequent loss to the system. This is similar to the findings of Leis and Miller (1976), who found that larvae of demersal-spawning reef fish (shorter pelagic duration) tended to be found closer to shore than larvae from pelagic-spawning reef fishes (longer pelagic duration). Some of the proposed physical mechanisms which can transport reef fish larvae back to their spawning site operate on the time scale of 2-3 months (e.g., Lobel and Robinson, 1986), consistent with the relatively high retention found in this study for a 3-month larval duration. Late-stage larvae of some reef fishes can occur at great distances from suitable adult habitat (e.g., Clarke, 1995; Victor, 1987), but are of unknown importance for local population persistence. This issue of long-distance dispersal may, however, be important for larval interchange in a metapopulation framework, which will be examined elsewhere for insular species in the Hawaiian Archipelago (Kobayashi, in preparation). The interannual pattern of retention (Fig. 2A) is consistent with observed large-scale changes in the central Pacific Ocean (e.g., Polovina et al., 1994); however, the exact mechanism remains unknown at this point. Larval settlement at Oahu examined by source

also appeared to be a proximity effect, with settlement negatively correlated with distance from Oahu. Larval duration was an important effect when examining Oahu settlement from the adjacent site at Necker (Fig. 6C); however, even at the longest durations, the numbers reaching Oahu from Necker did not surpass the number being retained around Oahu from Oahu on average (Table 2). Additional modeling is underway to better understand connectivity in the Archipelago and will address this on a finer spatial resolution, both in terms of source/sink dynamics and oceanographic input data.

There appears to be an interesting tradeoff between SST and chlorophyll-a with respect to seasonal spawning (Figs. 9B, 10B, 12B, 13B). Summer spawning is clearly conducive to placing the larvae into higher SST water masses; however, winter spawning clearly maximizes chlorophyll-a experienced by larvae. This dilemma does not appear to be mediated by seasonal retention (Fig. 2B) or seasonal nonsettlement (Fig. 8B). Early summer and late summer may be satisfactory compromises to best optimize these factors, thereby keeping both SST and chlorophyll-a at relatively high levels during the pelagic stages. The four spawning sites examined in this study generally fall along a latitudinal transect, and the resulting site-related patterns in SST and chlorophyll-a are consistent with oceanographic work in this area (Polovina et al., 2001; Seki et al., 2002).  The lowest SST and highest chlorophyll-a occur at the northernmost release site of Midway, which is well within the TZCF (Transition Zone Chlorophyll Front). At lower latitudes, there is a trend for higher SST values, as well as higher chlorophyll-a values. The latter may be due to increased nearshore processes (e.g., island effects) enhancing productivity around the larger islands in the Archipelago (e.g., Seki et al., 2001).

In summary, it has been shown that computer simulation may be a useful approach towards understanding important aspects of early life history and adult spawning ecology. Retention, transport, and environmental variables are shown to be expressed in complex spatial and temporal patterns. The utility of this approach depends critically on the passivity of larvae. Some late-stage fish larvae have been shown to be capable of directional orientation and active movement near the timing of settlement (e.g., Kingsford et al., 2002; Leis and Carson-Ewart, 1999; 2000; 2002; 2003; Leis et al., 2003; Tolimieri et al., 2004; Jeffs et al., 2003); however, it is quite likely that early life history stages (eggs and early-stage larvae) are passive drifters for a large part of the pelagic duration, and lobster phyllosoma have very limited swimming abilities. The findings of this simulation study can be used to pose further hypotheses and corroborate existing empirical evidence. In the latter case, for example, there are observed biogeographic patterns in the Hawaiian Archipelago which would benefit from a more quantitative mechanistic explanation, such as a higher rate of endemism being found at the northerly atolls (DeMartini and Friedlander, 2004), the faunal similarity between Johnston Atoll and the Main Hawaiian Islands (Kosaki et al, 1991), and the pattern of spread of introduced/invasive species such as the blue-lined snapper *Lutjanus kasmira* (Friedlander et al., 2002). Such corroboration could serve as potential ground-truthing for the modeling approach. Additionally, the SST and chlorophyll-a histories provide a useful environmental perspective to recent findings emphasizing the importance of larval physiological fitness (e.g., Berkeley et al., 2004) towards population maintenance. Incorporating demographic variability into the transport-modeling framework is a

logical next step. The modeling efforts as described here can help understand and predict recruitment success, when coupled with empirical observations and field experiments. A better understanding of oceanographic source-sink dynamics and connectivity throughout the Archipelago will be helpful towards design of marine protected areas (MPAs) and reserves (Cowen, 2002), and will contribute towards more effective management and resource utilization in the NWHI.

## ACKNOWLEDGEMENTS

Table 1. Summary of GAM analyses**.**

| Response variable | Predictor variable(s) |
|---|---|
| Larval retention (all data) | Year, Month, Site, and Duration |
| Larval settlement at Oahu (all data) | Site |
| Larval settlement at Oahu (separately by site) | Year, Month, and Duration |
| Larval non-settlement (all data) | Year, Month, Site, and Duration |
| Integrated SST history of retained larvae (separately by duration) | Year, Month, and Site |
| Integrated chlorophyll-a history of retained larvae (separately by duration) | Year, Month, and Site |

Table 2. Summary of larval settlement at Oahu, aggregated by year and month, from different spawning sites and for different larval durations. The average number reaching Oahu is out of 5,000 releases; the number of combinations with zero is out of 120 different year and month combinations per site/duration strata.

| Site | Duration | Average no. reaching Oahu | No. combinations with zero |
|---|---|---|---|
| Midway | 3-month | 0.00 | 120 |
| | 6-month | 0.00 | 120 |
| | 12-month | 5.10 | 66 |
| Maro | 3-month | 0.00 | 120 |
| | 6-month | 14.61 | 93 |
| | 12-month | 45.15 | 14 |
| Necker | 3-month | 55.61 | 82 |
| | 6-month | 85.52 | 29 |
| | 12-month | 98.12 | 0 |
| Oahu | 3-month | 732.73 | 8 |
| | 6-month | 297.02 | 2 |
| | 12-month | 126.47 | 0 |
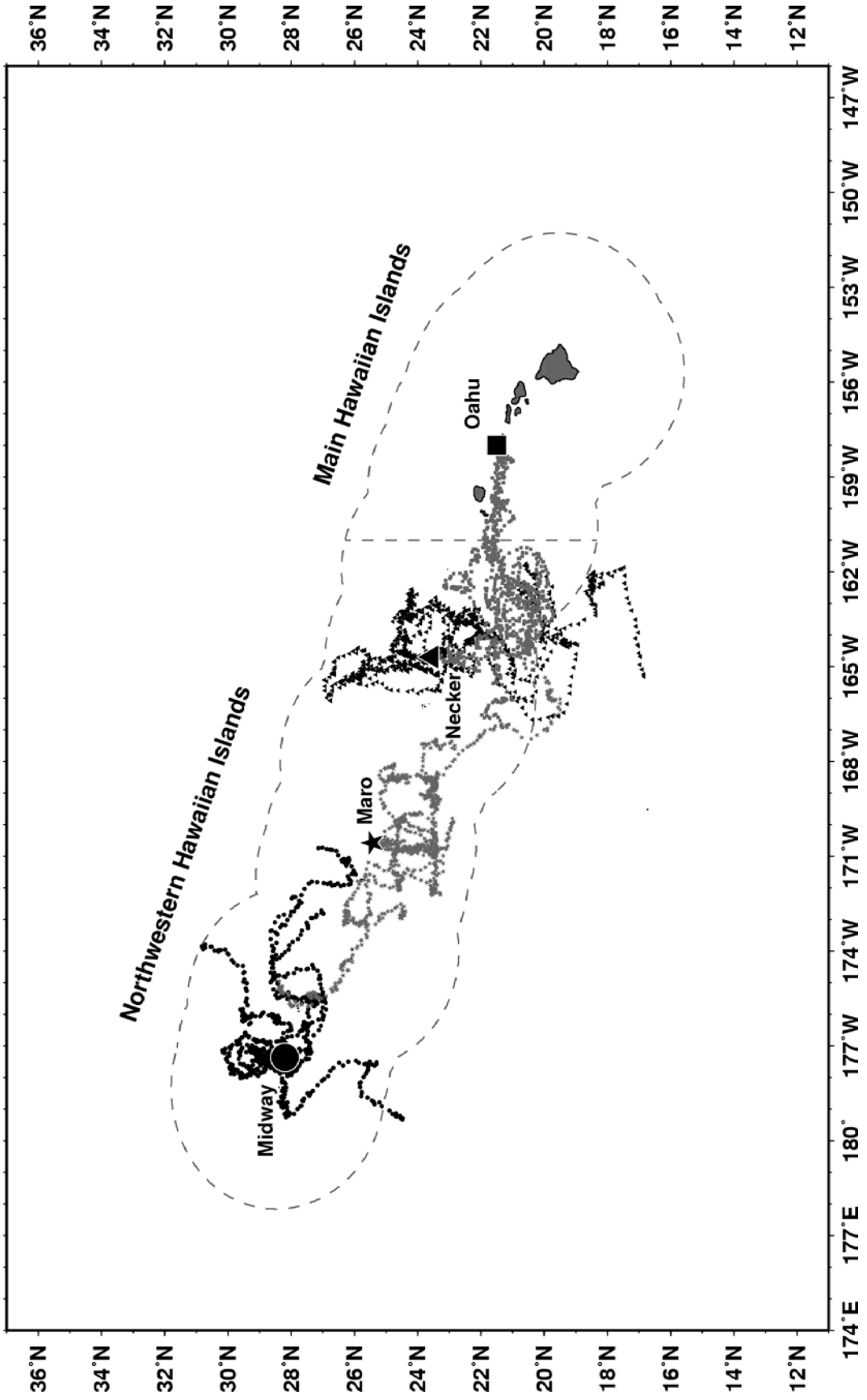
**Figure 1.** Map of Hawaiian Archipelago indicating larval release sites used in this analysis. Five sample releases from each site for a 6-month pelagic duration are shown for illustrative purposes only.
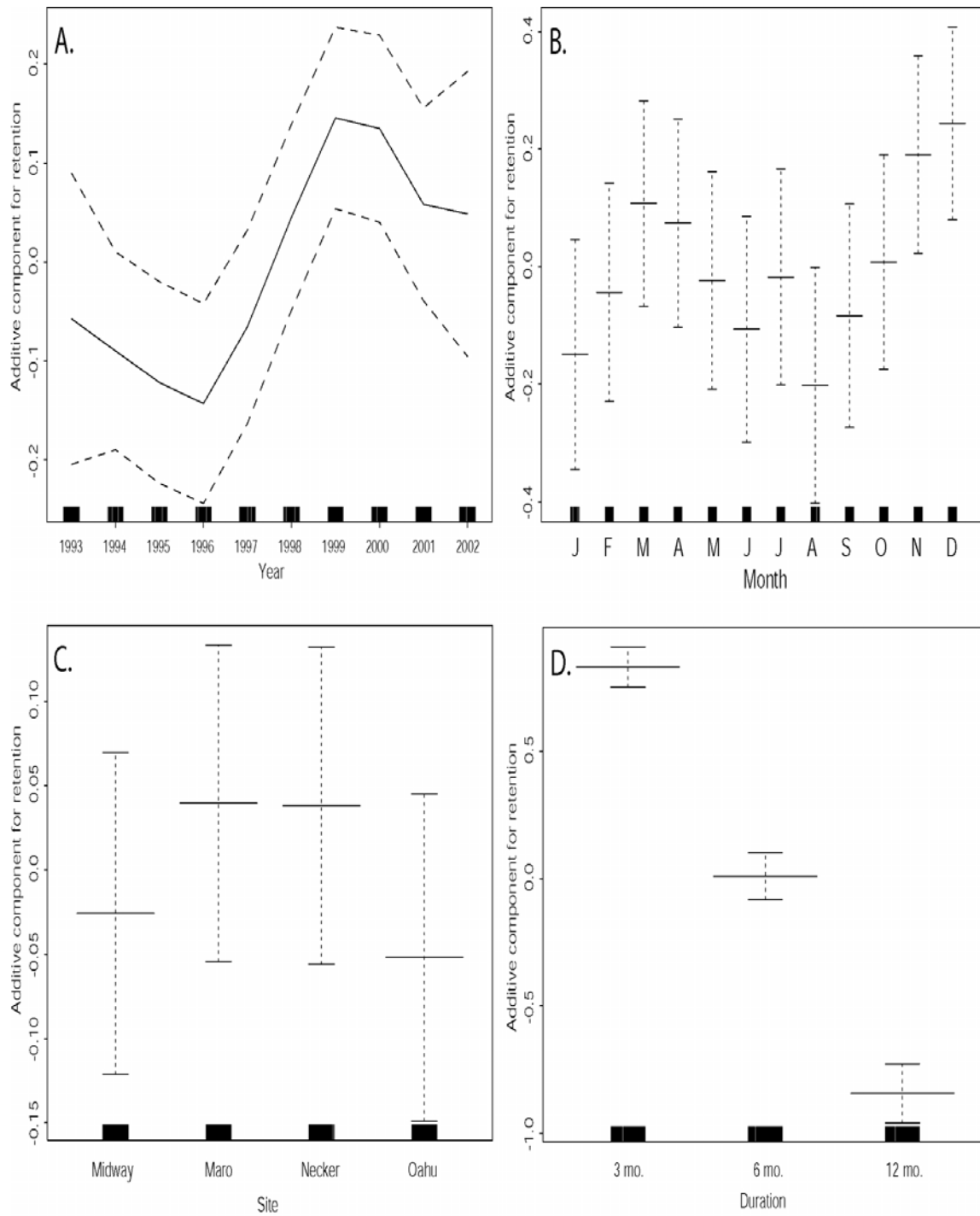
**Figure 2**. Results of GAM application to larval retention. The predictor variables are year (A), month (B), spawning site (C), and larval duration (D). C.I. are ±2 standard errors.
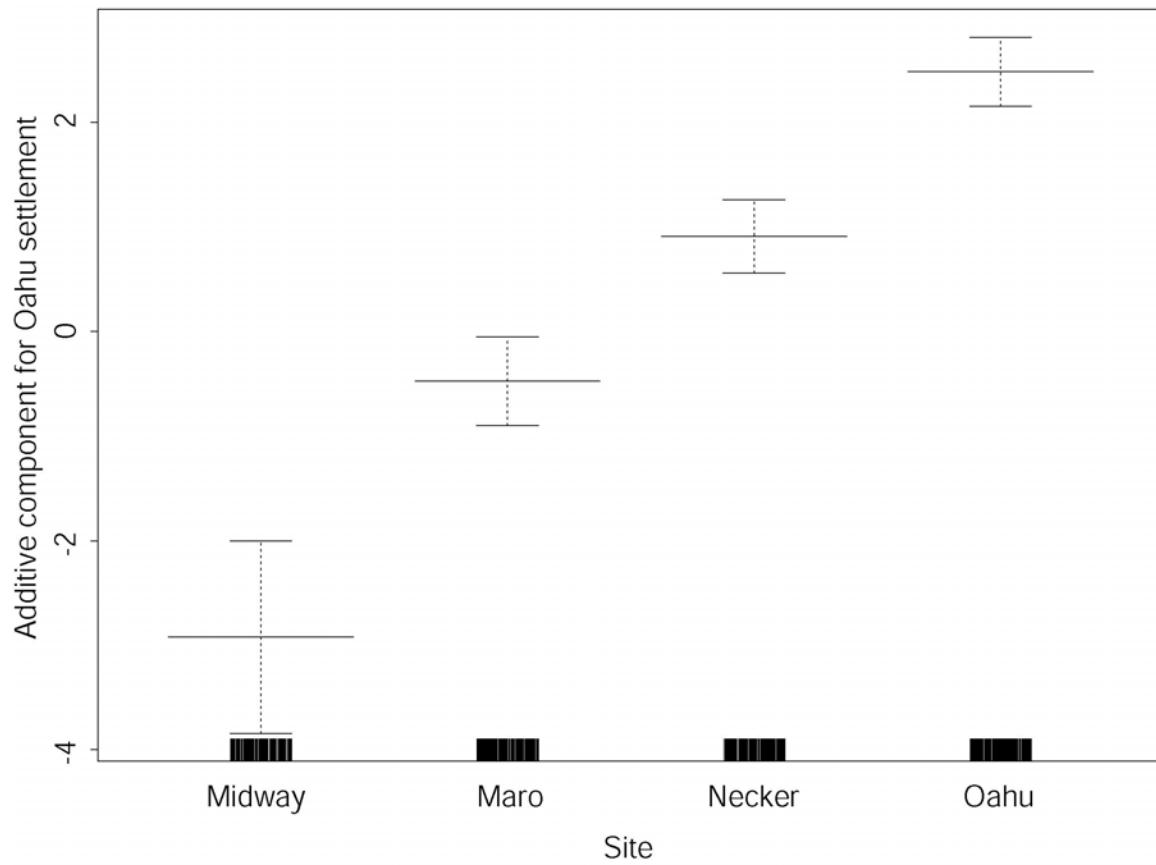
**Figure 3.** Results of GAM application to larval settlement at Oahu. The predictor variable is spawning site. C.I. are ±2 standard errors.
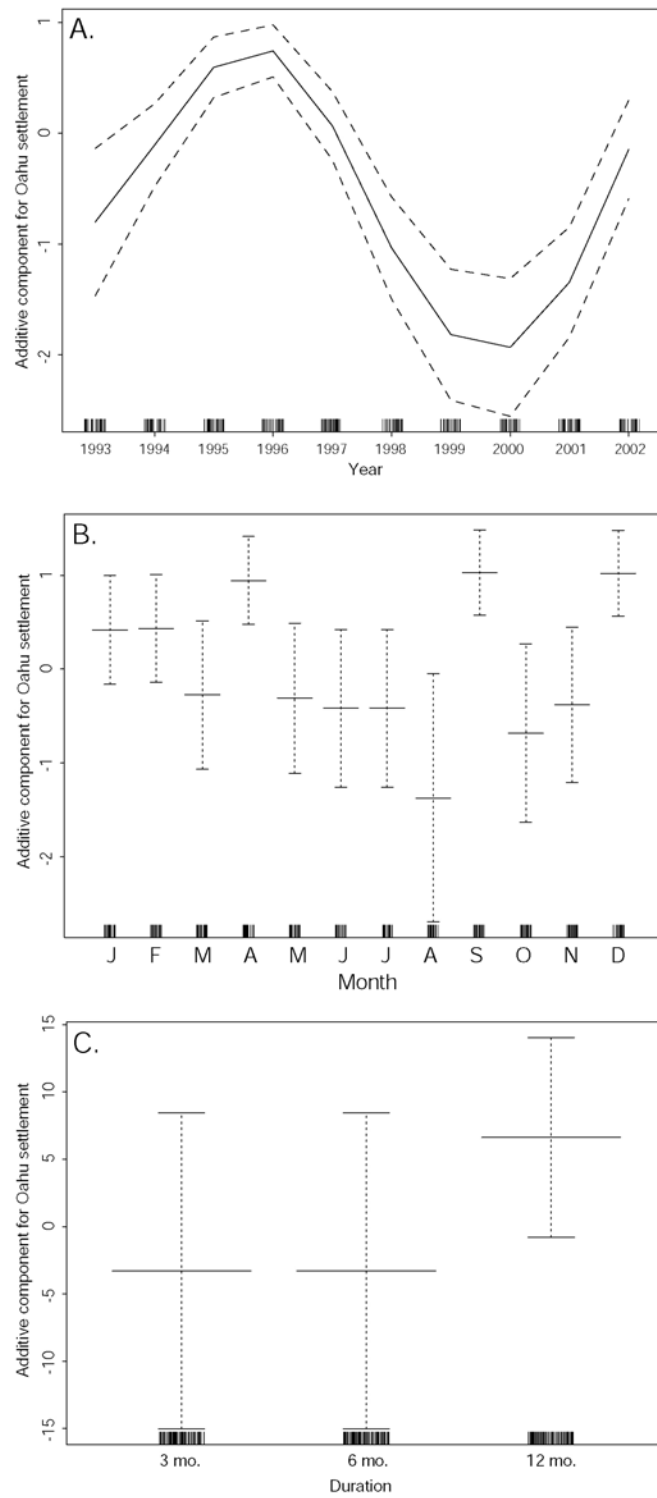
**Figure 4.** Results of GAM application to larval settlement at Oahu from Midway spawning. The predictor variables are year (A), month (B), and larval duration (C). C.I. are ±2 standard errors.
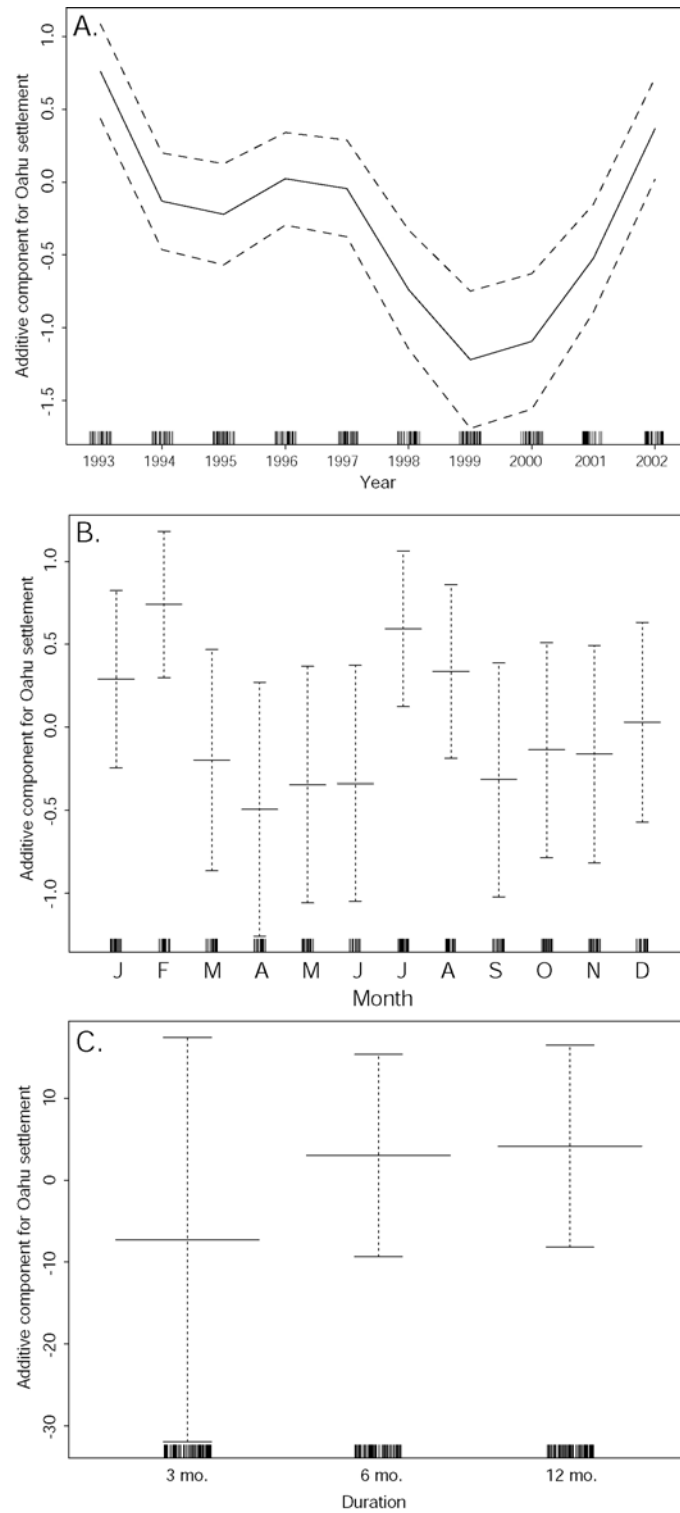
**Figure 5.** Results of GAM application to larval settlement at Oahu from Maro spawning. The predictor variables are year (A), month (B), and larval duration (C). C.I. are ±2 standard errors.
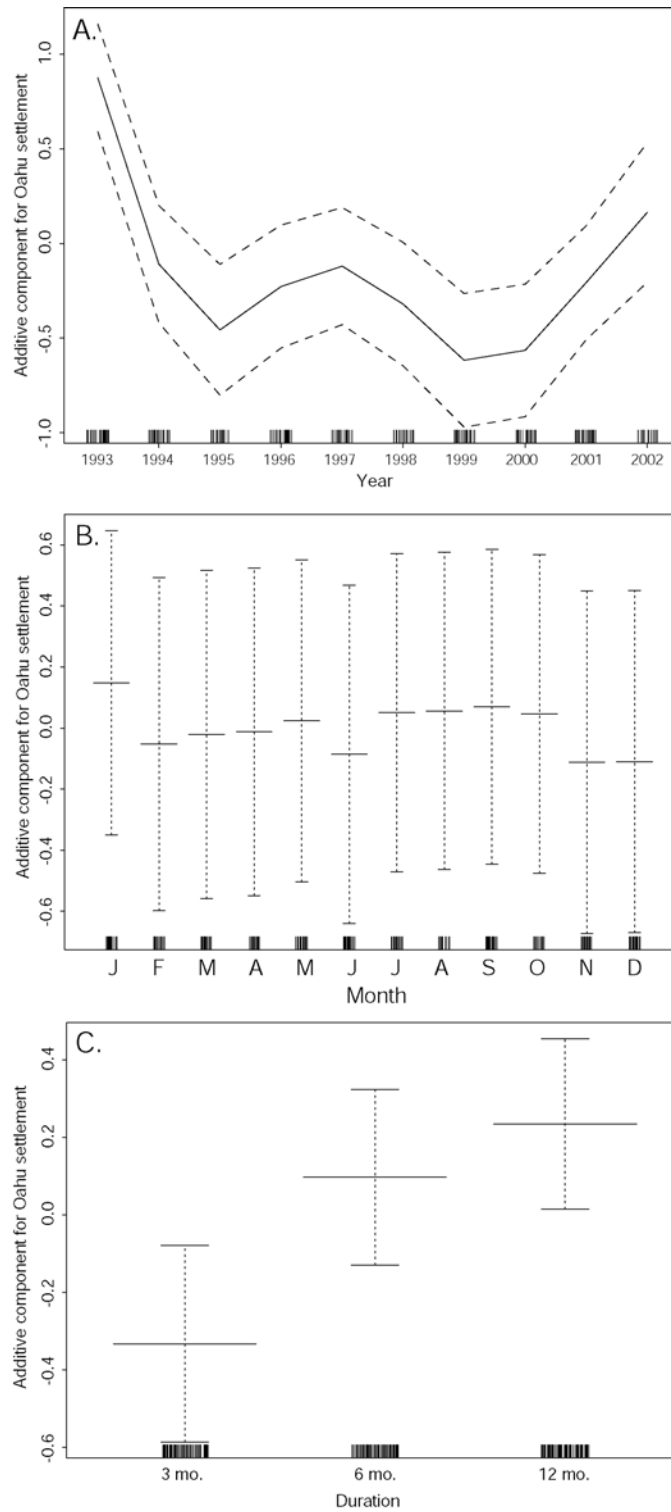
**Figure 6.** Results of GAM application to larval settlement at Oahu from Necker spawning. The predictor variables are year (A), month (B), and larval duration (C). C.I. are ±2 standard errors.
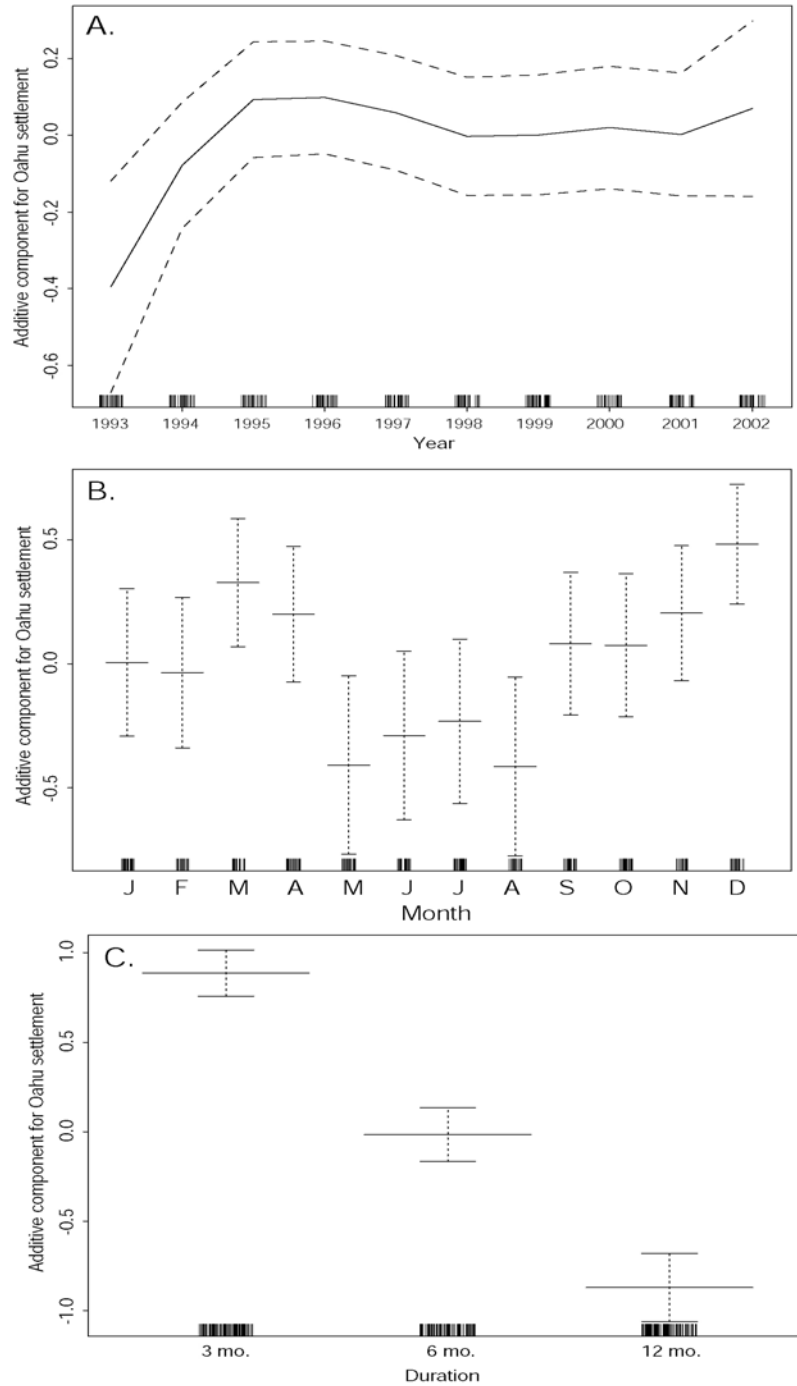
**Figure 7.** Results of GAM application to larval settlement at Oahu from Oahu spawning. The predictor variables are year (A), month (B), and larval duration (C). C.I. are ±2 standard errors.

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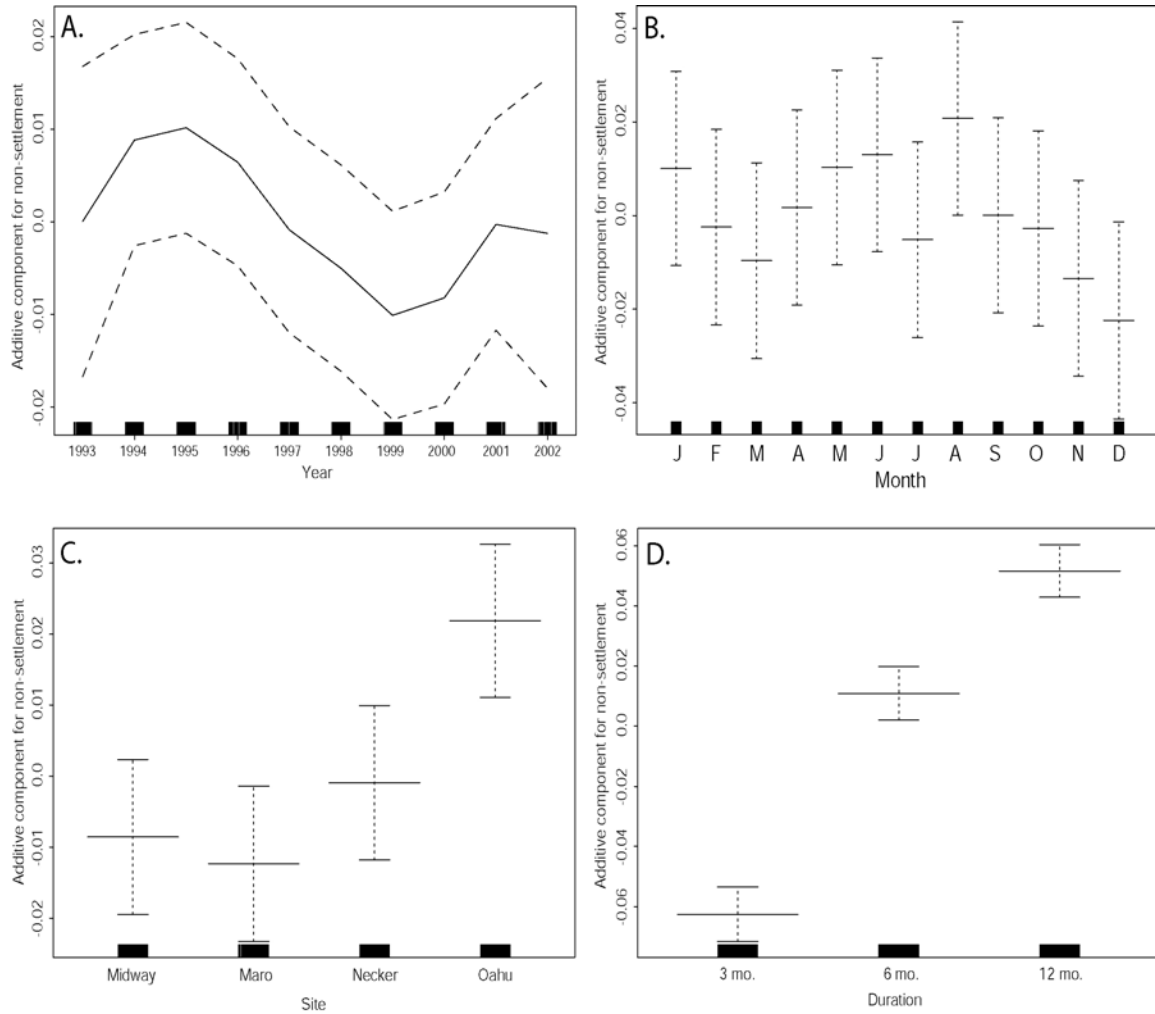


**Figure 8.** Results of GAM application to larval nonsettlement. The predictor variables are year (A), month (B), spawning site (C), and larval duration (D). C.I. are ±2 standard errors.
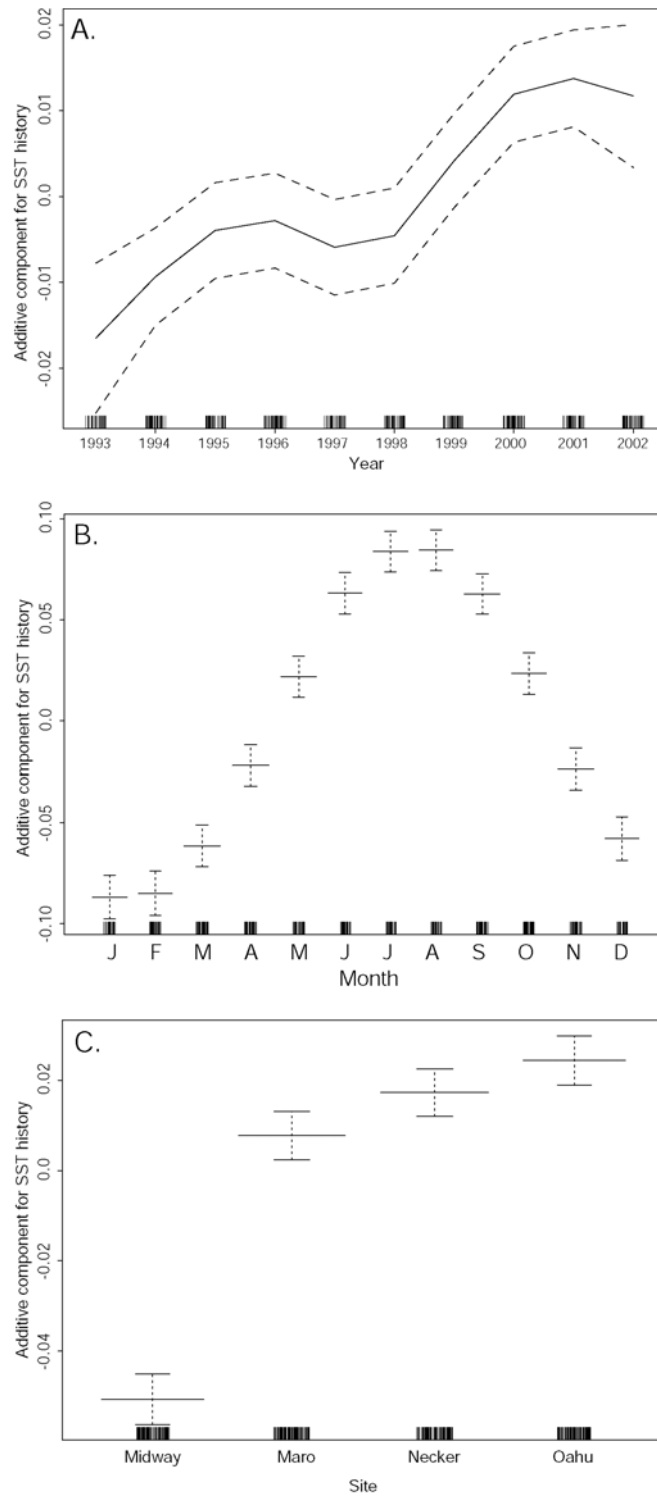
**Figure 9.** Results of GAM application to SST history of retained larvae after 3-month pelagic duration. The predictor variables are year (A), month (B), and spawning site (C). C.I. are ±2 standard errors.
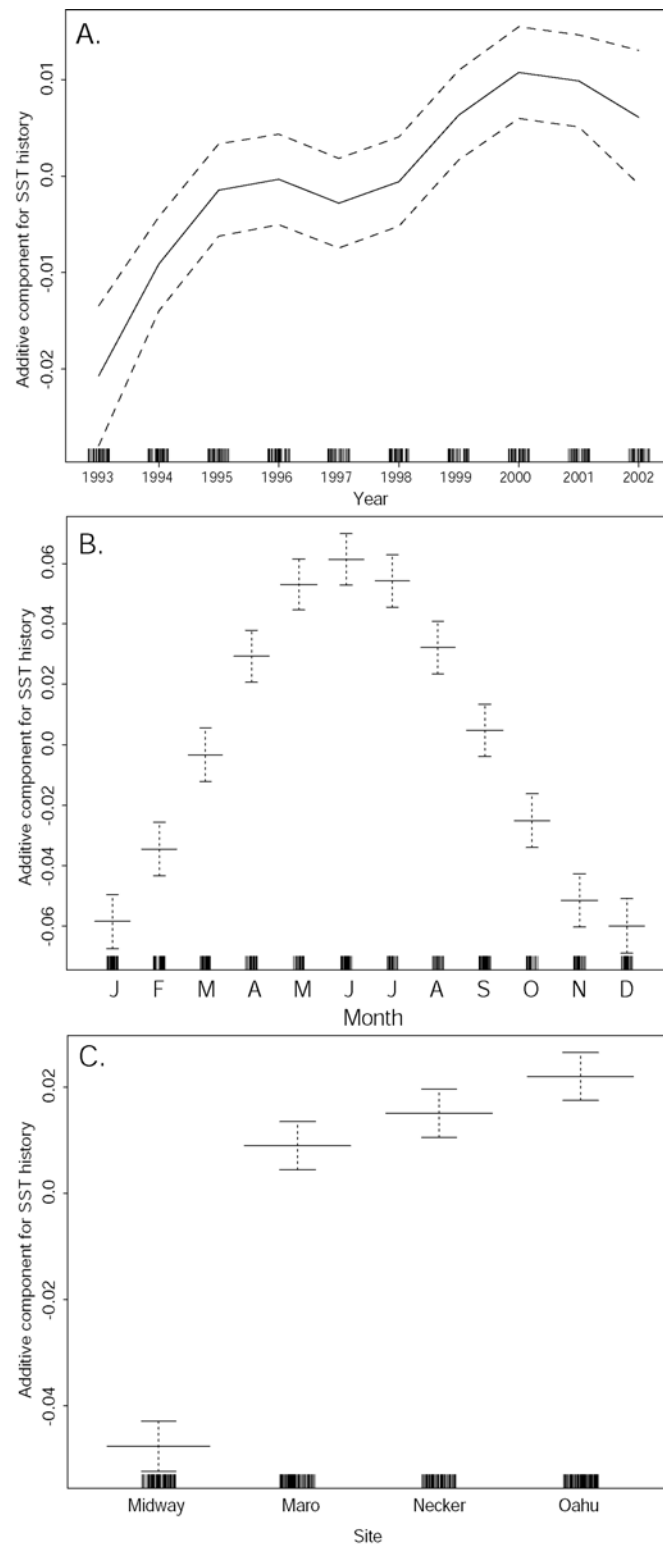
**Figure 10.** Results of GAM application to SST history of retained larvae after 6-month pelagic duration. The predictor variables are year (A), month (B), and spawning site (C). C.I. are ±2 standard errors.
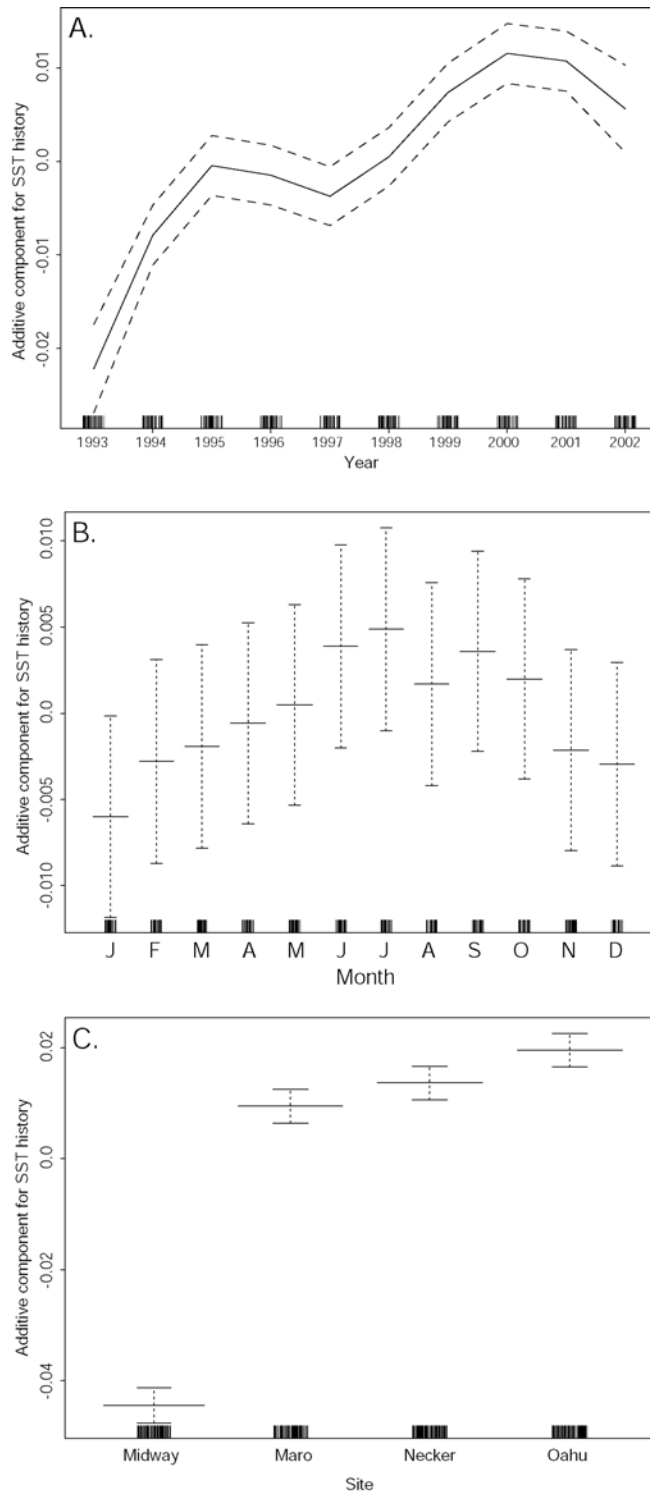
**Figure 11.** Results of GAM application to SST history of retained larvae after 12-month pelagic duration. The predictor variables are year (A), month (B), and spawning site (C). C.I. are ±2 standard errors.

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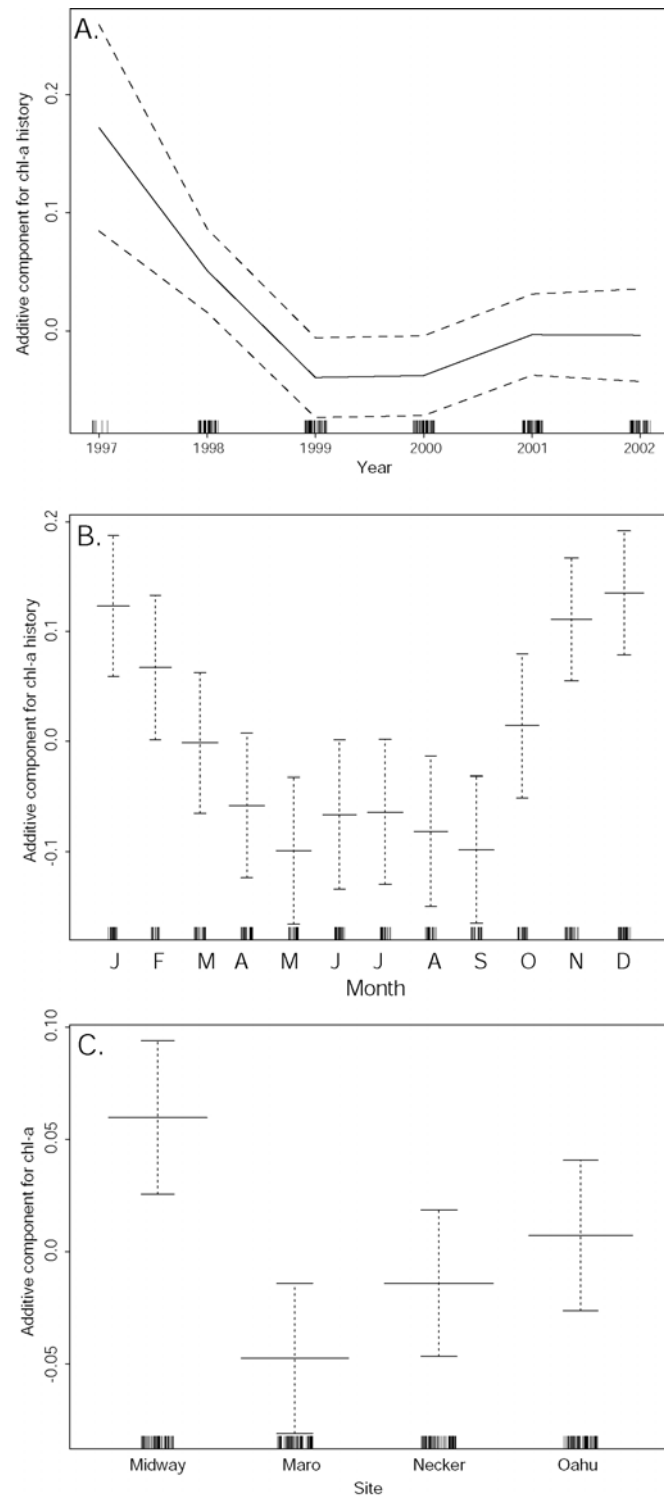


**Figure 12.** Results of GAM application to chlorophyll-a history of retained larvae after 3-month pelagic duration. The predictor variables are year (A), month (B), and spawning site (C). C.I. are ±2 standard errors.
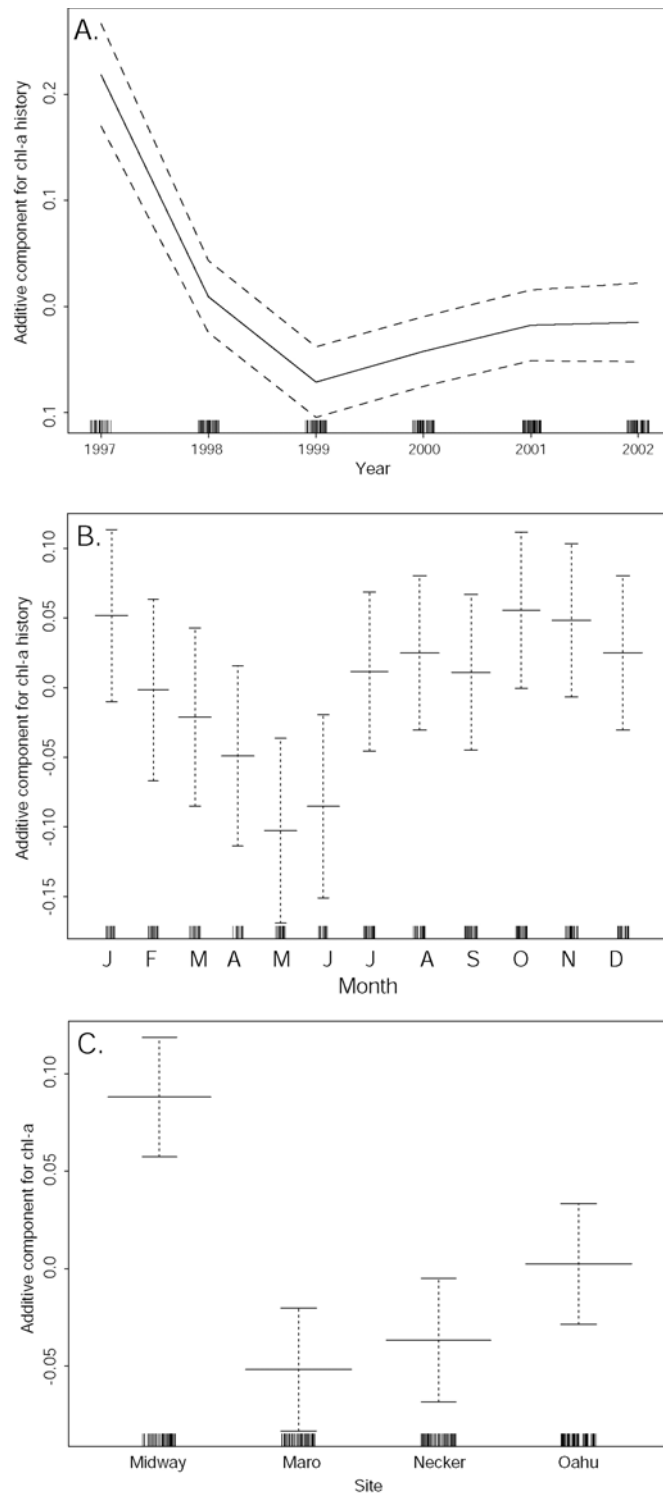
**Figure 13.** Results of GAM application to chlorophyll-a history of retained larvae after 6-month pelagic duration. The predictor variables are year (A), month (B), and spawning site (C). C.I. are ±2 standard errors.

386
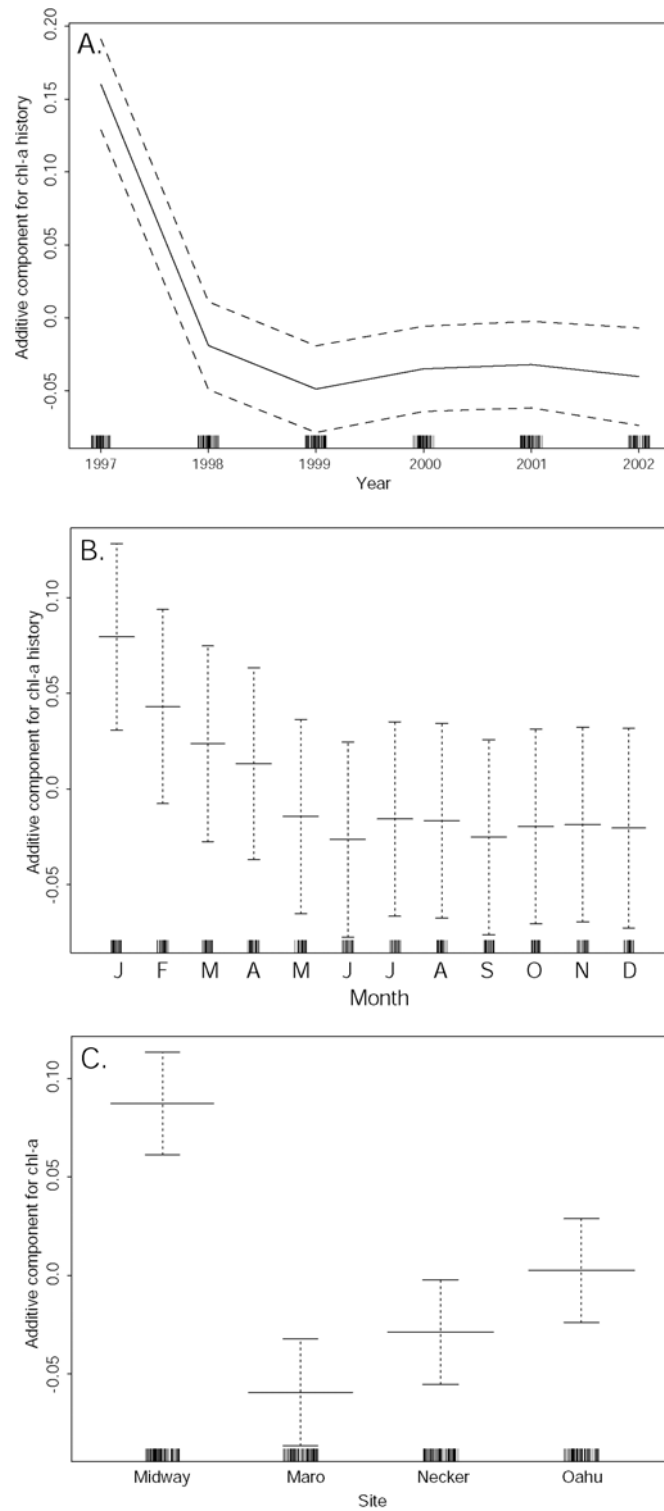


**Figure 14.** Results of GAM application to chlorophyll-a history of retained larvae after 12-month pelagic duration. The predictor variables are year (A), month (B), and spawning site (C). C.I. are ±2 standard errors.

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# DIEL TRENDS IN THE MESOPELAGIC BIOMASS COMMUNITY OF THE NORTHWESTERN HAWAIIAN ISLANDS OBSERVED ACOUSTICALLY

BY

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## ABSTRACT

The nighttime mesopelagic biomass occurring on and near six banks in the Northwestern Hawaiian Islands was investigated using a ship-based EK60 scientific echosounder. The locations investigated included French Frigate Shoals, Maro Reef, Lisianksi Island/Neva Shoals, Pearl and Hermes Atoll, Kure Atoll, and Midway Atoll. Surveys were designed to sample parallel and/or shore-normal at each site during different times of the night and during the day. A strong diel trend exists in the presence of midwater sound-scattering biota at all six locations visited. Dense communities of organisms accumulate on the edges of each island and the associated banks at night. The highest densities of organisms tend to occur in waters 30 meters or deeper, but significant increases in biomass were also observed at shallower depths. There was considerable temporal and spatial heterogeneity in the occurrence of the biota observed both between and within locations sampled. The biological composition of the observed biota is presently unclear but it resembles the mesopelagic boundary community that occurs in neritic waters off the Main Hawaiian Islands. The nightly influx of this biota into shallow waters is likely a significant, though poorly understood, component of these islands' reefs and nearshore ecosystems.

## INTRODUCTION

Sound-scattering layers (SSLs) are communities of organisms composed of various combinations of zooplankton, planktonic larvae, and micronekton. SSLs are found in many parts of the world's oceans and are characterized by a diel vertical migration from daytime subphotic habitats into surface waters at night. Vertically migrating SSLs are an important trophic link in pelagic food webs because they promote a downward transfer of energy from epipelagic waters into the deeper (>500 m), mesopelagic layers of the ocean (Roger and Grandperrin, 1976).

In the Main Hawaiian Islands (MHI), an island-associated SSL occurs that is known as the Mesopelagic Boundary Community (MBC) (Reid et al., 1991). This is a community of micronekton specifically adapted to the boundary region between the neritic and oceanic habitats. This community is made up of at least 23 species of fish,

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shrimp, and squid in 12 families.  During the day, the MBC is found in waters 400-700 m deep along the slopes of the islands, while at night it rises to within 10 m of the surface.

Recent work on the MBC has demonstrated that, in addition to migrating vertically at night, this community also moves horizontally towards shallower inshore waters (Benoit-Bird et al., 2001).  This net diagonal movement begins shortly before sunset and reaches its shallowest point at around the midpoint of the night. The MBC then reverses its movement so that it is back in deeper offshore waters by sunrise.  The shallowest depth reached by this migration is presently still unknown, but acoustic observations have detected the MBC in waters with a bottom as shallow as 30 m (Benoit-Bird and Au, 2004), and it is thought that it enters even shallower depths.

The influx of boundary community biomass into coastal waters on a nightly basis remains a poorly understood component of Hawaii's neritic habitat.  Stomach analyses of tuna (He et al., 1997), billfish (Skillman, 1998), bottomfish (Haight et al., 1993), and spinner dolphins (Norris et al., 1994; Benoit-Bird, 2004) have shown that boundary community prey represent an important component of their diets.  In addition, the occurrence of the MBC in waters shallow enough to overlap with coral reefs raises the possibility that a significant trophic relationship may also exist with this community between these two communities.

Reid et al. (1991) suggested that boundary communities are likely to occur globally in regions where land-associated mesopelagic species are found and that, consequently, an important, but still poorly understood ecological relationship exists between oceanic and island-associated near-shore habitats.  To examine this possibility over a broad geographic scale, the occurrence of mesopelagic biomass near islands and atolls in the Northwestern Hawaiian Archipelago was investigated using ship-based echosounders.  The objectives of this work were to establish whether diel migrations of biota into neritic waters are as common around the atolls of the Northwestern Hawaiian Islands (NWHI) as they are around the main Hawaiian Islands (MHI), and secondly, whether this nightly influx overlaps with coral reef habitat.

**METHODS**

The occurrence of the MBC and other mesopelagic biota was investigated acoustically using two Simrad EK60 echosounders operating at 38 kHz and 120 kHz.  Surveys were conducted using the NOAA ship *Oscar Elton Sette* during the 2003 NWHI Reef Assessment and Monitoring Program (RAMP) cruise, between 12 July and 17 August.  Both EK60 frequencies were set to operate at the maximum ping rate relative to the detected bottom, a pulse duration of 0.256 ms, a transmit power of 1000 Watts, a beam angle (-3 dB) of 7.1 degrees, and a transducer gain of 24 dB at 38 kHz and 25.1 dB at 120 kHz.  Both sounders were calibrated in September of 2004 and again in March of 2005.  Calibration values remained consistent within 0.5 dB.

Six locations in the NWHI Archipelago were examined.  These were: French Frigate Shoals (N23º45' N latitude, W166º10' W longitude), Maro Reef (N25º25' N

latitude, W170º35' W longitude), Neva Shoal/Lisianski Island (N26º04' N latitude, W173º58' W longitude), Pearl and Hermes Atoll (N27º50' N latitude, W175º50' W longitude), Midway Atoll (N28º12' N latitude, W177º22' W longitude), and Kure Atoll (N28º25' N latitude, W178º20' W longitude).  Acoustic surveys were conducted during a 6-hour time window at night and a 1-2 hour opportunistic time window during the day.  Each location was surveyed over a period of either 2, 3, or 4 days and nights.  A set of 2 to 4 systematic transect lines ranging in length from 3 to 6 nautical miles were acoustically sampled at a speed of 5-6 knots three times during the night (Fig. 1).  The placement of transect lines was balanced between the study's objectives, cruise logistics related to daytime diver-based operations, and local weather and sea conditions.  Different times relative to the middle of the night were examined to establish whether a net movement of biomass across and/or along transects took place.  The middle of the night was defined as the halfway point between sunset and sunrise, the time of which changed with increasing longitude.  Each transect was also sampled once during the day as cruise logistics permitted to give a day/night comparison.  In addition, to provide a comparison between data obtained in the NWHI and the boundary community known to occur in the MHI, a single nighttime transect along the leeward coast of the island of Oahu was conducted during a separate cruise on 9 April, 2004 with the same vessel.

Data were analyzed using Echoview 2.25.  To examine the relative abundance and distribution of biomass between and along transect lines, the sampled water column was divided into cells 100 m long by 5 or 10 m deep (deeper waters were divided into deeper cells).  Twenty percent of all the cells from each transect down to a depth of 180 m were randomly selected as the basis for statistical comparison between times.  Cells deeper than 180 m were excluded from the analysis due to the presence of time-varying gain-related noise with increasing depth.

The mean volume backscattering strength (Sv) for each cell was used as a relative measure of biomass (Throne, 1971; MacLennan and Simmonds, 1992).  Changes in Sv values were used as indicators that the total biomass and/or the relative composition of biomass had changed over time and space.  Larger (less negative) Sv values are indicative of an increase in biomass density, a shift in the species composition towards those with higher target strength, or an increase in target strengths due to changes in animal orientation or swim bladder volumes, or a combination of these (Deemer and Hewitt, 1995) (Fig. 2).  To represent the relative occurrence of biomass as a function of time, depth, and location along transects, each transect was divided into 3-5 segments, and the cells for each segment were averaged into depth bins of 5, 10, or 30 m.

Prior to calculating Sv, the data were visually inspected and pre-processed using Echoview's data exclusion utility to remove extraneous noise artifacts, such as false echoes arising from water turbulence related to the ship's motion.  In addition, the top 10 m of each transect was rejected from the analysis to avoid the confounding influence of wave-induced surface bubbles.   Volume backscatter was calculated only for waters 2 m or more above the bottom.

## RESULTS

In Table 1 we describe the statistical relationship between the daytime and nighttime occurrence of mid-water biota at the six locations surveyed. In all cases, more biomass occurred in the water column at night than during the day. There was considerable variability in the diel occurrence of biomass both temporally and spatially. This was the case within as well as between locations. More backscattered acoustic energy was consistently received with the 38- kHz echosounder than the 120- kHz system. Consequently, the summary findings detailed below for each location reflect only the 38- kHz data. A comparative analysis of the results obtained using both frequencies will be the subject of a future publication.

French Frigate Shoals

Three acoustic transects were conducted at French Frigate Shoals (FFS) (Fig. 1A). Transect A was adjacent and parallel to the reef flat, transect B was centrally located on the main bank of the shoals, and transect C was placed parallel to the slope of the bank. The diel difference was greatest along transect C, where dense layers of biota accumulated throughout the night (Table 1). The relative diel difference was approximately equal along transects A and B, but A had a greater absolute density of biomass during both daytime and nighttime.

For further analysis, each transect was divided into five equidistant 1.9- km segments. Table 2 reveals where biomass occurred as a function of depth and time. Along transects A and B, the occurrence of nighttime biota increased throughout the water column, but especially near the bottom 5-10 m. Increases were not homogeneous, but rather occurred in localized maxima or 'patches.' The densest patches along both transects occurred during the period preceding the middle of the night (2200h) and began to dissipate by 0300h. The increases in biota observed along transect C differed in that patches of biomass occurred as localized layers in the water column. Between two and three distinct layers occurred simultaneously during the early (2200h) and middle (0030h) periods of the night between 50 and 150 m. During the late period (0300h), distinct layers were still present but occurred deeper. Throughout the night, the densest aggregations occurred where a layer would come into contact with the bottom along the edge of the slope (Table 2, transect C, segment 'Edg').

To determine whether nocturnally present biota migrate horizontally from the slopes of the bank onto the shallows near the reef flat, we considered the relative occurrence of biomass in relation to the time of night. We expected that, if horizontal migration across the bank takes place through the night, two roughly equivalent local maxima of relative abundance would occur along transects B and C during the first and third quarters of the night (2200h and 0300h, respectively), and a local maximum would be observed along transect A during the midpoint of the night (0030h) (Fig. 3A). This was not the case, however (Fig. 3B). A similar analysis of relative biomass occurring along (rather than across) each transect as a function of time also did not match the predictions of large- scale horizontal movement, at least not within the time frame examined.

Maro Reef

Maro Reef was surveyed over the course of two days and nights, during which two shoal-normal transects were systematically sampled (Fig. 1B). Both transects initiated adjacent to the shallow reef flat and extended past the slope of the bank. For analysis, each transect was divided into five segments based on depth and distance from the reef flat: three 'shallow- bank' segments (length = 2.1 km for transect A, 2.9 km for transect B), an 'edge- of- bank' segment (length = 1.6 km for transect A, 1.2 km for transect B), and a 'slope- of- bank' segment (length = 1.5 km for transect A, 0.8 km for transect B). Biomass increases occurred throughout the length of both transects, but the highest densities accumulated on the 'edge- of- bank' segment in water between 30 and 90 m deep (Table 2). The layer was densest between 30 and 60 m deep where it impinged on the rising slope of the bank, but it extended well onto the bank along the 10 m closest to the bottom. This distribution pattern was relatively consistent throughout the three nighttime periods sampled, suggesting that only limited, if any, net horizontal movement normal to the reef flat took place within the time frame examined.

Neva Shoal/Lisianski Island

Three transects parallel to the reef flat were sampled at Neva Shoal over three days and nights (Fig. 1C). As at FFS, transect A was adjacent and parallel to the reef flat, transect B was located centrally on the main bank of the shoal, and transect C was placed parallel to the slope of the bank. Significant nightly increases in biomass were measured on transects A and C (Table 1). Transect B was not sampled during the day due to operational restrictions with the ship.

The difference in daytime vs. nighttime biomass density was considerably greater along the slope of the bank than near the reef flat. As was observed at FFS, there were predominant increases in biomass towards the bottom half of the water column near the reef flat (transect A), comparatively less biota along the middle of the bank (transect B), and a distinct layering of biomass centered between 30 and 90 m deep along the slope of the bank (transect C). As at Maro Reef, the layers found along the slope were densest where they impinged on the rising slope of the bank. An examination of the occurrence of biomass between and along transects in relation to the time of night, as described for FFS, also did not yield any clear evidence of net horizontal movement across the bank within the time frame considered. During the daytime, most of the remaining biota occurred in the middle of the water column, towards the southern ends of both transects A and C.

Pearl and Hermes Atoll

Pearl and Hermes Atoll was surveyed during four days and nights. Cruise logistics and favorable weather allowed four transects to be conducted on three sides of the Atoll (Fig. 1D). Transects A and B were shore-normal on the northeastern and southwestern corners of the Atoll, respectively. Both transects initiated adjacent to the

shallow reef flat and extended past the slope of the bank.  For analysis, each transect was divided into five 1,400- m segments representing different depth strata and distances from the reef flat.  These were labeled using the same nomenclature employed at Maro Reef.

Transects C and D were both on the southern side of the Atoll, parallel to shore and to one another.  Transect C extended over a long segment of both declining and inclining slope, dropping to a depth of approximately 650 m in between and leveling off into a bank on the western end.  For analysis, transect C was divided into four depth strata: a 'slope- of- bank' ('Slo') segment, an 'edge- of- bank' ('Edg') segment, and two 'shallow- bank' ('Shb') segments.  Transect D was offshore of C and was mostly over water greater than 1,000 m deep.  For analysis, it was divided into a 'deep- water' segment, a 'slope- of- bank' segment, and an 'edge- of- bank' segment.

Transect A had the lowest nighttime Sv values of the four, but exhibited a distinct layer of biomass centered at the 31-60- m depth range throughout the night (Table 2).  This layer occurred along the entire transect, but was densest mid-water along the 'edge' and 'slope' segments.  A second, more localized layer was associated with the bottom below approximately 60 m, primarily along the middle 'shallow- bank' segment (Table 2, transect A, Shb2).

Transect B exhibited a similar distribution pattern as transect A, but with a considerably higher density of biomass along the shallowest two segments of the bank (Table 2, transect B, Shb1 and Shb2).  In addition, the dense patch of biota occurring along the middle 'shallow- bank' segment (Shb2) persisted into the day, although it disassociated itself from the bottom and became concentrated in a layer centered approximately 20 m above the bottom.

A dense layer of biota centered between 31 and 60 m deep occurred along the length of transect C.  This layer was densest near the bottom of the 'edge' and first 'shallow- bank' ('Edg' & Shb1) segments during the middle of the night.  The layer scattered somewhat and descended deeper as the night wore on, but a notable density of biomass remained in both 'shallow- bank' segments (Shb1 & Shb2) during the pre-dawn hours and persisted there during the day.

Transect D was dominated by deeper waters than transects A, B and C.  However, as with the other three transects, a layer of biota centered between 31 and 60 m deep occurred there during the majority of the night.  Also consistent with the other three transects was the higher concentration of biomass at the lower depths of the 'edge' segment.  In contrast with transects C and B, however, low densities of 'edge'-associated biota remained during the day.

Midway Atoll

Two transects parallel to the southern slope of Midway Atoll were sampled during two days and nights (Fig. 1E).  Transect A extended from the center of the Atoll's southwestern bank to near the entry channel into the lagoon.  The bottom along this transect gradually sloped upward from a maximum depth of 97 m on the western end to a minimum depth of 46 m on the eastern end.  Transect B ran parallel to A along the edge and slope of the Atoll.   The depth along transect B varied widely between 423 m and 91 m.

Transect A exhibited a nocturnal increase in biomass throughout the water column, but especially towards the eastern end below 20 m.  The abundance of biota remained high throughout most of the night and began to decrease prior to sunrise (0530h).  It persisted the longest towards the eastern end of the transect, which was adjacent to a steeper slope than the western end and was therefore characteristic of the 'edge' bathymetry described for other locations in the Archipelago.

Transect B differed in the distribution of biomass between the western and eastern end.  The western end was characterized by a distinct biomass layer near the surface and an accumulation near the bottom, separated by low densities in the middle of the water column, particularly at 0300h.  On the eastern end, the surface layer became denser and reached deeper, but no accumulation near the bottom was observed.  Toward sunrise, the distribution pattern changed considerably, with the bulk of the biota occurring at the lower depths of the western end, most likely representing the downward phase of the diel migration cycle.

Kure Atoll

Kure Atoll was surveyed during two days and nights.  Two transects were sampled parallel to the Atoll's western slope (Fig. 1F).  Transect A was the shallower of the two with nearly homogeneous depths.  Transect B was parallel to A, approximately 2.3 km further offshore.  The bottom of transect B sloped upward on the northern end, but was roughly constant in depth towards the southern end.

A nocturnal increase in biomass occurred throughout the water column along transect A during the middle of the night (0030h) and gradually decreased in density as the night wore on, particularly along the bottom half of the water column (Table 2). Transect B was characterized by dense aggregations below approximately 100 m and a secondary, more diffuse layer towards the surface.  The densest patches observed along transect B occurred during the latter part of the night (0300h) along the northern end.  A distinct patch persisted there into the last phase of the night (0530), but was entirely gone by daytime.

Waianae, Oahu

A single 6.3- km transect was conducted parallel to the northern Waianae coast of Oahu during the middle of the night in waters between 45 m and 120 m deep.  The average volume backscattering strength calculated for Waianae was near the median of the distribution of all the NWHI transects for both frequencies (Table 1).   The concentration of biomass was patchy, with a distinct mid-water layer occurring towards the northern end and a more bottom-associated layer towards the southern end.  The highest observed density was found along the edge of a descending slope towards the southern end.  The density and distribution pattern of the biota encountered off Waianae was not distinct in any notable way from the range of the patterns observed in the NWHI.

**DISCUSSION**

The study's primary objective was to answer the question: are diel migrations of biota into neritic waters common in the NWHI? We indicate that they are. Increases in nocturnal mid-water biomass were noted at all locations and along each transect surveyed. However, considerable spatial and temporal heterogeneity characterized the occurrence of this biota. Each site exhibited localized maxima in densities that tended to peak during the middle of the night and gradually subside prior to sunrise. During the day, most locations, regardless of depth, exhibited a substantial decrease and even total absence of the sound-scattering biota observed at night.

Although there was much variability, certain spatial patterns in the occurrence of this nighttime biota did emerge. The most consistent and dense aggregations were observed on and near the edges of the slopes of the atolls and shoals visited. The band of water between 30 m and 90 m deep nearly always had one or more distinct layers associated with it, usually throughout the night. These layers typically extended well beyond the slope, both offshore and towards the shore or reef flat. Interestingly, the layers often had well-defined upper boundaries, usually below 20 m deep. This may be tied to avoidance of light reflected from the moon, which can lead to greater predation (Gliwicz, 1986; Gal et al, 1999). Conversely, there appeared to be no avoidance of the benthos, although this changed during the day when, on the few occasions where a layer did persist into daytime hours, there was always a clear separation from the bottom (e.g., Pearl & Hermes Atoll transect B).

The second major objective was to determine whether the migratory biota observed near the slopes of atolls enters coral reef habitat. This point remains unresolved. There was clearly a nocturnal influx of biota into the water column at sites with depths commonly associated with coral reef habitat (~20-40 m), such as transect A at French Frigate Shoals (FFS). However, the data obtained did not reveal an identifiable, horizontally migrating 'front' of organisms that might account for this biomass, as has been observed in the MHI (Benoit-Bird et al 2001; Benoit-Bird and Au, 2004). Therefore, we presently cannot exclude the possibility that at least some of the biota observed arose from within or near the bottom locally. Benoit-Bird and Au (2004) have reported that the average horizontal migratory rate of micronekton off Oahu is 1.7 km h$^{-1}$. So, it is possible that biota observed over reef habitats within 2-3 km of an atoll's slope migrated there from deep waters quickly following sunset, and therefore did not appear as a moving front during the time frame we sampled. However, this is unlikely for the interior of large banks such as FFS and Maro Reef, where the reef flat is more than 10 km from the bank's slope.

Regardless of origin, the finding of consistently higher nocturnal biomass densities over reef habitat is important because it suggests that traditional daytime biological assessments may not capture all the trophic relationships present on the reef and may under-represent certain groups. This is relevant to efforts aimed at creating ecological models for the NWHI. For example, Friedlander and DeMartini (2002) reported that over 54% of the total fish biomass observed on reefs in the NWHI consists of apex predators, raising the intriguing question of how so many top-level consumers

are trophically supported.  A part of the answer may lie with the nocturnal influx of biota reported here.

Another unresolved issue is the taxonomic makeup of the biota observed. Logistical restrictions did not allow trawling for samples during acoustic data collection. Consequently, we can say relatively little about the identity of the organisms that occur at the various locations sampled.  The fact that more backscattered acoustic energy was consistently received with the 38- kHz echosounder (vs. 120-kHz)than 120 kHz is suggestive of micronekton rather than zooplankton, since the smaller zooplankters would be expected to reflect more acoustic energy at the higher of the two frequencies (MacLennan and Simmonds, 1992).  In addition, the fact that the limited data obtained off the Waianae coast of Oahu fell in line with mean Sv values from the NWHI further points to biota related to the mesopelagic boundary community.

In summary, it is reasonable to conclude that the nocturnal composition of biota in neritic waters off atolls and islands in the NWHI Archipelago is substantially different from what is observed there in the daytime.  This should be carefully considered when planning ecosystem assessments or trying to model trophic relationships based on observed biomass.  To better understand the ecological importance of these diel migrations, future surveys will need to resolve questions about the biological makeup of biota at different sites.  In addition, engaging in long-term monitoring of migration trends and correlated oceanographic conditions will yield important insights into the dynamics of these communities and possibly provide information on long-term patterns in the health of neritic ecosystems.

## ACKNOWLEDGEMENTS

400
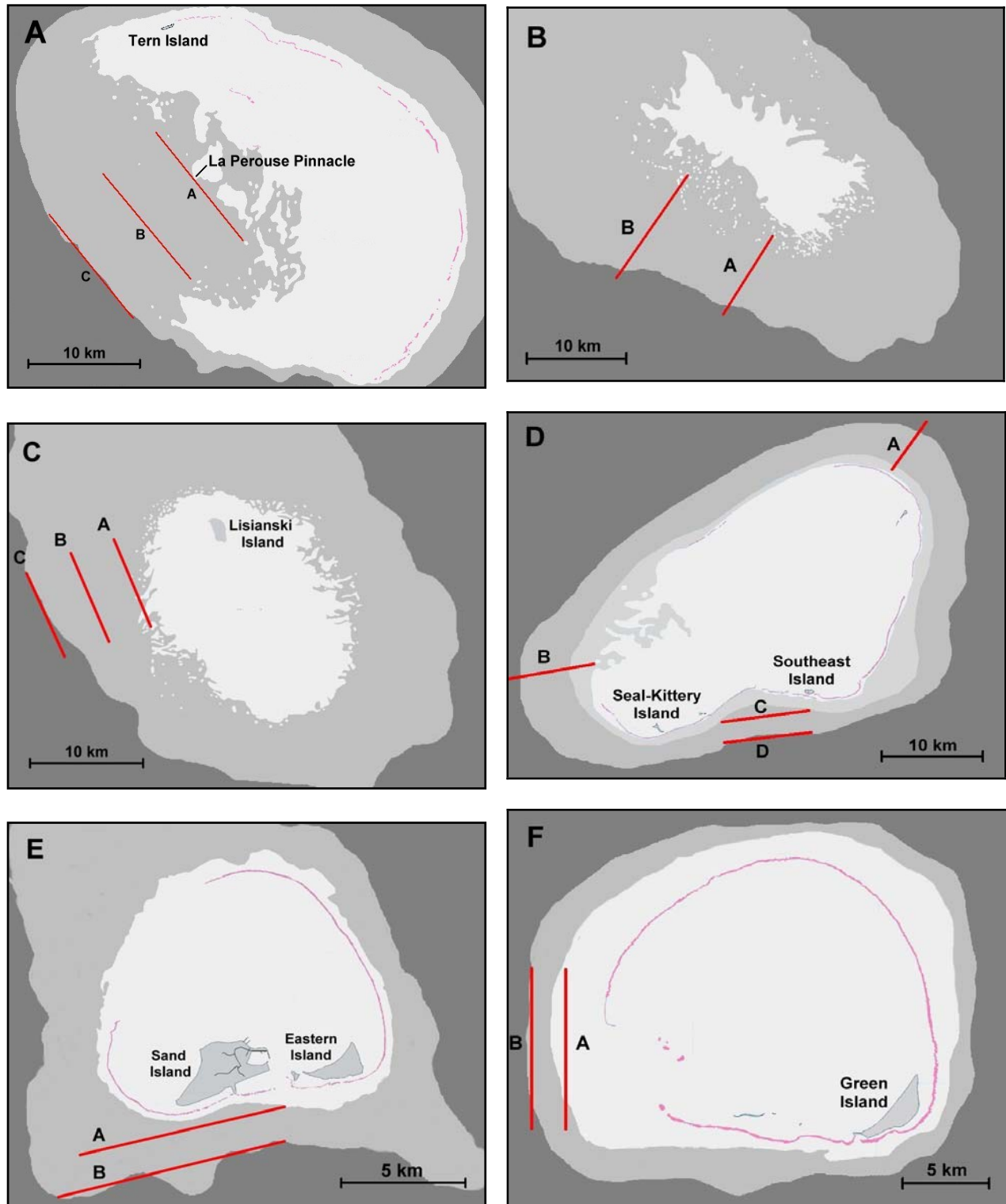


**Figure 1**. Acoustically sampled transect lines at French Frigate Shoals (A), Maro Reef (B), Lisianski Island/Neva Shoal (C), Pearl and Hermes Atoll (D), Midway Atoll (E), and Kure Atoll (F).
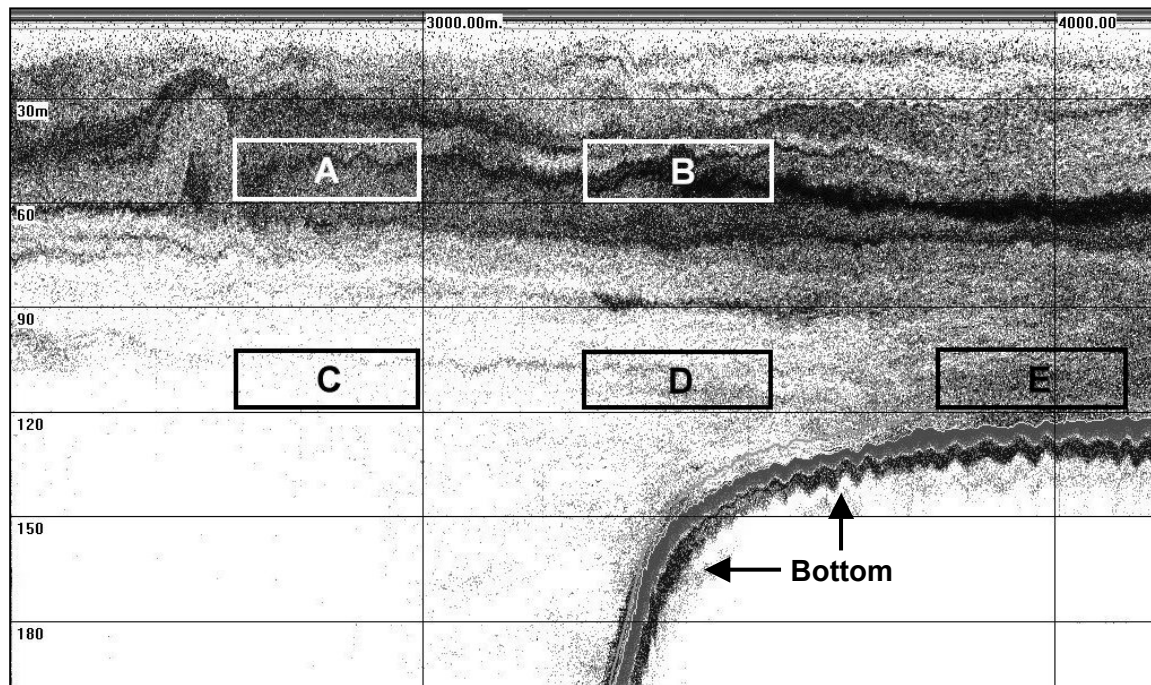
**Figure 2.** Nocturnal aggregation of biota observed with the 38-kHz echosounder along transect C at Pearl and Hermes Atoll. The figure illustrates the relationship between the relative density of biomass and volume backscattering strength (Sv). Cell A = -61.5 dB; Cell B = -56.3 dB; Cell C = -73.4 dB; Cell D = -67.3 dB; Cell E = -64.3 dB.
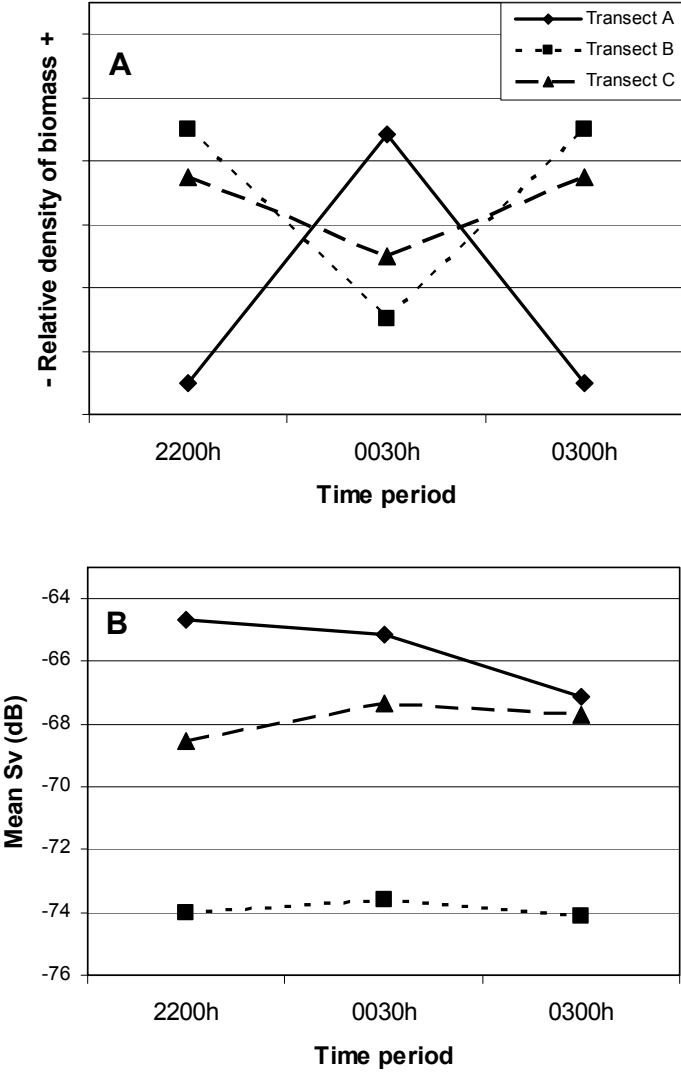
**Figure 3.** Relative biomass density along the transect at FFS. For a hypothesized nocturnal migration across the bank, the expected pattern (A) was not observed (B).

Table 1.  Table of nocturnal vs. diurnal mean Sv values measured for each transect sampled.  Statistical comparisons are based on two-sample t-tests.

| | Transect | Mean Sv (dB) 38 kHz | | | | Mean Sv (dB) 120 kHz | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Day | Night | Δ | P | Day | Night | Δ | P |
| French Frigate Shoal | A | -70.06 | -65.15 | -4.91 | <0.001 | -74.45 | -69.67 | -4.78 | <0.001 |
| | B | -77.94 | -73.58 | -4.36 | <0.001 | -81.84 | -76.21 | -5.63 | <0.001 |
| | C | -74.64 | -67.35 | -7.30 | <0.001 | -83.43 | -76.54 | -6.88 | <0.001 |
| Maro Reef | A | -77.35 | -69.19 | -8.16 | <0.001 | -84.41 | -77.11 | -7.30 | <0.001 |
| | B | -75.31 | -69.58 | -5.73 | <0.001 | -82.79 | -76.35 | -6.43 | <0.001 |
| Lisianski / Neva Shoal | A | -73.14 | -70.99 | -2.16 | 0.017 | -73.86 | -70.39 | -3.46 | 0.006 |
| | B | N/A | -72.34 | -- | -- | N/A | -75.10 | -- | -- |
| | C | -74.57 | -64.93 | -9.64 | <0.001 | -78.13 | -71.62 | -6.51 | <0.001 |
| Pearl & Hermes Atoll | A | -76.36 | -69.74 | -6.62 | <0.001 | -80.67 | -76.28 | -4.39 | <0.001 |
| | B | -72.96 | -68.45 | -4.51 | 0.007 | -79.15 | -76.28 | -2.87 | 0.013 |
| | C | -74.93 | -66.61 | -8.31 | <0.001 | -82.26 | -74.41 | -7.86 | <0.001 |
| | D | -77.55 | -68.96 | -8.59 | <0.001 | -84.91 | -77.62 | -7.28 | <0.001 |
| Midway Atoll | A | -75.35 | -64.79 | -10.56 | <0.001 | -74.76 | -68.95 | -5.82 | <0.001 |
| | B | -77.57 | -69.42 | -8.14 | <0.001 | -84.00 | -77.38 | -6.62 | <0.001 |
| Kure Atoll | A | -74.38 | -67.95 | -6.42 | <0.001 | -76.43 | -71.68 | -4.75 | <0.001 |
| | B | -76.91 | -70.78 | -6.13 | <0.001 | -84.41 | -77.83 | -6.58 | <0.001 |
| Waianae, Oahu | A | N/A | -67.86 | -- | -- | N/A | -74.30 | -- | -- |

Table 2. The volume backscattering strength (Sv) measured along each transect as a function of water column depth during different times of the night and during daytime. Gray-scaled cells represent relative acoustic backscatter at 38 kHz. Darker cells represent greater backscatter. *Shb*: shallow bank; *Slo*: slope; *Edg*: edge; *Deep*: > 500 m deep. A solid (____) base indicates the cell includes the bottom, a dashed (_ _ _) base indicates the cell partly includes the bottom, and a dotted (……) base indicates the cell does not include the bottom.

## French Frigate Shoals

### Transect A

| Depth (m) | 2200 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | 0030 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | 0300 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | Day Shb1 | Shb2 | Shb3 | Shb4 | Shb5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-15 | -68.9 | -66.9 | -67.9 | -66.7 | -66.0 | -67.8 | -67.4 | -67.0 | -64.3 | -64.5 | -67.5 | -67.6 | -67.8 | -65.9 | -65.4 | -68.2 | -67.3 | -66.3 | -65.9 | -74.9 |
| 16-20 | -69.0 | -65.8 | -66.1 | -65.3 | -65.7 | -66.9 | -66.1 | -66.5 | -64.1 | -63.6 | -66.6 | -67.3 | -67.4 | -66.1 | -65.3 | -66.9 | -67.6 | -69.0 | -68.0 | -75.5 |
| 21-25 | -64.6 | -61.5 | -61.2 | -60.3 | -63.6 | -64.8 | -64.4 | -65.8 | -62.7 | -62.1 | -67.0 | -68.4 | -68.2 | -67.9 | -68.3 | -70.9 | -75.5 | -73.2 | -70.4 | -72.1 |
| *Avg. depth* | ← 24.1 → |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

NW ←→ SE

### Transect B

| Depth (m) | 2200 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | 0030 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | 0300 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | Day Shb1 | Shb2 | Shb3 | Shb4 | Shb5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-15 | -77.1 | -76.0 | -76.5 | -70.2 | -74.7 | -74.6 | -74.6 | -73.1 | -73.5 | -77.0 | -74.4 | -74.8 | -75.7 | -75.5 | -75.2 | -73.1 | -73.1 | -75.1 | -74.0 | -80.0 |
| 16-20 | -77.1 | -75.5 | -76.6 | -72.0 | -72.5 | -73.9 | -74.1 | -73.6 | -72.6 | -76.7 | -73.9 | -73.7 | -74.7 | -74.7 | -73.6 | -76.5 | -75.7 | -77.3 | -77.1 | -82.3 |
| 21-25 | -76.3 | -74.1 | -75.3 | -69.9 | -69.4 | -73.5 | -73.5 | -73.8 | -72.6 | -75.0 | -72.9 | -73.0 | -74.4 | -74.6 | -73.6 | -79.6 | -79.5 | -78.9 | -80.8 | -83.8 |
| 26-30 | -73.7 | -73.4 | -74.3 |  |  | -71.3 | -73.2 | -73.1 |  |  | -72.4 | -73.2 | -74.9 |  |  | -75.5 | -75.7 | -82.1 |  |  |
| *Avg. depth* | ← 30.8 → |  |  | 27.2 | 23.5 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

### Transect C

| Depth (m) | 2200 Slo1 | Edg | Slo2 | Slo3 | Slo4 | 0030 Slo1 | Edg | Slo2 | Slo3 | Slo4 | 0300 Slo1 | Edg | Slo2 | Slo3 | Slo4 | Day Slo1 | Edg | Slo2 | Slo3 | Slo4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-30 | -72.0 | -71.5 | -75.4 | -76.7 | -73.8 | -76.5 | -74.2 | -74.3 | -71.7 | -70.5 | -70.0 | -73.0 | -73.5 | -71.3 | -71.2 | -75.3 | -72.2 | -73.2 | -74.4 | -74.9 |
| 31-60 | -66.9 | -66.5 | -67.4 | -69.8 | -70.4 | -70.6 | -71.0 | -67.4 | -67.8 | -71.4 | -66.1 | -66.8 | -68.2 | -70.8 | -70.1 | -76.4 | -75.5 | -75.3 | -75.0 | -75.8 |
| 61-90 | -66.1 | -66.4 | -63.5 | -66.5 | -67.6 | -65.4 | -64.1 | -64.1 | -69.8 | -72.2 | -66.8 | -69.7 | -73.2 | -73.6 | -72.1 | -74.9 | -73.6 | -74.6 | -74.8 | -77.5 |
| 91-120 | -68.6 | -61.1 | -65.0 | -61.6 | -60.1 | -62.6 | -59.9 | -62.7 | -64.9 | -68.0 | -64.8 | -63.5 | -65.5 | -67.2 | -66.2 | -74.4 | -74.3 | -74.4 | -73.7 | -75.3 |
| 121-150 | -70.5 | -61.9 | -72.8 | -69.1 | -63.4 | -61.4 | -62.1 | -64.7 | -62.3 | -65.6 | -63.4 | -62.8 | -66.2 | -63.8 | -64.2 | -74.4 | -70.2 | -76.0 | -74.4 | -75.7 |
| *Avg. depth* | 239 | 149 | 249 | 175 | 206 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

## Maro Reef

### Transect A

| Depth (m) | 2200 Shb1 | Shb2 | Shb3 | Edg | Slo | 0030 Shb1 | Shb2 | Shb3 | Edg | Slo | 0300 Shb1 | Shb2 | Shb3 | Edg | Slo | Day Shb1 | Shb2 | Shb3 | Edg | Slo |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-30 | -72.5 | -71.5 | -66.8 | -66.5 | -67.1 | -72.4 | -68.9 | -65.5 | -64.8 | -66.8 | -71.1 | -68.5 | -68.0 | -69.5 | -67.1 | -81.4 | -76.9 | -74.1 | -70.2 | -79.9 |
| 31-60 |  |  |  | -61.6 | -68.1 |  |  |  | -62.5 | -70.9 |  |  |  | -62.8 | -68.2 |  |  |  | -70.3 | -71.9 |
| 61-90 |  |  |  | -63.6 | -69.5 |  |  |  | -65.5 | -71.2 |  |  |  | -61.5 | -70.3 |  |  |  | -79.7 | -77.5 |
| 91-120 |  |  |  |  | -70.3 |  |  |  |  | -72.3 |  |  |  |  | -70.2 |  |  |  |  | -82.7 |
| 121-150 |  |  |  |  | -70.7 |  |  |  |  | -72.5 |  |  |  |  | -71.6 |  |  |  |  | -81.7 |
| *Avg. depth* | ← 30.7 → |  |  | 66.5 | 393 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

NE ←→ SW

### Transect B

| Depth (m) | 2200 Shb1 | Shb2 | Shb3 | Edg | Slo | 0030 Shb1 | Shb2 | Shb3 | Edg | Slo | 0300 Shb1 | Shb2 | Shb3 | Edg | Slo | Day Shb1 | Shb2 | Shb3 | Edg | Slo |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-30 | -71.2 | -70.5 | -67.5 | -70.2 | -70.4 | -72.0 | -70.2 | -65.9 | -66.4 | -71.5 | -70.7 | -69.0 | -68.4 | -70.6 | -72.2 | -79.1 | -76.8 | -75.3 | -79.1 | -77.3 |
| 31-60 |  |  |  | -66.0 | -64.2 |  |  |  | -61.2 | -63.9 |  |  |  | -63.0 | -66.8 |  |  |  | -76.8 | -67.4 |
| 61-90 |  |  |  | -67.3 | -65.4 |  |  |  | -65.0 | -66.1 |  |  |  | -62.6 | -66.0 |  |  |  | -75.3 | -77.1 |
| 91-120 |  |  |  |  | -70.5 |  |  |  |  | -74.3 |  |  |  |  | -69.7 |  |  |  |  | -78.4 |
| 121-150 |  |  |  |  | -75.7 |  |  |  |  | -74.4 |  |  |  |  | -74.9 |  |  |  |  | -79.4 |
| *Avg. depth* | ← 33.2 → |  |  | 63.9 | 325 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

## Lisianski/Neva Shoal

### Transect A

| Depth (m) | 2230 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | 0100 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | 0330 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | Day Shb1 | Shb2 | Shb3 | Shb4 | Shb5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-15 | -70.2 | -69.9 | -71.2 | -72.0 | -72.3 | -73.7 | -73.6 | -72.9 | -74.7 | -71.6 | -74.0 | -74.0 | -73.8 | -74.2 | -70.3 | -70.5 | -72.0 | -74.6 | -68.1 | -67.7 |
| 16-20 | -72.1 | -70.7 | -71.3 | -71.9 | -72.1 | -73.3 | -73.4 | -72.6 | -73.8 | -69.2 | -73.6 | -73.7 | -73.2 | -73.6 | -69.7 | -72.7 | -74.8 | -77.9 | -70.1 | -67.7 |
| 21-25 | -74.7 | -71.7 | -71.6 | -72.0 | -68.7 | -73.0 | -72.7 | -71.4 | -71.7 | -63.7 | -73.1 | -73.5 | -72.2 | -71.2 | -66.5 | -76.8 | -79.8 | -81.1 | -71.5 | -67.2 |
| 26-30 | -76.1 | -71.7 | -64.1 | -65.3 | -70.3 | -72.5 | -69.2 | -63.9 | -66.0 | -64.0 | -72.9 | -71.4 | -67.2 | -64.2 | -72.0 | -77.6 | -74.8 | -74.0 | -73.3 | -76.6 |
| *Avg. depth* | ← 28.8 → |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

North ←→ South

### Transect B

| Depth (m) | 2230 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | 0100 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | 0330 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | Day Shb1 | Shb2 | Shb3 | Shb4 | Shb5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-15 | -69.9 | -72.3 | -71.7 | -69.6 | -68.1 | -71.2 | -70.5 | -71.0 | -70.2 | -70.6 | -71.7 | -75.9 | -74.8 | -75.7 | -73.9 | n/a | n/a | n/a | n/a | n/a |
| 16-25 | -71.4 | -73.8 | -72.4 | -70.0 | -68.2 | -71.9 | -71.6 | -71.8 | -71.5 | -70.6 | -71.9 | -75.3 | -73.4 | -72.9 | -72.6 | n/a | n/a | n/a | n/a | n/a |
| 26-35 | -72.1 | -72.4 | -72.4 | -70.5 | -65.2 | -73.6 | -73.5 | -73.1 | -71.7 | -69.6 | -71.1 | -73.3 | -71.7 | -70.1 | -68.1 | n/a | n/a | n/a | n/a | n/a |
| *Avg. depth* | ← 32.0 → |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

### Transect C

| Depth (m) | 2230 Edg1 | Edg2 | Edg3 | Edg4 | Edg5 | 0100 Edg1 | Edg2 | Edg3 | Edg4 | Edg5 | 0330 Edg1 | Edg2 | Edg3 | Edg4 | Edg5 | Day Edg1 | Edg2 | Edg3 | Edg4 | Edg5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-30 | -65.1 | -65.5 | -63.7 | -66.2 | -66.9 | -69.9 | -67.2 | -66.7 | -67.1 | -68.4 | -73.3 | -71.3 | -71.8 | -72.2 | -72.7 | -72.0 | -72.7 | -73.1 | -70.4 | -72.3 |
| 31-60 | -58.9 | -59.0 | -57.0 | -59.2 | -60.8 | -65.6 | -65.6 | -63.0 | -62.8 | -63.2 | -66.3 | -64.8 | -65.7 | -65.3 | -69.9 | -75.4 | -75.3 | -73.9 | -67.6 | -69.4 |
| 61-90 | -65.0 | -59.0 |  |  | -58.1 | -63.5 | -59.7 |  |  | -59.8 | -63.5 | -56.0 |  |  | -64.6 | -80.4 | -80.8 |  |  | -77.5 |
| 91-120 |  |  |  |  | -68.4 |  |  |  |  | -66.0 |  |  |  |  | -69.5 |  |  |  |  | -80.7 |
| *Avg. depth* | 87.7 | 71.7 | 67.4 | 54.7 | 103 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

## Pearl & Hermes Atoll

### Transect A

| Depth (m) | 2200 Shb1 | Shb2 | Shb3 | Edg | Slo | 0030 Shb1 | Shb2 | Shb3 | Edg | Slo | 0300 Shb1 | Shb2 | Shb3 | Edg | Slo | Day Shb1 | Shb2 | Shb3 | Edg | Slo |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-30 | -72.5 | -71.7 | -73.2 | -71.8 | -71.3 | -70.1 | -71.3 | -72.8 | -72.4 | -70.9 | -71.2 | -71.7 | -71.7 | -71.0 | -70.8 | -79.3 | -80.3 | -79.0 | -78.3 | -78.6 |
| 31-60 | -68.0 | -68.5 | -67.6 | -65.8 | -65.9 | -68.5 | -68.5 | -66.7 | -66.3 | -66.1 | -68.7 | -69.0 | -68.0 | -67.1 | -67.0 | -75.9 | -74.6 | -74.9 | -75.5 | -74.4 |
| 61-90 |  | -67.8 | -68.9 | -71.1 | -71.0 |  | -65.3 | -69.8 | -70.4 | -72.1 |  | -66.0 | -71.3 | -73.1 | -72.2 |  | -78.8 | -75.5 | -76.4 | -75.5 |
| 91-120 |  |  |  | -70.9 | -73.3 |  |  |  | -72.9 | -74.5 |  |  |  | -71.5 | -72.9 |  |  |  | -77.8 | -76.6 |
| 121-150 |  |  |  |  | -71.5 |  |  |  |  | -71.7 |  |  |  |  | -74.2 |  |  |  |  | -76.9 |
| *Avg. depth* | *48.0* | *72.0* | *85.3* | *103* | *357* | | | | | | | | | | | | | | | |

### Transect B

| Depth (m) | 0030 Shb1 | Shb2 | Shb3 | Edg | Slo | 0300 Shb1 | Shb2 | Shb3 | Edg | Slo | 0445 Shb1 | Shb2 | Shb3 | Edg | Slo | Day Shb1 | Shb2 | Shb3 | Edg | Slo |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-30 | -65.8 | -64.5 | -70.6 | -64.0 | -67.8 | -67.3 | -69.5 | -71.5 | -70.8 | -69.3 | -70.1 | -70.1 | -72.6 | -69.6 | -69.1 | -69.2 | -64.1 | -73.4 | -79.4 | -81.1 |
| 31-60 | -57.1 | -51.8 | -69.8 | -65.3 | -69.0 | -56.5 | -68.5 | -67.9 | -67.0 | -68.8 | -59.0 | -66.2 | -68.4 | -66.9 | -67.7 | -68.3 | -56.0 | -75.0 | -76.4 | -75.3 |
| 61-90 |  | -49.0 | -70.2 | -70.8 | -73.0 |  | -68.4 | -73.8 | -72.2 | -69.4 |  | -53.5 | -71.4 | -72.2 | -73.0 |  | -69.7 | -72.4 | -78.0 | -77.3 |
| 91-120 |  |  |  | -65.4 | -78.1 |  |  |  | -73.8 | -74.0 |  |  |  | -73.4 | -74.1 |  |  |  | -75.6 | -75.5 |
| 121-150 |  |  |  |  | -78.9 |  |  |  |  | -77.9 |  |  |  |  | -76.1 |  |  |  |  | -79.1 |
| *Avg. depth* | *26.2* | *63.0* | *78.1* | *105* | *363* | | | | | | | | | | | | | | | |

### Transect C

| Depth (m) | 0030 Slo | Edg | Shb1 | Shb2 | 0300 Slo | Edg | Shb1 | Shb2 | 0530 Slo | Edg | Shb1 | Shb2 | Day Slo | Edg | Shb1 | Shb2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-30 | -67.9 | -70.2 | -65.4 | -69.6 | -65.8 | -65.0 | -64.3 | -63.9 | -62.4 | -66.8 | -67.5 | -69.4 | -67.6 | -68.5 | -66.3 | -67.6 |
| 31-60 | -61.3 | -62.8 | -61.2 | -61.2 | -64.3 | -63.6 | -59.6 | -53.7 | -67.0 | -70.7 | -64.3 | -66.2 | -70.3 | -72.4 | -68.9 | -68.8 |
| 61-90 | -65.4 | -60.0 | -56.6 |  | -67.6 | -64.0 | -56.3 |  | -75.0 | -77.7 | -70.7 |  | -79.1 | -80.4 | -77.4 |  |
| 91-120 | -71.0 | -62.0 |  |  | -66.5 | -60.3 |  |  | -75.1 | -77.0 |  |  | -80.1 | -80.7 |  |  |
| 121-150 | -73.6 |  |  |  | -71.3 |  |  |  | -76.0 |  |  |  | -81.4 |  |  |  |
| *Avg. depth* | *441* | *128* | *108* | *46.7* | | | | | | | | | | | | |

East ⟷ West

### Transect D

| Depth (m) | 0030 Deep | Slo | Edg | 0300 Deep | Slo | Edg | 0530 Deep | Slo | Edg | Day Deep | Slo | Edg |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-30 | -67.0 | -68.1 | -67.0 | -67.0 | -66.9 | -64.9 | -69.3 | -70.0 | -72.6 |  | -75.8 | -76.6 |
| 31-60 | -65.1 | -64.5 | -64.8 | -64.1 | -65.6 | -64.6 | -68.5 | -71.2 | -73.7 | -75.1 | -73.3 | -72.4 |
| 61-90 | -68.9 | -65.4 | -65.7 | -66.4 | -68.9 | -70.9 | -75.3 | -77.8 | -80.6 | -78.5 | -79.1 | -79.6 |
| 91-120 | -72.7 | -67.9 | -64.0 | -68.3 | -71.3 | -75.8 | -75.1 | -77.3 | -77.8 | -79.6 | -79.6 | -80.1 |
| 121-150 | -77.6 | -72.5 | -59.4 | -73.7 | -72.6 | -73.8 | -76.7 | -78.8 | -68.9 | -80.6 | -76.4 | -79.3 |
| *Avg. depth* | *>1000* | *287* | *198* | | | | | | | | | |

**Mean Sv (dB)**
- >=-63.5
- -63.6 to -66.5
- -66.6 to -69.5
- -69.6 to -72.5
- <=-72.6

## Midway Atoll

### Transect A

| Depth (m) | 0030 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | 0300 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | 0530 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | Day Shb1 | Shb2 | Shb3 | Shb4 | Shb5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-30 | -65.7 | -65.8 | -67.2 | -67.8 | -65.5 | -65.5 | -68.9 | -70.7 | -64.8 | -60.4 | -67.0 | -68.5 | -67.8 | -67.1 | -65.6 | -67.7 | -76.9 | -64.5 | -67.7 | -68.3 |
| 31-60 | -67.7 | -64.5 | -61.6 | -59.5 | -58.8 | -66.2 | -64.5 | -64.7 | -58.5 | -53.6 | -71.1 | -73.5 | -69.5 | -63.4 | -71.0 | -67.4 | -69.3 | -74.8 | -69.5 | -76.8 |
| 61-90 | -65.0 | -62.7 |  |  |  |  | -64.2 | -61.2 |  |  |  | -71.1 | -75.0 |  |  |  | -75.8 | -79.0 |  |  |
| *Avg. depth* | *86.0* | *69.8* | *53.9* | *45.5* | *43.7* | | | | | | | | | | | | | | | |

West ⟷ East

### Transect B

| Depth (m) | 0030 Edg | Slo1 | Shb | Slo2 | Slo3 | 0300 Edg | Slo1 | Shb | Slo2 | Slo3 | 0530 Edg | Slo1 | Shb | Slo2 | Slo3 | Day Edg | Slo1 | Shb | Slo2 | Slo3 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-30 | -68.7 | -69.3 | -65.9 | -65.2 | -66.3 | -66.9 | -64.3 | -64.9 | -65.8 | -68.7 | -66.9 | -68.9 | -70.7 | -70.5 | -70.0 | -72.9 | -75.6 | -73.6 | -71.6 | -71.4 |
| 31-60 | -71.7 | -70.2 | -66.9 | -64.7 | -63.3 | -67.1 | -68.1 | -69.6 | -70.0 | -68.0 | -71.8 | -71.0 | -73.2 | -74.6 | -77.3 | -73.7 | -73.9 | -72.5 | -72.2 | -72.4 |
| 61-90 | -70.2 | -68.0 | -67.8 | -65.6 | -67.4 | -73.1 | -74.3 | -71.7 | -71.9 | -70.8 | -72.8 | -68.8 | -77.2 | -82.2 | -83.4 | -77.8 | -79.7 | -80.3 | -78.5 | -79.3 |
| 91-120 | -71.7 | -71.7 |  | -71.9 | -73.3 |  |  |  | -75.1 | -74.0 | -66.2 | -68.8 |  | -79.6 | -76.4 |  |  |  | -81.3 | -81.6 |
| 121-150 | -72.1 | -71.9 |  | -74.0 | -79.6 | -73.3 | -77.2 |  | -75.2 | -79.5 | -63.4 | -66.9 |  | -79.0 | -83.1 | -80.1 | -81.6 |  | -80.5 | -81.5 |
| 151-180 | -64.3 | -63.9 |  | -72.4 | -79.3 | -64.5 | -70.2 |  | -74.9 | -78.2 | -64.5 | -67.1 |  | -78.2 | -81.5 | -76.6 | -77.5 |  | -79.6 | -80.8 |
| *Avg. depth* | *190* | *183* | *98.3* | *231* | *366* | | | | | | | | | | | | | | | |

## Kure Atoll

### Transect A

| Depth (m) | 0030 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | 0300 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | 0530 Shb1 | Shb2 | Shb3 | Shb4 | Shb5 | Day Shb1 | Shb2 | Shb3 | Shb4 | Shb5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-30 | -67.9 | -68.1 | -69.7 | -67.4 | -66.1 | -70.4 | -69.6 | -68.4 | -70.1 | n/a | -71.9 | -70.9 | -71.7 | -72.2 | -71.7 | -73.6 | -72.7 | -75.9 | -72.8 | -70.3 |
| 31-60 | -68.0 | -68.5 | -68.8 | -67.9 | -66.9 | -71.7 | -67.8 | -68.4 | -70.5 | n/a | -72.8 | -74.4 | -79.0 | -81.4 | -79.3 | -76.4 | -74.8 | -80.9 | -76.9 | -76.5 |
| *Avg. depth* | | | *55.4* | | | | | | | | | | | | | | | | | |

North ⟷ South

### Transect B

| Depth (m) | 0030 Edg1 | Edg2 | Edg3 | Edg4 | Edg5 | 0300 Edg1 | Edg2 | Edg3 | Edg4 | Edg5 | 0530 Edg1 | Edg2 | Edg3 | Edg4 | Edg5 | Day Edg1 | Edg2 | Edg3 | Edg4 | Edg5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10-30 | -71.1 | -71.4 | -71.7 | -71.7 | -71.3 | -71.1 | -71.7 | -72.9 | -72.3 | -71.5 | -71.7 | -73.0 | -72.6 | -73.7 | -73.9 | -73.7 | -74.6 | -71.6 | -72.4 | -74.0 |
| 31-60 | -71.1 | -71.0 | -71.6 | -71.4 | -72.7 | -72.0 | -72.0 | -71.6 | -70.8 | -71.4 | -70.0 | -73.2 | -77.3 | -77.6 | -78.2 | -74.7 | -71.2 | -73.6 | -74.7 | -74.7 |
| 61-90 | -75.4 | -76.6 | -73.5 | -72.6 | -72.5 | -76.6 | -75.9 | -68.0 | -71.0 | -70.1 | -68.1 | -73.6 | -83.1 | -82.6 | -82.6 | -83.4 | -81.3 | -76.7 | -75.1 | -81.5 |
| 91-120 | -73.8 | -73.9 | -68.4 | -68.1 | -65.6 | -67.2 | -68.6 | -65.3 | -68.8 | -67.9 | -65.3 | -74.7 | -77.3 | -82.4 | -82.5 | -84.6 | -84.5 | -84.3 | -79.9 | -81.1 |
| 121-150 | -69.1 | -65.4 |  |  |  | -62.9 | -62.5 |  |  |  | -69.9 | -68.9 |  |  |  | -83.0 | -83.0 |  |  |  |
| 151-180 | -61.9 |  |  |  |  | -62.4 |  |  |  |  | -69.6 |  |  |  |  | -74.9 |  |  |  |  |
| *Avg. depth* | *175* | *156* | *127* | *118* | *116* | | | | | | | | | | | | | | | |

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# BATHYMETRIC ATLAS AND WEBSITE
# FOR THE NORTHWESTERN HAWAIIAN ISLANDS

BY

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## ABSTRACT

Until recently the only bathymetric data available in the Northwestern Hawaiian Islands (NWHI) came from single-beam charting surveys that were conducted before World War II. In many cases these data were poorly located, and individual banks could be mischarted by several kilometers. Because detailed bathymetric data are required for a variety of management and research purposes, including designation of boundaries for the NWHI Coral Reef Ecosystem Reserve, updating of nautical charts, and for ecosystem-based management (e.g., formulating benthic habitat maps and designating essential fish habitat), a consortium of National Oceanic and Atmospheric Administration (NOAA) and University of Hawaii scientists are collaborating to make data collected during mapping expeditions to the NWHI available to the public. Bathymetric data collected through August 2003 are combined to provide a baseline for planning future expeditions and for scientific and management use. Thirty maps span the NWHI from Kure Atoll to western Kauai. IKONOS satellite data provide sufficiently reliable estimated depths only to 16 m for the shallowest banks and islands. LIDAR data (0-30 m) are available at Kure, Midway, and Pearl and Hermes Reef.; mid-depth (15-100 m) multibeam coverage is 80% complete at Midway while all other areas have limited coverage at the 50-m boundary line.; deeper multibeam coverage (100-600+ m) is available from Nihoa to Lisianski Island, and limited multibeam coverage exists in depths greater than 600m. Methods used for registration and processing of the data are described, statistics are presented for the amount of area surveyed to date, and estimates are provided for level of effort to complete surveying in the NWHI.

## INTRODUCTION

The Northwestern Hawaiian Islands (NWHI) is a chain of small islands and submerged banks stretching approximately 2,200 km west-northwest from the Main Hawaiian Islands (MHI) to Kure Atoll. In December 2000, the Northwest Hawaiian

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Islands Coral Reef Ecosystem Reserve (CRER), which is estimated to cover 351,195 km², was created by Executive Order 13178. Because this region was last surveyed in the 1930s, data on nautical charts were inaccurate (Evans et al., 2004), particularly with respect to horizontal positioning of the sounding data, and insufficient to define depth-dependent management boundaries (Table 1) that are needed for use in the NWHI CRER. In addition to improving charting and boundary designations, better mapping data are needed to fulfill requirements of a number of other federal statutes, and initiatives also require mapping data, including (e.g., the Endangered Species Act, the Magnuson-Stevens Fishery Conservation and Management Act, and the Coral Reef Conservation Program's (CRCP) plan to map all U.S. coral reefs by 2009).

Table 1. NWHI CRER boundary information required. Italics represent boundaries not mapped in 2002.

| Boundary (fm) | Boundary (m) | Island/Reef/Bank Where Boundary is Required (Minimum Set of Boundaries) |
|---|---|---|
| 25 | 46 | *Nihoa*, Necker, Gardner, Maro, Lisianski, |
| 50 | 92 | Laysan |
| 100 | 183 | Nihoa, Necker, French Frigate Shoals, Gardner, Maro, Laysan, Lisianski, *Pearl and Hermes*, *Kure* |

      In 2002, NOAA and University of Hawaii scientists collaborated on a NWHI cruise to define these boundaries and to satisfy other urgent management requirements. Numerous NOAA agencies, including the National Marine Sanctuaries' (NMS) CRER, the CRCP, the Pacific Island Fisheries Science Center's (PIFSC) Coral Reef Ecosystem Division (CRED), the Western Pacific Regional Fishery Management Council (WPRFMC), and the Office of Coast Survey (OCS) provided funding and personnel for this collaborative cruise. The University of Hawaii's (UH) Hawaii Mapping Research Group (HMRG) and the Hawaii Undersea Research Laboratory (HURL) also provided personnel and support during cruise KM0206 aboard UH's R/V *Kilo Moana*. In order to most efficiently plan for mapping the required boundaries, NOAA and UH scientists combined existing bathymetric data from single-beam and multibeam echosounders, airborne LIDAR data, and "estimated depths" from IKONOS satellite imagery (Stumpf and Holderied, 2003). During the 26-day cruise in October/November 2002, all required boundaries except for those indicated in italics in Table 1 were mapped. The bathymetric data from the two *Kilo Moana* multibeam sonars were processed on board the vessel, and 27 maps were produced. The cruise data were processed independently by participants from NOAA's OCS and are being used to update nautical charts. Over 38,000 km² were mapped, primarily in water depths of 40-2,000 m.

      NOAA and UH scientists cooperatively produced the *"Bathymetric Atlas of the Northwestern Hawaiian Islands: A Planning Document for Benthic Habitat Mapping,"*

a draft of which was introduced at the May 2003 NWHI science workshop sponsored by NMS. Multibeam and single-beam bathymetry, LIDAR data, and IKONOS-estimated depths were combined to produce a series of 30 maps for the atlas. Additional data collected at Midway in August 2003 using CRED's 25-ft. survey launch R/V *AHI* (Acoustic Habitat Investigator) are being presented here. These data are not included in the printed atlas, but have been added to a Web version (http://crei.nmfs.hawaii.edu/ BathyAtlas). Periodic updates to both printed and Web versions of the atlas are planned as new data become available from further mapping in the NWHI.

## METHODS

Depth data described in this paper were produced from single-beam and multibeam sonars, an aerial LIDAR system, and IKONOS satellite imagery. Each of the data sources for the atlas and Website data are described with a discussion of characteristics and accuracy.

Sonar Data

A sonar (Sound Navigation And Ranging) uses one or more transducers to project sound down through the water column; the sound waves are reflected by the seafloor and received at the survey vessel by the sonar receiver(s). The time between the transmission of the sound, termed "ping,", and the resulting echo from the seafloor is measured accurately and combined with information about the speed of sound in water to calculate the water depth. (water depth = sound velocity/time). Single-beam sonars produce only a single sounding directly underneath the vessel with each ping, while multibeam sonars are designed to produce numerous depth measurements (multiple beams form a "swath") perpendicular to the survey vessel's track out to angles as wide as a total swath width of 150 degrees (~7.5 times water depth). In order to provide accurate positions and depths, multibeam sonars are coupled with GPS-based navigation sensors and motion sensors that measure vessel pitch, roll, heave, heading, and yaw. Single-beam sonars also require accurate navigation, but generally no high-resolution motion sensors. Depending upon transmitter and receiver configurations, the beam size, number of beams, and accuracy can vary widely.

Simrad EK50 single-beam sonar data were collected aboard the NOAA Ship *Townsend Cromwell* along the entire NWHI chain in 2001 and 2002. Ship position from shipboard GPS sensors was integrated with the depth data in real time. The data collection software that was used averages the incoming signal over five pings to reduce noise in the waveform data that also are collected. This averaging, as well as the large size of the beam, can reduce the accuracy of the output by as much as a factor of 10, and a single depth value can represent relatively large, averaged areas of the seafloor. Depth spikes were manually removed from the data. A ship's draft correction of 3.5 m also was also applied in post-processing. The sound velocity used for calculation of water depth was 1,500 m/sec.

Archival National Ocean Service (NOS) depth data, some of which dates back to the 1930s, also were used in limited areas; these were obtained from the National Geophysical Data Center. Multiple-source files were consolidated into single files for each bank and converted from the Old Hawaiian datum into NAD83. Metadata for each NOS data set used in the atlas have been developed to the extent possible, given the lack of documentation available for the original surveys. Based on GPS surveys of the emergent land areas in the NWHI conducted in 1999, sounding data for atolls with emergent land areas were relocated into positions that matched the GPS surveys. The assumption used for these position shifts was that the sounding data were internally consistent for each island group, even though they were not in the correct position. Only those areas with emergent lands (Laysan, Lisianski, Midway) to use as reference points were shifted successfully. Raita Bank and Brooks Banks bathymetry data were not moved, nor were data from Maro Reef, due to a lack of visible reference points. Of the sonar data used, these data must be considered to have the lowest accuracy.

Simrad EM120 multibeam bathymetry and imagery data were collected aboard the *Kilo Moana* between Kauai and Lisianski Islands on cruise KM0206 in depths of ~100 m and greater. The EM120 is a 12-kHz, 191-beam, bathymetric sonar system capable of hydrographic charting and seafloor acoustic backscatter imaging in water depths up to 11,000 m. Angular coverage is up to 150 degrees depending on depth, and beams are 1x2 degrees. Width of coverage is generally six times water depth up to 2,000 m, with a maximum swath width of 20 km. GPS data in the WGS-84 datum were obtained from an Applanix POS-MV model 320, which also measured pitch, roll, yaw, and heave. These position and motion data, as well as corrections for sound velocity, were integrated into the multibeam data in real time, but no tidal corrections were made. The bathymetry data were processed using a combination of Science Applications International Corporation's (SAIC) SABER software (Simmons et al., 2001), MB-System (Caress and Chayes, 1995), and Generic Mapping Tools (GMT) (Wessel and Smith, 1998). Bathymetric data were processed aboard ship using SABER to remove artifacts manually; preliminary grids also were also produced aboard ship using GMT and MB-System. No significant biases were observed in the EM120 bathymetric data.

Simrad EM1002 multibeam sonar bathymetry and imagery data were collected on KM0206 in depths of ~20-1,000 m. The EM1002 is a 95-kHz, 111-beam system with an angular coverage of up to 150 degrees. The width of the coverage is about 1,500 m in deeper waters (7.4 times water depth in shallower water), and beams are 2x2 degrees in size. EM1002 multibeam and backscatter data were collected and processed at sea identically to the EM120 data. A systematic sinusoidal bathymetry anomaly was observed in flat, shallow areas during periods of large swells, and analysis indicated the anomaly resulted from improper heave correction. The magnitude of this error (<0.4 m) is within system specifications. While the shallow data are certainly usable as bathymetry, caution must be used when interpreting the data so that the sinusoidal artifact is not assumed to be sand waves.

SeaBeam 210 multibeam sonar bathymetry data were collected aboard the UH R/V *Kaimikai-O-Kanaloa (KOK)* in 2000-2002. The SeaBeam 210 multibeam sonar system installed aboard the *KOK* is a 12-kHz, 16-beam, hull-mounted, roll- and- pitch-

compensated, bathymetric deep seafloor mapping system capable of ensonifying a swath equal to 70-80% of the water depth. SeaBeam 210 does not have backscatter capability. The SeaBeam data were processed by HURL personnel using MB-System, and some artifacts remain in the data, particularly in shallow waters for which this low-frequency system is not designed.

Reson 8101ER multibeam sonar bathymetry and imagery data were collected using the NOAA survey launch R/V *AHI*, which was deployed only at Midway from the NOAA Ship *Oscar Elton Sette* in August 2004. The Reson 8101 is a 240-kHz, 101-beam system with an angular coverage of up to 150 degrees, has a maximum swath width of ~350 m, and a depth range of ~250+ m. Navigation and attitude data were obtained from an Applanix POS-MV and integrated using SAIC's ISS-2000 real-time survey system. Corrections for sound velocity, pitch, roll, heave, draft, and predicted tides were applied to the data in real time. The bathymetry data were processed using SAIC's SABER software to manually remove artifacts and to recorrect for verified Midway tides and sound velocity.

## Aerial and Satellite Data

LIDAR bathymetric data were obtained using the airborne LADS MKII system at Kure Atoll, Midway Atoll, and Pearl and Hermes Atoll. These data were collected for comparison with the IKONOS-estimated depth data (Stumpf and Holderied, 2003). The aircraft ground speed is about 150 knots, resulting in a 4x4-m laser spot spacing across a swath of ~200 m. The maximum water penetration (where a return was reported) in the clearest water in this area exceeded 60 m. The survey met International Hydrographic Standards for accuracy of order 1. Vertical precision of measured relative water depth was 0.5 cm, as indicated by the cross-line comparisons. To determine height relative to mean lower low water, the standard datum for bathymetry, a tidal correction for Midway Island was applied (80 km from Kure and 130 km from Pearl and Hermes) because tide gauges were not present at either Kure or Pearl and Hermes.

IKONOS-estimated depth data are derived from 4-m multispectral imagery. The IKONOS satellite system provides multispectral data with three visible bands (blue, green, red) and one near-infrared (near-IR) band. IKONOS data were collected primarily to provide information for benthic habitat analysis in the NWHI (NOAA Publication 2003), but it was also possible to derive estimated depths from these data. Two algorithms were used to derive estimated depths. The standard bathymetry algorithm has a theoretical derivation (Lyzenga, 1978) but also incorporates empirical tuning as an inherent part of the depth-estimation process. A new depth-estimation model, developed by Stumpf and Holderied of NOAA's Biogeography Program, used the reflectance for each satellite imagery band, calculated with the sensor calibration files and corrected for atmospheric effects. Estimated depth data from both methods were compared with the LADS LIDAR data. Although Stumpf and Holderied's method allows calculation of estimated water depths in deeper waters, only estimated depth data down to 16 m were selected for inclusion in this atlas, due to uncertainty levels up to 30% in deeper water.

Data Synthesis

After processing the individual data types using appropriate methods, data were combined using MB-System and GMT. In these grids, data are prioritized by using the data with highest accuracy for each grid cell, so that *Kilo Moana* and *AHI* multibeam data are used whenever available, followed by LIDAR data, IKONOS-estimated depths, *KOK* multibeam data, and, last, single-beam values.

## RESULTS

The first draft of the *Bathymetric Atlas of the NWHI* was presented at the May 2003 NWHI Symposium; these data were used as input to NOAA's *"Mapping Moderate Depth Habitats of the U.S. Pacific Islands with Emphasis on the Northwestern Hawaiian Islands: an Implementation Plan,"* vol. 2, August 2003, and gridded data products were made publicly available at http://crei.nmfs.hawaii.edu/BathyAtlas in January 2004. NMS published the printed atlas (Miller et al., 2004), and copies were made available in November 2004 at the NWHI Third Symposium.

In the *Bathymetric Atlas of the NWHI*, 30 chart areas are used to display the NWHI area. A series of four figures is presented for each of 30 charts. Each four-page group of figures (Fig. 1) in the atlas includes maps "a", "b", "c", and "d.". Map "a" displays the location of each individual map (bold) in relation to all other maps. The bathymetry data shown in the "a" charts are predicted from satellite altimetry. The "b" plot represents only acoustic or satellite sources that provide both imagery and bathymetry data, and all data presented in the "b" plots were gridded at 60-m grid cell size. Map "c" displays the composite maps of all data sources, including IKONOS, EM-120, EM-1002, LIDAR, CRED, and NOS single-beam data. All data, except for the two single-beam data sources, were gridded at a 60-m grid cell size using MB-System. The single-beam data are not gridded, but plotted over the underlying grids as points. Map "d" shows the locations of each different data types as point plots; multibeam data points are decimated by a factor of 100. All of these figures are also available for download at the BathyAtlas web site.

Multibeam- and IKONOS-estimated depth data were combined for Midway Island as shown in Figure 2. These high-resolution bathymetric data show extensive spur and groove formations on the NW side of the Midway reef crest (Fig. 3) and provide evidence for possible previous stands of the sea at ~ 45- and 60-m depths.

## DISCUSSION

Because of the need for accurate base maps, it is important to understand how much and what kind of mapping has been done, what mapping needs to be done, in what water depths, priorities for mapping specific areas or depth ranges, and how long it might take to complete this mapping using candidate technologies.
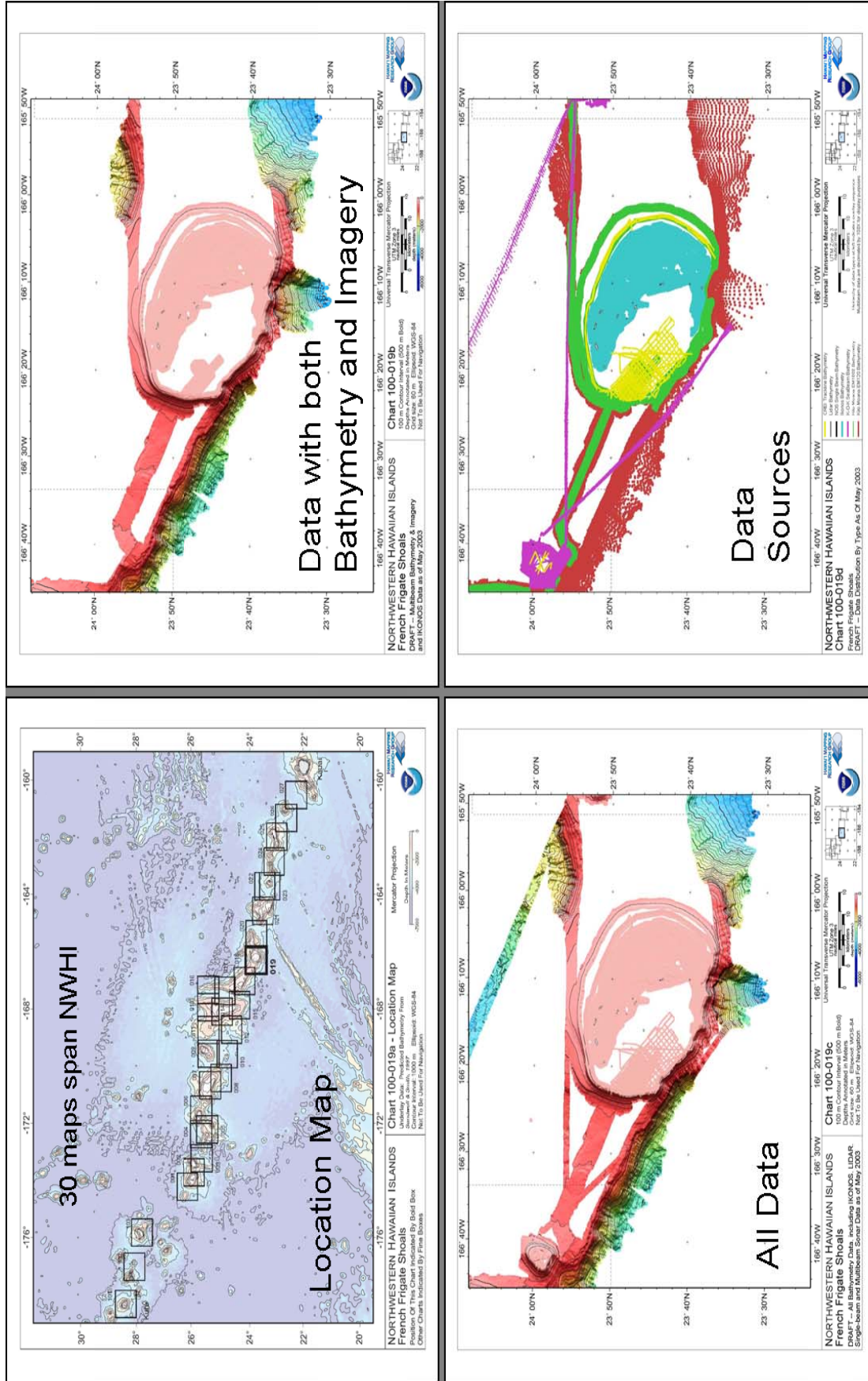
**Figure 1.** Example "a," "b," "c," and "d" maps from Bathymetric Atlas of NWHI. See website at http://crei.nmfs.hawaii.edu/BathyAtlas/.
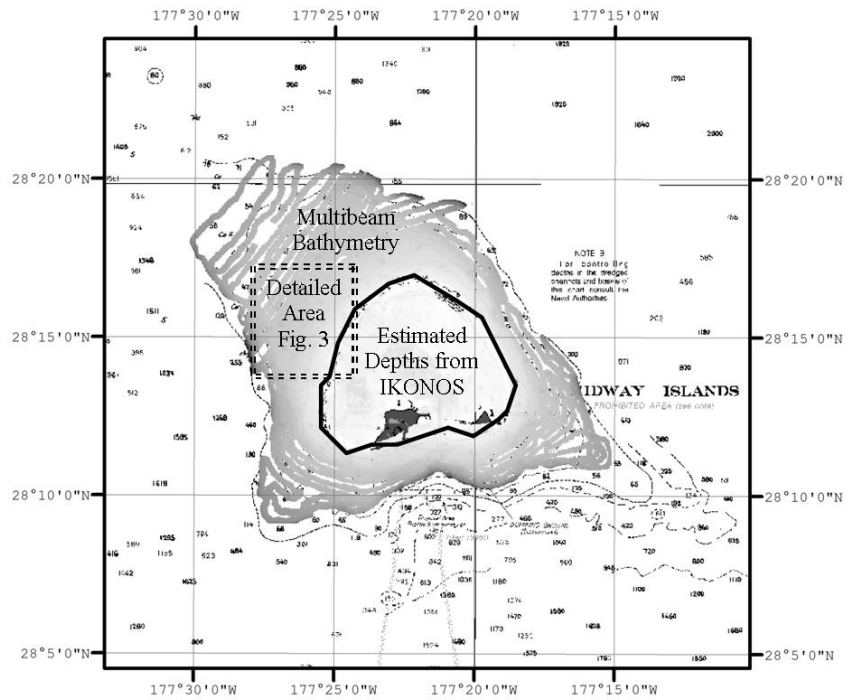
**Figure 2.** Hillshade of Midway multibeam and IKONOS-estimated depth data.
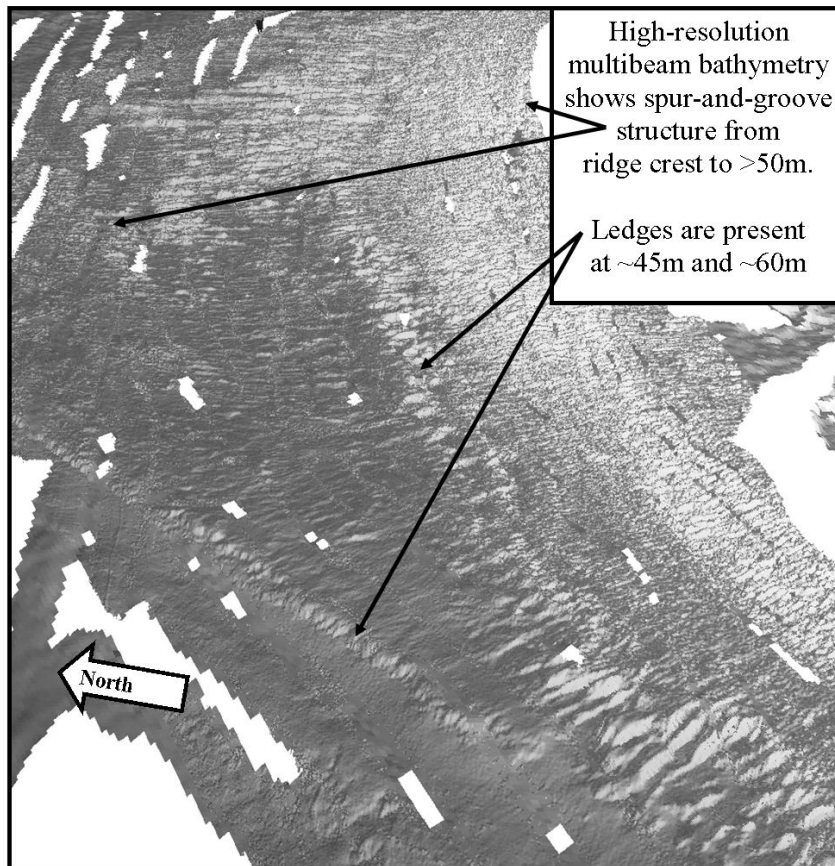


**Figure 3.** Detail of Midway multibeam hillshade on the NW side of the bank.

Mapping Estimates

In Table 2 we present an analysis of areas by water depth (in fathoms, because fathoms are used on existing nautical charts) included in the NWHI. These estimates were made as part of the document *Mapping Moderate Depth Habitats of the U.S. Pacific Islands with Emphasis on the Northwestern Hawaiian Islands: an Implementation Plan*. The CRER encompasses a total of 351,195 km$^2$ of which 13,708 km$^2$ are in the 0-100 fm range that is of primary interest for coral reef managers.

After presentation of the *Bathymetric Atlas of the NWHI* at the May 2003 NWHI Symposium, NMS identified the needs for statistics regarding how much mapping had been done. NMS incorporated these statistics (Table 3) into the atlas and published the final printed document. The areal extents of existing bathymetry data in the five depth ranges (0-10 fm; 10-100 fm; 100-200 fm; 200-500 fm; and greater than 500 fm) shown in Table 3 are subtracted from the total CRER areas shown in Table 2 to provide an estimate of the remaining areal extent that still needs to be mapped in the NWHI CRER. The results are presented in Table 4. Table 4 illustrates that the area within the 0-10 fm boundaries are 99% completed using derived depths from IKONOS imagery, but the critical 10-100 fm area that must be mapped using multibeam sonars is only 45% complete. Note that the total area in Table 2 in less than 10 fathoms (~18 m) of water is estimated at less than the actual area already mapped shown in Table 3. This is the result of inaccuracies in the older nautical charts as well as the methods used for estimation; however, the overall rough estimates are sufficient to determine approximately how much area is left to be mapped.

Mapping Capabilities and Operational Estimates

The primary systems and vessels for mapping in the NWHI in the immediate future are the NOAA Ship *Hi'ialakai*, which had two multibeams installed in early 2005 (mapping capability 10-3,000+ m); the NOAA survey launch R/V *AHI* (mapping capability 5-250+ m); and the NOAA Ship *Oscar Elton Settee,* which has no multibeams, but is used to collect a variety of other data.

To determine how long it might take to map specific areas, an understanding of operational factors is required. The four primary operational parameters affecting survey efficiency are: water depths and corresponding swath widths of individual sonars; vessel speed required to produce acceptable data; survey standards that must be met for data collection (e.g., density and overlap of data); and weather and sea conditions. A number of assumptions are necessary to produce realistic estimates:

- Average effective swath width of sonars on *AHI* and *Hi'ialakai* is assumed to be five times the water depth until limits of range are reached. On the *AHI,* the maximum swath width of ~350 m is reached in 70-m water depth and then remains constant to depths of up to 300 m.
- Almost all mapping (except for Midway) that has been done to date in the 120-1200-fm range was done as part of 2002 boundary surveys in the deeper part of this range (50 m and greater). Because surveying in shallower water is much more time consuming than surveying in deeper water, estimates in this depth range are being made for 30-40 m where the majority of the bank tops in the NWHI are located.

Table 2: Estimates of total NWHI areas based upon nautical chart information.

| Area Description | Area (km$^2$) |
|---|---|
| NWHI CRER | 351,195 |
| Area Between 0-10 fm (0-18 m) | 1,541 |
| Area Between 10-100 fm (18-183 m) | 12,167 |
| Area Between 100-1,000 fm (183-1830 m) | 46,435 |
| Area in CRER > 1,000 fm (> 1830 m) | 304,760 |

Table 3: Estimates of areas mapped in the NWHI as of November 2004.
(See Bathymetric Atlas of NWHI for estimates of areas for specific banks)

| Mapped Areas (in square kilometers) | | | | | | Bathymetry Data (in linear nautical miles) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Less than 10 fm (18 m) | Between 10-100 fm (18-183 m) | Between 100-200 fm (183-366 m) | Between 200-500 fm (366-915 m) | Greater than 500 fm (915 m) | IKONOS | K-O-K SeaBeam | Kilo Moana EM1002 / EM120 | CREI Single Beam | LIDAR | NOS Single Beam |
| 1,759 | 5,478 | 2,454 | 6,550 | 53,778 | 1,848 | 7,946 | 57,509 | 5,157 | 181 | 26,952 |

Table 4. Estimates of area remaining to be mapped in NWHI as of Nov. 2004.

| Area Description | Total Area (km$^2$) | Area Mapped (km$^2$) | Remaining to be Mapped (km$^2$) | % Mapped |
|---|---|---|---|---|
| NWHI CRER | 351,195 | 70,018 | 281,177 | 19.9% |
| NWHI 0-10 fm* (0-18 m) | 1,541 | 1,759 | 0* | 99.9% |
| NWHI 10-100 fm (18 -183 m) | 12,167 | 5,478 | 6,689 | 45.0% |
| NWHI 100-1000 fm** (183-1830 m) | 46435 | 35,893 | 10,542 | 77.3% |
| CRER > 1000 fm*** | 304,760 | 26,887 | 277,874 | 8.8% |

\*      Incorrect initial estimation of total area inside the 10 fm (18 m) boundary.

\*\*      Area mapped between 100-1000 fm (183-1830 m) was calculated using Table 3 100-200 fm plus 200-500 fm plus one-half of area greater than 500 fm.

\*\*\*      Area mapped CRER greater than 1,000 fm (1830 m) was calculated using one-half of area greater than 500 fm.

- Minimal overlap will be needed in water depths less than 20 m. In general, multibeam mapping will not be attempted in 0-20 m depths.
- Ninety-five percent coverage of all areas is desirable.
- No mapping will be planned in depths greater than ~3,000 m due to sonar limitations.
- Mapping speeds required for acceptable data quality will be calculated at 5-7 knots in water depths less than 100 m and 10 knots on the ship in greater water depths.
- Multibeam data will be collected for 8 hrs/day using survey launch and 10 hrs/day on multimission cruises.  On dedicated mapping cruises, this estimate of 10 hrs/day is also used, because it is critical also to collect photographic and video validation data in order to create benthic habitat maps.
- In general, it is wise to make conservative assumptions with respect to weather; sea conditions; operational needs such as conductivity, temperature, and depth (CTD); equipment failure; transits; and survey efficiency.  A conservative estimate of 50% efficiency is commonly used.

Table 5 presents ship and launch survey efficiencies, given the assumptions above. From this table it can easily be seen that surveying in the shallow (10-50 fm) areas that make up a large portion of the NWHI is a very slow process. CRER banks cover only ~6.7 km² per day, compared to over 1,000 km² per day in the 1,000-1,500-fm depth range.

Table 5.  Survey efficiencies.

| Water Depth Ranges (fm) | Average Depth (m) | Vessel | Speed (kts) | Speed (km/hr) | Swath Width (km) | Coverage (km²/hr) | Hrs/ Day | Coverage (km²/day) | Effi- ciency | Adj. Coverage (km²/day) |
|---|---|---|---|---|---|---|---|---|---|---|
| 10-100 | 30 | Either | 6 | 11.1 | 0.15 | 1.7 | 8 | 13.3 | 0.5 | 6.7 |
| 10-100 | 75 | Ship | 8 | 14.8 | 0.375 | 5.56 | 10 | 55.6 | 0.5 | 27.8 |
| 100-1000 | 1000 | Ship | 10 | 18.5 | 5 | 92.6 | 10 | 926 | 0.5 | 463 |
| 1000-1500 | 2500 | Ship | 10 | 18.5 | 12.5 | 231.5 | 10 | 2315 | 0.5 | 1157.5 |

Applying these metrics to the overall NWHI areas allows a rough estimation of the time it could take to map in the NWHI (Table 6).  The 120-1,200-fm banks have been divided into two separate areas. The first is based upon an estimation that 80% of the bank areas occur in approximately 10-25-fm of water and that either the *AHI* or the *Hi'ialakai* might be used to map in these areas at speeds of 5-7 knots. The second division is based upon the assumption that the *Hi'ialakai* would be used to map in the steep deeper areas that make up an estimated 20% of the 50-100-fm area.  Approximately 803, 10-hr survey days are estimated for mapping the 10-25-fm areas, while only ~311 days are required to map in waters greater than 25 fm.

Table 6.  Estimation of time needed to map NWHI CRER.

| Area Description | Remaining to be Mapped (km$^2$) | Adj. Coverage (km$^2$/day) | 10-hr Survey Days |
|---|---|---|---|
| NWHI CRER | 281,177 | | **1114** |
| NWHI 0-10 fm (0 – 18 m) | 0 | | |
| NWHI 10-100 fm (18-183 m) (80% - AHI or ship) | 5351 | 6.7 | **803** |
| NWHI 10-100 fm (18 – 183 m) (20% - Ship only) | 1337 | 27.8 | 48 |
| NWHI 100-1000 fm (183-1830 m) | 10,542 | 463 | 23 |
| CRER > 1000 fm (> 1830 m) | 277,874 | 1157.5 | 240 |

Mapping Priorities

   Given the extensive areas to be mapped and the number of days needed to map these areas, a unified mapping strategy must be adopted to map priority areas most efficiently. Furthermore, numerous groups have priorities for mapping in the NWHI, including NMS, CRER, CRCP, WPRFMC, the Pacific Islands Regional Office (PIRO), and USFWS. In preparation of the *Pacific Moderate Depth Mapping Implementation Plan*, a survey was done of NWHI stakeholders to determine what depths are of greatest interest for mapping.  The consensus was that boundaries needed for management decisions are the first mapping priority; areas in waters between 20 and 400 m were the second priority, because these areas are critical to bottomfish fisheries in the area; completion of aerial or satellite mapping in waters less than 20 m is third priority, but these areas already are covered relatively well by IKONOS imagery; and that water depths greater than 400 m are of lowest priority.

        In terms of which specific islands, atolls, and banks should be mapped and when, stakeholders have been queried several times over the past 2 years to determine changing priorities as mapping has progressed.  The current consensus for prioritization of future multibeam mapping in the NWHI can be summarized as follows:

- Finish boundary mapping at Nihoa (25 fm), Kure (100 fm) and Pearl and Hermes (100 fm).
- Map in high-priority management areas where quantities of biological, oceanographic, and habitat data have been collected over the past 4 years in 0-400 m in order to facilitate efficient production of benthic habitat maps. These areas include French Frigate Shoals, Maro Reef, Necker Island, Laysan Island, and Lisianski Island.
- Continue mapping at submerged banks where submersible and bottomfishing data have been collected.

- Continue mapping deeper areas between islands, atolls, and banks on transits between islands.

Suggested strategies for optimizing survey efficiency include:

- Continuous updates of survey coverage are critical to efficient mapping. It is planned that the UH Pacific Islands Benthic Habitat Mapping Center will maintain an up-to-date database of survey coverage in the NWHI.
- Plan mapping expeditions to focus on one particular island, bank, or atoll, rather than mapping small, scattered portions of the chain in a single cruise (e.g., map as much of Kure, Pearl and Hermes, and/or Nihoa as possible when mapping the highest priority boundary areas).
- If it is not possible to cover all of an area at once, determine if perhaps coverage less than the targeted 95% may be an option.
- Begin mapping using widely spaced lines to determine the complexity and variability of habitats around an island, bank, or atoll. Then, if it is not possible to provide 95% or greater coverage, areas of particular interest can be chosen for complete coverage.
- Maximize mapping efficiency by providing guidelines for running transit lines for all *Hi'ialakai* cruises to the NWHI and all ships with multibeam sonars (e.g., *Kilo Moana*) that might be transiting through the area.
- On *Hi'ialakai* cruises, when mapping is not the primary focus of the scientific mission, ensure that personnel are available onboard to run the sonars in cases where no night operations are planned.

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# ECOLOGY AND ENVIRONMENTAL IMPACTS



NOAA Photo by Kyle Koyanagi

# PRECIOUS CORALS AND SUBPHOTIC FISH ASSEMBLAGES

BY

FRANK A. PARRISH[1]

## ABSTRACT

Telemetry studies of monk seal movements at French Frigate Shoals identified two areas where seals were focusing their foraging at subphotic depths. Submarine surveys (1998, 2000, and 2001) were used in these areas to locate beds of deep-water corals. In an attempt to link the density, size, or biomass of subphotic fish (potential seal prey) with the presence of deep-water corals, a comparison of areas with and without deep-water corals was conducted. Areas with tall morpho-types of deep-water corals (e.g., *Gerardia* sp.) often supported greater fish densities than adjacent areas without deep-water corals. The prey-evasion guild of "bottom hiders" was the fish group most commonly seen using the coral branches as shelter. However, an analysis of fish and coral data accounting for habitat effects indicated fish and deep-water corals co-occur in areas of high relief, each likely exploiting improved flow conditions, with little inter-dependence.

## INTRODUCTION

Recent documentation of monk seals (*Monachus schauinslandi*) visiting beds of deep-water corals prompted a hypothesis that seals may have more success in obtaining subphotic prey around deep-water coral beds, because the shelter afforded by the corals continually aggregates fish from the diffuse surroundings. This notion is an extension of findings from foraging research conducted at shallower depths where seals were found to repeatedly target specific foraging habitat types (Parrish et al., 2000), including filamentous deep-water black coral colonies (Parrish et al., 2002). If the French Frigate Shoals (FFS) seal colony is at or approaching carrying capacity for foraging as suggested by some research (Gilmartin et al., 1993; Gilmartin and Eberhardt, 1995), seals may be choosing to dive deeper to explore nearby subphotic depths rather than swim to distant, neighboring banks to feed. Habitats at depths below the photic boundary are understandably less diverse than shallower sites. The lack of scleratinian corals and macroalgae generally leaves only the geologic composition of the substrate and the scale of bottom relief to provide habitat. Patches of deep-water corals are one of the few exceptions that diversify the substrate. It is unknown whether fish (seal prey) are associated with the coral "trees," using them facultatively. This work explores potential links between deep-water corals and the fish assemblages that could be prey for monk

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seals. In particular, two deep-water corals, *Corallium* (pink coral) and *Gerardia* (gold coral) which are targeted commercially, were used to represent the two primary forms of coral trees found among deep-water corals (Fig.. 1). *Corallium* is a crustose octocoral
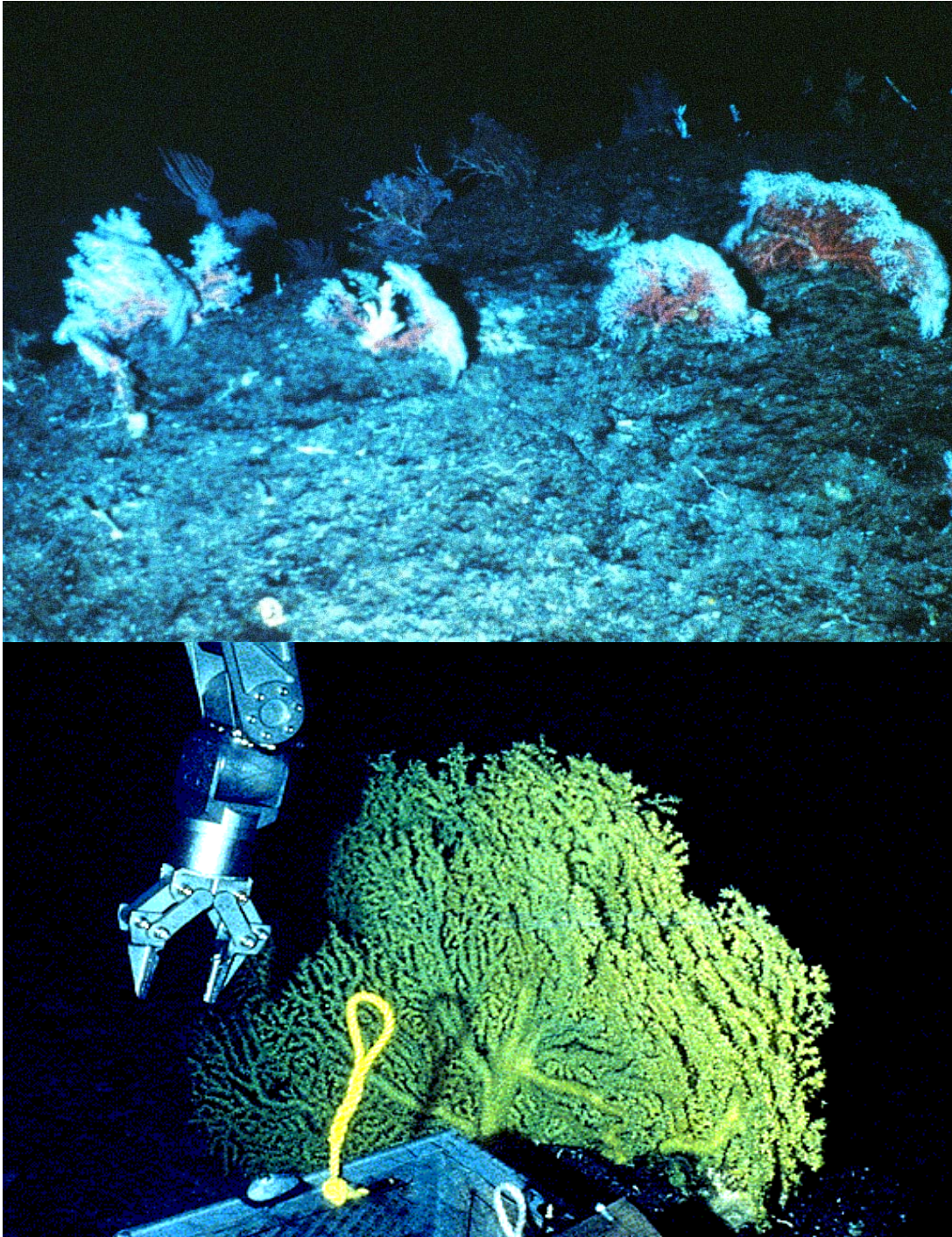


**Figure 1**. Representative morphology of the two genera of deep-water corals assessed in this work. *Corallium* sp. (pink coral) form colonies less the 30 cm in height (top) whereas *Gerardia* sp. (gold coral) grows to 150 cm in height (bottom).

which occurs in pink (*C. secundum*) and red (*C. lauuense*) species reaching heights of 30 cm.  For the purposes of this work, I will refer to all *Corallium* (pink and red) as pink coral.  *Gerardia* sp. is an imposing hexacoral with flexible branches that grows to heights of well over 100 cm.  Both genera are known to colonize locations of high flow (Grigg, 1993) and were found at the two subphotic sites visited by FFS seals.

## METHODS

Submersible Survey Methodology

All the subphotic data were collected in a series of submersible dives using the *Pisces V*, *Pisces IV,* and *RCV-150* to survey depths between 300 and 500 m (1998, 2000, and 2001).  Dive sites, hereinafter referred to as stations, included Makapuu, Keahole, and Cross Seamount in the Main Hawaiian Islands (MHI) and Brooks Bank, East French Frigate Shoals (FFS) Platform, and WestPac Bank in the Northwestern Hawaiian Islands (NWHI) (Fig. 2). Submersible surveys at each station consisted of four transects covering a 3,600 m$^2$ swath of bottom along the 350 m, 400 m, 450 m, and 500 m contours. However, the physiography of the slope varied considerably and often dictated restructuring of transects within the depth range.  The submersibles were three-person vehicles with the pilot situated in the center and observers on either side.  Each person can see an illuminated bottom area of ~55 m$^2$ through view ports directed diagonally forward and down. The cumulative view from the three view ports (adjusted for overlap) provides an effective illuminated survey area of ~120 m$^2$.  A video camera on each side of the submersible was operated continuously, and the edited video feed from the cameras was recorded throughout the dive.  The *RC-150* is a remotely operated vehicle (ROV); the pilot and observers watch a live video feed aboard the ship while the tethered vehicle navigates below.  This camera views a bottom area of ~46 m$^2$ .
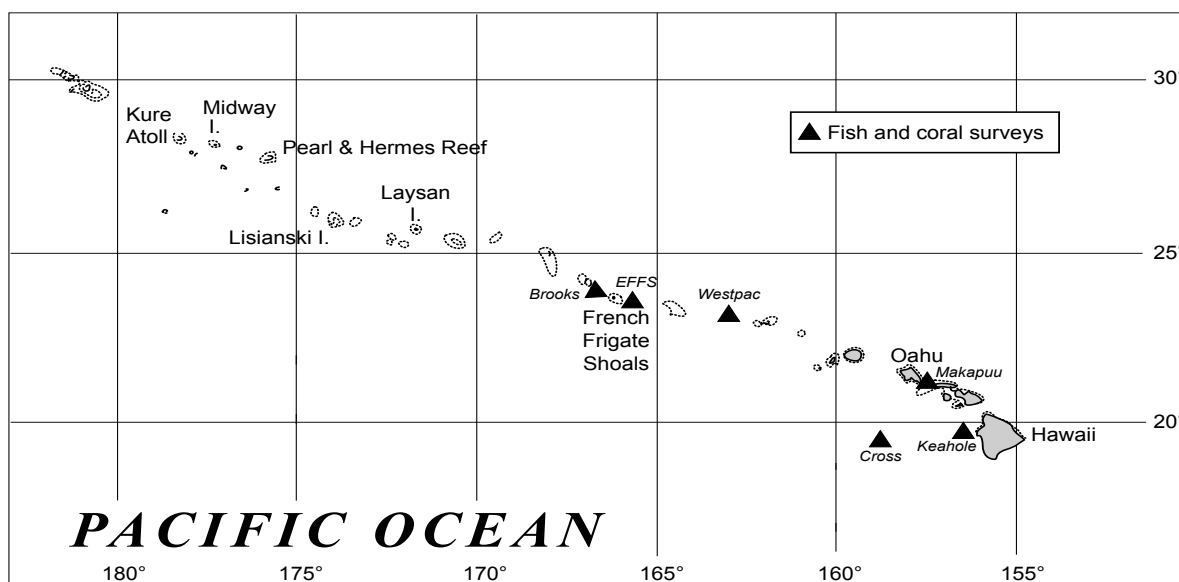


**Figure 2**.  Map of the Hawaiian Archipelago with locations of dive stations.

Fish and corals were identified to genus, if not species, and visual counts of fish with their lengths and corals with their heights were recorded cumulatively for 5-min segments to obtain numerical density and size structure information. A brief break (~30 sec) was taken between each segment. This pseudo replication technique is common in ecological sampling (Oksanen, 2001) and has been used effectively to survey fish assemblages from *Pisces* and *RCV-150* submersibles in prior studies (Moffitt and Parrish, 1992; Parrish et al., 2002). A laser reference scale was projected on the bottom within the view of the video cameras used on each of the submersibles to assist the observers in estimating the lengths of fish and height of corals. In addition to the fauna, the surveys logged substrate type and relief scale using three categories. Substrate was divided into categories of sand, carbonate hard bottom, and basalt/manganese. Relief was divided into categories of flat, even bottom called "hardpan" (< 15 cm relief); uneven bottom "outcrops" (15- 90 cm); and steep surfaces such as "pinnacles" or cliffs (>90 cm). Any fish seen orienting close to a coral tree (presumably using it as shelter) was recorded. All fish taxa were divided into one of four prey-evasion guilds including bottom hider, bottom fleer, bottom camouflage, and midwater fleer.

The opportunistic nature of these submersible surveys and modifications to the study design because of weather and mechanical problems resulted in a temporally unbalanced data set. Surveys were conducted in 1998, 2000, and 2001 during the fall of each year (September to November). For some stations, multiple dives were made in the same year; at other stations dives were separated by years. For this reason, "year" was not included as a variable in the analysis.

Analysis

The fish and coral data were nonnormally distributed, and could not be normalized by conventional transformations. For this reason, all analyses relied on nonparametric techniques. Coral preferences for substrate and relief were assessed using Mann-Whitney (M-W) and Kruskal-Wallis (K-W) tests, respectively. The association of fish with each of the two coral genera was assessed individually. To test the null hypothesis for fish numerical density, fish length, and fish biomass density, all pseudo replicates of sites with corals were pooled and compared to those without corals using a Mann-Whitney test. A Wilcoxon related samples test was run using the variable station to compare pseudo replicates with and without corals. Spearman correlations were used to determine the degree of association between variables identified as relevant in the prior analyses. In circumstances where there was reason to suspect colinearity between explanatory variables, a parametric partial correlation analysis was used to describe the linear association between two variables while controlling for the effects of a third. The size structure of trees that had fish hiding in them was then compared to the size structure of trees without fish to see whether fish preferentially sheltered in the largest trees. Descriptive statistics were computed to describe the species and seal-evasion guilds that comprise the fish assemblages found in the trees. Sample sizes for all analyses were adequate to detected differences at large-effect sizes with alpha at 0.01 and a power of 0.80.

**RESULTS**

Habitat Description

The stations varied in their topography, habitat and corals. Details of the substrate, relief, and coral type for each of the stations are presented in Table 1. Some stations were on summits, such as Cross Seamount, whereas others were on the flanks of islands and shallow banks, such as Brooks Bank or Makapuu Point. The bottom substrate and relief at these sites ranged from a homogenous continuum of one type to a combination of all types at a single site, such as the FFS Platform.

Table 1. Number of pseudo replicates, mean depth, prevalent substrate type, relief type and coral type for each of the known coral beds at various stations in the Hawaiian Archipelago during 1998, 2000, and 2001. FFS stands for French Frigate Shoals.

| Station | No. pseudo replicates | Mean Depth (m) | Primary substrate | Primary relief | Coral type |
|---------|-----------------------|----------------|-------------------|----------------|------------|
| Brooks | 127 | 485 | Carbonate/basalt | Pinnacle | Pink-R* / gold |
| FFS | 275 | 379 | Basalt | Pinnacle | Gold |
| WestPac | 141 | 368 | Carbonate | Hardpan | Pink |
| Makapuu | 126 | 398 | Carbonate | Hardpan | Pink |
| Keahole | 70 | 387 | Carbonate/basalt | Outcrop | Pink-R* / gold |
| Cross | 158 | 389 | Basalt | Pinnacle | Gold |

\* Pink-R indicates *Corallium lauuense*.

Other than a general depth range and the assumption that areas of high water flow over exposed bottom were needed for successful coral growth, there was no basis found for predicting where the coral beds would occur. Coral composition varied among stations. Some stations had more gold coral (*Gerardia* sp.) or more pink coral (*Corallium* sp.). A few stations had the two taxa intermixed (Table 1). Density of coral colonies in the beds was higher for pink coral (mean 88±(sd)149/ha) than for gold coral (mean 42±(sd)54/ha). When a submersible transect first encountered a coral bed, the initial sightings of individual corals would increase quickly to a high numerical density within the span of a single pseudo replicate, making coral presence-absence type analyses viable. Gold coral was found in significantly greater density on manganese/basalt substrate (MW Z=-6.18 P<0.01) and differed by relief type (KW, $\chi^2$=164.9 df=2 P<0.01). *Post-hoc* multiple comparisons attributed the relief significance to greater densities of gold corals encrusting "pinnacle"-type relief versus the flat or outcrop relief types (Tukey Q=11.5 & 12.1, P<0.05). Most of the pinnacles surveyed were composed of manganese/ basalt which probably explained the substrate differences identified above. In contrast, the density of pink coral was significantly higher on carbonate substrate (MW, Z= 83.4, P<0.01) and flat bottom (KW, $\chi^2$=54.9, P<0.01; Tukey Q=5.5 & 6.2, P<0.05).

Fish Diversity, Density, and Biomass

The surveyors counted and sized 13,295 fish in a total of 897 pseudo replicates. Depth was positively correlated with fish size ($r_S$ =0.154, P<0.01) but negatively correlated with fish numerical density ($r_S$ = -0.303, P<0.01). A total of 42 taxa were identified.  Many of these fish were eel-shaped and moved more slowly than shallow-water species.  The number of taxa did not change appreciably between areas with coral (w/gold n=41, w/pink n=39) and those without (w/o gold n=42, w/o pink n=40).  The top 20 taxa identified in this analysis comprised 94% of the total number of fish sampled and are listed in Table 2.  Eleven of these taxa were present at all stations.  The absence of some taxa from some stations did not fit any obvious latitudinal or physiographic pattern.  All taxa were used in the analysis of fish and coral association, because it is not known which of the fish taxa are eaten by seals. Multiple dives at each station generated a median of 150 pseudo replicates for each station.  As with many field studies, it was not possible to balance sampling across substrate, relief, and coral type for all stations, but all types were well represented in the data.

Table 2.  The top 20 fish taxa ranked by the number of pseudo replicates in which each taxon was seen.  Also included is the mean number of fish per pseudo replicate where each taxon was sighted and the seal prey-evasion guild (BC=bottom camouflage, BF=bottom fleer, BH=bottom hider, MF=midwater fleer).

| Rank | Taxa | Mean No. | Evasion guild |
|------|------|----------|---------------|
| 1 | *Symphysanodon maunaloae* | 56.1 | BH |
| 2 | *Polymixia* spp. | 5.6 | BF |
| 3 | *Congridae* | 2.9 | BF |
| 4 | *Scorpaenidae* | 2.0 | BC |
| 5 | *Beryx* spp. | 3.6 | BF |
| 6 | *Myctophidae* | 21.6 | MF |
| 7 | *Hollardia goslinei* | 1.8 | BH |
| 8 | *Epigonidae* | 12.2 | BH |
| 9 | *Moridae* | 1.5 | BF |
| 10 | *Chloropthalmus proridens* | 2.6 | BC |
| 11 | *Antigonia* sp. | 3.0 | BH |
| 12 | *Chrionema chryseres* | 2.5 | BC |
| 13 | *Owstonia* sp. | 2.2 | BF |
| 14 | *Grammicolepis brachiusculus* | 1.7 | MF |
| 15 | *Grammatonotus* spp. | 13.4 | BH |
| 16 | *Macrouridae* | 1.9 | BF |
| 17 | *Ijimaia plicatellus* | 2.2 | BF |
| 18 | *Chaunax* spp. | 1.2 | BC |
| 19 | *Satyrichthys* spp. | 1.9 | BF |
| 20 | *Synaphobranchidae* | 1.7 | BF |

Effect of *Gerardia* Sp. (Gold Coral)

Gold corals were found at depths from 350 to 516 m (N=199 replicates), and supported significantly greater fish densities (MW, Z= -2.9, P<0.01) than tracts of bottom in the same depth range without gold coral (N=399 replicates). An analysis comparing across related samples (within station) of coral (N=191) to non-coral (191) pseudo replicates similarly indicated significantly greater densities of fish around gold coral (Wilcoxon Z=-3.34, P<0.01). However, persistent high counts of *Symphysanodon maunaloae* at the east FFS station strongly influenced the analysis. If the FFS station is excluded, no difference in numerical density is evident in either the pooled (MW Z= -3.1, P=0.76) or related sample comparison (Wilcoxon Z=-0.316, P=0.75). Fish body size did not differ significantly between sites with gold coral and sites without (MW, Z= -1.0, P=0.312 or Wilcoxon Z=-1.35, P=0.17).

Relief type significantly affected fish numerical density (KW, $\chi^2$=25.5 df=2 P<0.01) and fish size (KW, $\chi^2$=9.1 df=2 P=0.01). Follow-up comparisons indicated that all differences were associated with pinnacle relief. Significantly more fish were found around pinnacles (Tukey, Q= 5.0 & 3.5, P<0.05), and these fish were on average smaller (Tukey, Q= 52.0 & 60.7, P<0.05). A potential for covariance with sources of high relief existed between the fish data and gold coral data, so all the variables with depth were assessed using Spearman correlations. Weak correlations were evident between the density of gold coral and fish numerical density ($r_s$=0.12, P<0.01) and relief scale ($r_s$=0.37, P<0.01). However, the positive association between coral density and fish numerical density was lost ($r_s$=0.02, P=0.34) in a partial correlation when the effects of relief were controlled.

Effect of *Corallium* Sp. (Pink Coral)

Pink coral was documented at depths of 328-573 m. Fish numerical density, length, and biomass density in areas with pink coral (N=312 pseudo replicates) were not significantly different from those without pink coral (N=557 pseudo replicates) within this range (MW, Z= -0.016 to -1.6, P=0.093 to 0.98). Comparing across related samples (within station) of coral (N=215) to non-coral (215) pseudo replicates similarly indicated no significant differences associated with the presence of pink coral (Wilcoxon Z= -0.26 to 1.06, P=0.28 to 0.79). In some beds, the relatively small pink corals are intermixed with the much larger gold corals (Brooks Bank, Cross Seamount, Keahole Point), potentially confounding the comparisons. The analysis was rerun using only data from the stations of WestPac Bank and Makapuu Pt. to address exclusively beds of pink coral, and still no effect was detected for any of the fish data (MW, Z= -0.89 to -3.8, P=0.37 to 0.55). Similarly, follow up correlations indicated that pink coral had no significant effect on fish numerical density, body length or biomass density ($r_s$= -0.03 to -0.01, P=0.62 to 0.85).

Evasion Guild Comparison

The numerical density of the seal prey was compared between areas with and without corals. Areas with gold coral were found to have significantly more bottom hiders (MW, Z= -4.03, P<0.001)(Fig. 3). However, again this finding lost significance when the FFS site was excluded (MW, Z= -1.4, P=0.14). The body lengths of evasion guilds were indistinguishable between areas with and without gold coral (MW, Z=-0.027 to -0.205, P=0.10 to 0.98) except for the bottom camouflage guild (MW, Z= -2.8, P<0.01). Again this difference disappeared if the FFS station was dropped (MW, Z= -1.3,
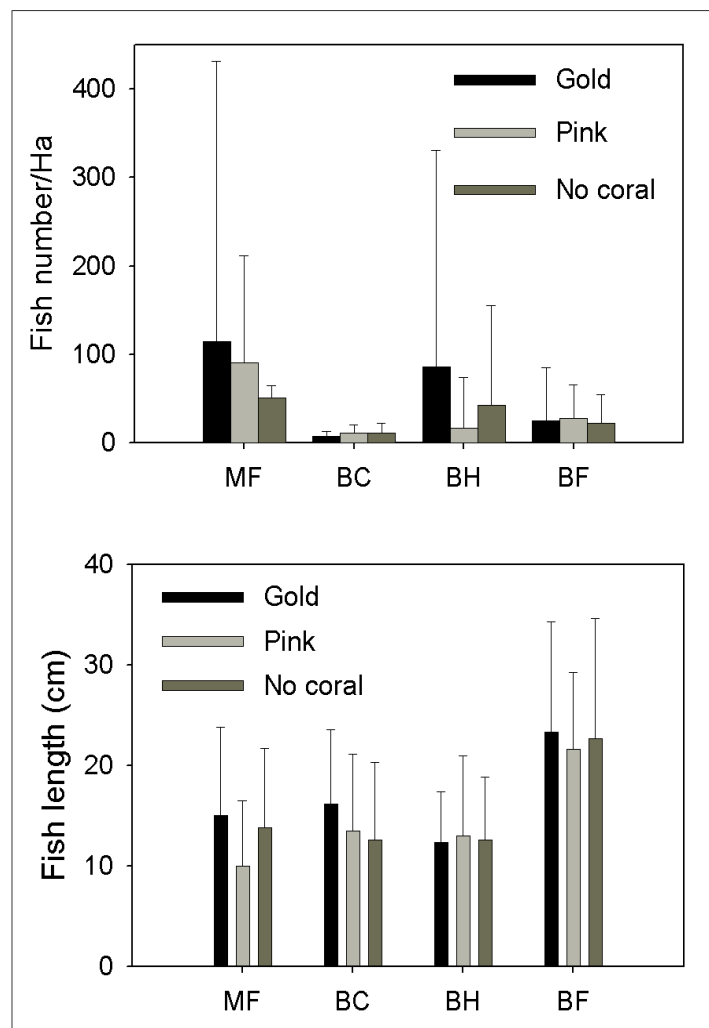


**Figure 3.** Numerical density (top) and body length (bottom) of fish data divided into seal prey evasion guilds with values for sites with gold, pink, and no coral (MF=midwater fleer, BC=bottom camouflage, BH=bottom hider, BF=bottom fleer). The error bars indicate the standard deviation.

P=0.17). Due to the intermixing of the small pink coral with the larger gold corals at a number of stations, this analysis was limited to stations that were exclusively pink coral (Makapuu and WestPac Beds). None of the guilds differed significantly between sites with and without pink coral (MW, Z= -0.44 to -1.85, P=0.064 to 0.66).

Corals as Shelter for Monk Seal Prey

Using data from all stations surveyed Archipelago-wide (N=1,452 pseudo replicates), only 93 pseudo replicates documented fish using coral trees as shelter. These 286 fish represented 13 taxa and are listed in Table 3. All these taxa were seen commonly using abiotic sources of benthic relief, so none are thought to be exclusively dependent on coral colonies. Almost all were bottom hiders (>90%). Based on the survey counts, an estimated 2,900 gold coral colonies, 11,916 pink colonies, and 79,397 colonies of other coral types (ranging from single filamentous whips to tall branched trees) were inspected during these surveys. The survey counts above should not be construed as actual numbers of coral colonies, because they probably include counts of some of the same colonies on successive survey years. The height of coral colonies ranged from 5 to 180 cm for gold coral and 5 to 60 cm for pink coral (Fig. 4). Most of the fish (73%) were seen with the taller gold coral colonies.

Table 3. List of taxa that used coral colonies as shelter, with the number of pseudo replicates in which they were observed, the mean number of fish counted, the mean standard length of the fish, and the mean height of the host colonies in centimeters.

| Taxa | Pseudo replicates | Mean No. fish (sd) | Mean size (cm) | |
|---|---|---|---|---|
| | | | Fish length | Coral height |
| *Symphysanodon maunaloae* | 98 | 16.3 (19.8) | 13.6 | 100 |
| *Antigonia* sp. | 62 | 1.6 (0.8) | 11.9 | 75 |
| *Hollardia goslinei* | 36 | 1.2 (0.4) | 11.1 | 108 |
| *Grammicolepis brachiusculus* | 7 | 1.2 (0.4) | 25.7 | 103 |
| *Moridae* | 6 | 1.0 (na) | 18.0 | 100 |
| *Stethopristes eos* | 6 | 1.0 (na) | 9.1 | 150 |
| *Epigonidae* | 5 | 6.5 (6.9) | 5.0 | 100 |
| *Beryx* spp. | 5 | 5.0 (na) | 15.0 | 120 |
| *Congridae* | 5 | 2.5 (2.1) | 28.0 | 132 |
| *Scorpanidae* | 4 | 1.3 (0.6) | 16.2 | 103 |
| *Cytonemis* | 4 | 1.0 (na) | 7.5 | 64 |
| *Macrouridae* | 1 | 1.0 (na) | 40.0 | 135 |
| *Synaphobranchidae* | 1 | 1.0 (na) | 40.0 | 70 |
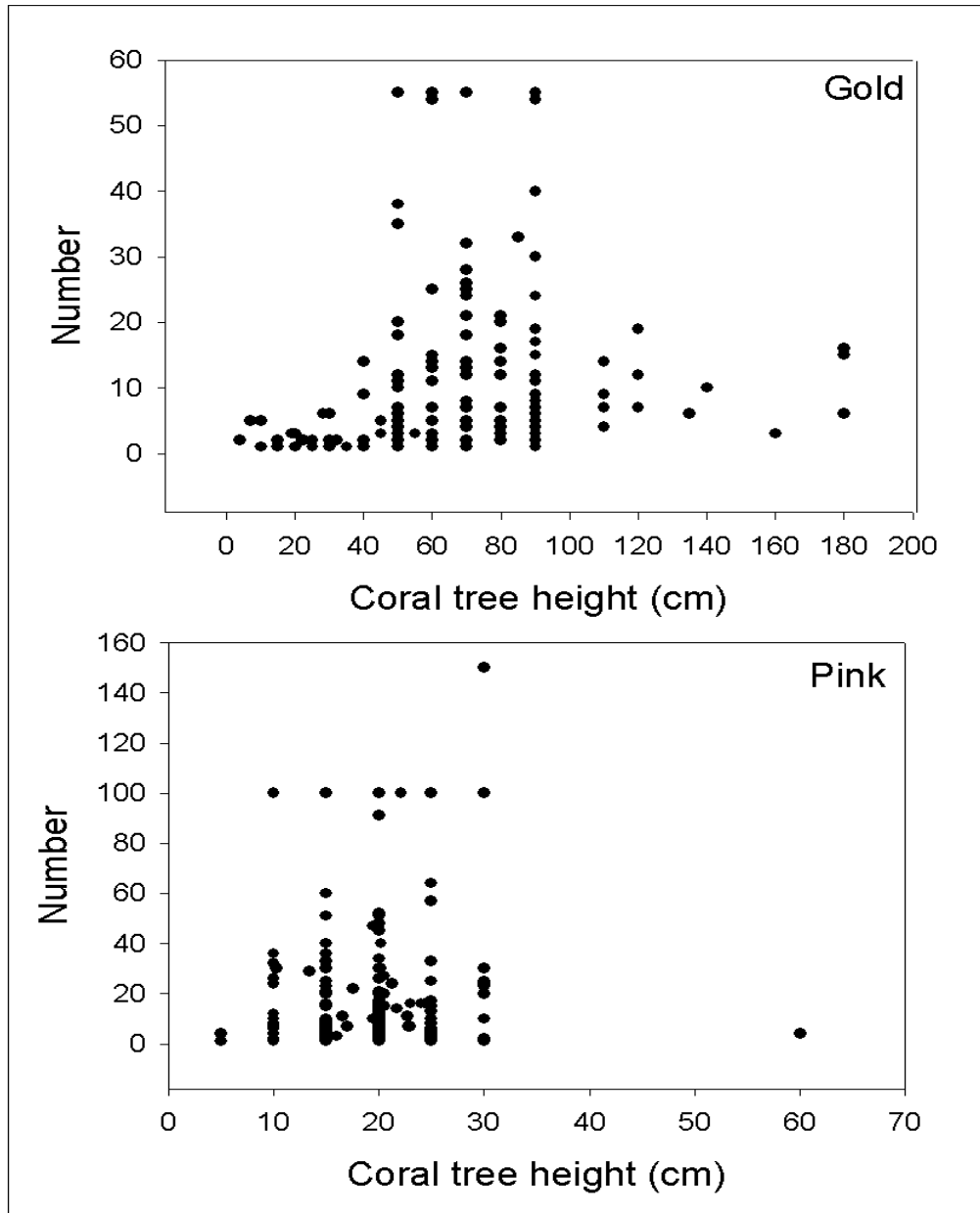
**Figure 4**. Median height of gold (top) and pink (bottom) coral trees for each 5-min survey segment with coral.

## DISCUSSION

Substrate and Relief

There were obvious differences among the substrate, relief type, and corals at each of the stations. It appears that the two coral types prefer different habitat configurations. Habitat measures used in this work were limited to three types of

substrate (sand, carbonate, basalt/manganese) and three relief categories (hardpan, outcrops, and pinnacles).  Even with this crude resolution, it was clear that the carbonate hardpan of the Makapuu station looked the same as that at the WestPac station, and that both supported dense populations of pink coral.  The basalt pinnacles on the summits of Cross Seamount and the FFS Platform were similar, and each was encrusted with gold coral.  Brooks and Keahole were a mix of basalt and carbonate outcrops, and both supported gold and the *Corallium lauuense* variety of pink coral.  Although these habitat associations were for the most part consistent, coral success also is related clearly to localized water flow, a variable not measured in this study.  High-relief features can divert water movement and enhance localized water flow, in which corals thrive.  This would explain why the scale of relief was the only bottom variable that significantly influenced gold coral.  Gold trees were grouped on the tops of pinnacles, on the top edges of cliffs, and along sharp bends in walls.  All these bottom features intensify water flow and probably improve the corals' growth.  Indeed, on a number of dives working in gold coral beds, the submersible was forced to hide from the current until the flow abated, and on one occasion the submersible was pinned against a cliff face by the strength of the local current.

An association with topographic features and flow was not identified for pink coral.  The two largest beds (Makapuu and WestPac) were on hardpan, nearly devoid of relief.  It may be that the low-standing, crustose fan of pink coral is better suited to more unidirectional or lower-speed flow than the more intense and perhaps multi-directional flow in which gold corals thrive. Future work is planned to determine the water flow characteristics with which the two corals associate.

Fish Assemblage

Avoidance of the submersible and its projected light field varied among fish species.  Most of the fish were slow-moving and appeared oblivious to the submersible until nearly struck by the vehicle.  Infrequent, large transient fish such as snappers and mackerel moved out of the light field, but these were a small fraction of the fish assemblage, and many were too large to be considered seal prey. These fish surveys were appropriate to address two types of fish assemblages — coral-sheltering assemblages and aggregated assemblages.  Surveying fish that use coral colonies as shelter is straightforward.  Fish seen in the trees were considered to be sheltering.  However, determining when fish were aggregated was often difficult.  At shallower depths, aggregating effects have been documented in both benthic systems (Anderson et al., 1989) and pelagic systems (Gooding and Magnuson, 1967).  The degree to which fish are concentrated around a source of shelter varies by taxa, so counting the fish around corals is as important as counting fish in the coral branches.  The 5-min psuedo replicate survey effectively encompasses the coral and the immediate surroundings.  Of the top 20 fish taxa, none appeared exclusively associated with either of the coral types examined. The high densities of *Symphysanodon maunaloae* at the FFS station and *Polymixia* at the WestPac station were atypical of the other stations surveyed.  The occurrence of other taxa was comparable across all stations.  Of the top 20 taxa, only *Polymixia* and eels

(Congridea, Ophicthidae) were documented as prey from prior scat analyses (Goodman-Lowe, 1998).  However, a large number of eel fragments (mostly vertebra) in the scats were classified as "unidentified eels," and many of the eels and eel-like fish in the top 20 taxa could be some of these unidentified eels.

Corals and Fish Assemblages

Generally, fish are attracted to habitats for food or shelter. This work only tested whether fish were in higher concentrations in and around the corals and did not address the reasons.  We expected gold coral would be more of a fish attractant than pink coral due to its large size and flexible nature.  However, gold coral also has polyps that illuminate when brushed.  Thus, a fish moving through the branches of the tree might cause it to glow, attracting attention and bringing other conspecifics or predators.

Based on the fish counts alone, greater fish numerical density occurred in areas with gold coral.  However, when the known effects of bottom relief (Friedlander and Parrish, 1998) and depth (Thresher and Colin, 1986; Chave and Mundy, 1994) are accounted for, the relationship with gold coral loses statistical significance.  This makes it hard to attribute any increase in fish density to the presence of gold coral.  Areas with high relief (e.g., pinnacles, walls) constrict water movement and increase flow speed, and both corals and fish benefit by feeding on the increased delivery of drifting particulates (detritus and zooplankton).  There is no clear evidence that the coral colonies aggregate a fish community.  All that can be said is that corals and fish exploit the same type of high relief and high flow habitats.

Pink corals were less associated with bottom relief features, and there was no identified co-occurrence with fish as there was with the gold corals.  The lack of shelter afforded by the smaller pink corals and the flat pavement bottom they colonize could explain the lack of fish.  Another possibility is that gold and pink coral exploit significantly different flow regimes, and fish do better in the gold coral flow regime.  However, understanding this situation will require a separate investigation.  Tall coral trees, most often gold coral, were used as shelter by some fish. Other coral genera fish used as shelter included the taller trees of *Callogorgia*, *Calyptrophora*, and *Leiopathes*.

Evaluation of fish data using seal prey-evasion guilds showed significantly more bottom hiders around gold coral.  No other guilds were associated with gold or pink coral.  Bottom hiders typically maintain position and shelter around a source of relief and opportunistically feed on the passing drift.  Hence, these fish have evolved to make use of relief and high-flow sites irrespective of the presence of corals.  Fish co-occur with corals, but obligate interdependency is not supported by the data.

Few studies have been done on fish associations with deep-water corals.  In the Atlantic, Husebo et al. (2002) compared fish catches from longlines and gillnets deployed at areas with coral beds (*Lophelia pertusa*) and at areas without coral.  They reported significantly more *Sebastes marinus* (a bottom hider) in area with corals and that they were  at least similar to numbers of two other species.  They attributed the greater numbers of *S. marinus* to the fish's use of the corals' physical relief as shelter.  Their results are consistent with the increased number of bottom hiders observed in

Hawaiian coral beds. However the Husebo et al. (2002) study was only able to account for habitat effects in a general sense. *Lophelia pertusa* grows on exposed rock outcrops and pinnacles and not in the mud flats that the authors reported as the habitat surrounding the bed, making it difficult to isolate the effects of the coral. Syms and Jones (2001) tested the importance of soft corals in the fish community by conducting baseline surveys of some test reefs, then removing the corals, and then resurveying the fish community for a period of 2 years. The baseline surveys on the test reefs revealed that higher fish abundance is correlated with density of soft corals. However, the experimental removal of soft corals resulted in no change to the fish assemblage over a 2-year period of monitoring. This may be a shallow-water example of corals and fish co-occurring in optimal conditions (e.g., high flow). Recent surveys by Boland and Parrish (2005) of fish assemblages in relation to shallow-water black coral trees (*Antipathes dichtoma*) found that the fish assemblage uses the trees generally as shelter much as they used other comparable abiotic relief. Few taxa were documented to rely exclusively on the coral colonies. Based on the available literature, corals and fish appear to co-occur in high densities at areas of relief and high flow. Subphotic fish in Hawaiian waters appear to use deep-water corals interchangeably with abiotic relief sources with no significant difference. However, it is important to remember that all the present surveys were conducted during the day and at the same time of year, so any nocturnal or seasonal differences in fish association with corals were undetected.

## ACKNOWLEDGEMENTS

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# ECOLOGICAL CHARACTERISTICS OF CORAL PATCH REEFS AT MIDWAY ATOLL, NORTHWESTERN HAWAIIAN ISLANDS

BY

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## ABSTRACT

Ecological aspects of coral patch reefs were studied from 1981 to 1985 in Welles Harbor, Midway Atoll. Water temperatures varied from 17°C in February to 28°C in August. Sizes of reefs studied were described by mean area (59 m²), mean volume (52 m³), vertical relief (<1 m), and inter-reef isolation (100 m). Considerable temporal change in reef size occurred due to large winter swells shifting bottom sand. Six common species accounted for 70% of all individual fish visually censused over 4 years. Overall fish assemblage composition ranged from 11 to 46 fish/10 m², from 3 to 14 species. Numerical abundance and species richness for all fish (pooled) strongly correlated with physical reef substrate characteristics of area, volume, and vertical relief during summer. Species diversity (H') was not correlated with the substrate variables, suggesting similarity in the structure of fish communities among different sizes of patch reefs. Daily surveillance for presence of large transient taxa suggested that visits by sharks, large jacks, monk seals, sea turtles, and dolphins were infrequent. Density estimates were made for all conspicuous invertebrate megafauna during initial and final assessments. Six common taxa provided 90% of these counts; nearly half were sea urchins. Percent cover also was recorded for coral and algal species on the patch reefs. Cover by live coral was low (about 7%) and dominated by a few species. Mean algal cover ranged from 32 to 77%. Such information on ecological characteristics of reefs may aid in understanding complex ecological processes and provides an earlier reference for current ecosystem studies.

## INTRODUCTION

Coral reef communities are among the most ecologically diverse systems known, including many ecological interactions among fish, coral, other invertebrates, and algae (Hixon, 1997). Many coral reefs are patchy in spatial distribution. Abiotic and biotic factors of the reef environment can affect the distribution patterns of fish assemblages (Hobson, 1980; Sale, 1980; Friedlander and Parrish, 1998). These factors include reef structural attributes (e.g., reef size, substrate complexity, patch isolation, and depth),

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environmental variables (e.g., water temperature, suspended sediment, current, and sand movement), and direct or indirect effects of other biota (e.g., algae, corals, other invertebrates, and nonteleost vertebrates) (Luckhurst and Luckhurst, 1978; Bohnsack, 1979; Carpenter et al., 1981; Sale and Douglas, 1984; Walsh, 1985; Green et al., 1987; Roberts and Ormond, 1987; Clarke, 1988; DeFelice and Parrish, 2001, 2003). Behavioral interactions among fishes, such as predation and competition, also can influence the abundance of these populations, as well as benthic community structure (Sale, 1980; DeMartini and Friedlander, 2006).

Reef fish communities from the geographically isolated Hawaiian Archipelago are characterized by low species richness, high endemism (~21% of the inshore species, many of which are abundant, and increasing with latitude), and the presence of mesoscale eddies, which may help retain planktonic larvae (Gosline and Brock, 1960; Lobel and Robinson, 1986; Hourigan and Reese, 1987; Lobel, 1989; Randall, 1996; DeMartini and Friedlander, 2004; Firing et al., in press). Most species are small and site-attached or have limited home ranges. All trophic guilds are represented, although most species are generalists, exhibiting wide diet overlap (Hobson, 1974; Sale, 1980; Parrish, et al., 1985).

Patch reefs are natural habitat structures composed of coral and rock substrate that are isolated across sand from other reefs. They are usually of small to moderate size (e.g., < 100 m across), but numerous in many shallow nearshore environments. Patch reefs are valuable for some ecological studies because they support relatively isolated communities with diverse and abundant fauna, and are of manageable size for assessment with replication (Nolan, 1975; Sale, 1980, 1984; Clarke, 1988; Ault and Johnson, 1998). Some investigators have assumed they are closed systems (following larval settlement) and that they reveal patterns representative of much larger reefs (Smith and Tyler, 1975; Jones and Chase, 1975). However, the validity of these assumptions has been questioned (Clarke, 1988; Robertson, 1988; Ault and Johnson, 1998; Schroeder and Parrish, 2005). The degree of isolation between patch reefs can affect migration rates by fish that are not fully site attached. Some species use small patch reefs only as a juvenile nursery habitat before relocating to more extensive reefs.

The present study describes the structure of fish communities and related ecological characteristics of 'natural' patch reefs within the lagoon at Midway from 1981 to 1985. Midway is a high-latitude coral atoll characterized by: 1) isolation in the mid-Pacific, 2) a subtropical climate, with a wide seasonal water temperature range, 3) many species that are common on shallow reefs and attain large sizes in the NWHI, but occur only rarely or in deep water farther southeast, and 4) lagoon reefs that are essentially free of fishing pressure (Gosline & Brock, 1960; Mauck, 1975; Hobson, 1980, 1984; Randall et al., 1993; Friedlander and DeMartini, 2002). These reefs and their associated communities were generally representative of a protected inshore biotype, common in the northwestern portion of the Hawaiian Archipelago.

## METHODS AND MATERIALS

Study Area

Coral patch reefs were studied during 1981-1985 within Welles Harbor, in the SW quarter of Midway Atoll (centered about 28°12' N latitude, 177°24' W longitude) of the Northwestern Hawaiian Islands (NWHI) (Fig. 1). Midway, located at the northern limit of the subtropics, experiences more pronounced seasonal extremes than the lower latitude (19° N to 22° N latitude) high Hawaiian Islands, some 2,000 km to the SE. The lagoon averages 10 km in diameter and is surrounded by a barrier reef except along the W and NW sides. The four patch reefs studied were among many scattered within the SW section (~2 km W of Sand Island and ~2 km E of the western barrier reef) of the shallow (5-10 m), sand-bottom lagoon. These 'natural' patch reefs were selected based on general similarity in broad characteristics (e.g., size, substrate composition, vertical relief, water depth, isolation across sand, and apparent fish assemblage composition) with those occurring within the Welles Harbor study area. While parts of the Midway Islands and its lagoon had experienced major disturbances in previous decades (e.g., harbor dredging, landfill, and marine recreation by U.S. Navy personnel), the reefs in the section of the lagoon for this study had experienced no known recent fishing disturbance (pers. comm., Midway Koral Kings Dive Shop). Measured water temperatures at Midway ranged from 17°C in February to 28°C in August. Currents were usually negligible or slight from the south (i.e., rarely ≥ 1 knot) .Large oceanic swells from the NW often created strong bottom surge during winter. Underwater horizontal visibility was usually 10-20 m, except when rare storms greatly increased turbidity.



**Figure 1**. Typical coral patch reef (station 3C) in Welles Harbor, Midway Atoll (Photo: R. Schroeder).

Reef Physical Characteristics

Major physical attributes of each patch reef were measured at the beginning of the study (July-August 1981 and July-August 1982), and repeated during the final sampling period (July-August 1985). Initial attributes of two replacement reefs (for originals covered by sand during the winter of 1983-84) were measured in August 1984 (see Results and Discussion). Reef physical characteristics were measured because major differences in patch reef size and structure could significantly influence the composition of the fish community (Helfman, 1978; Sale and Douglas, 1984; Clarke, 1988). Also, significant temporal changes in the reef substrate could affect other ecological characteristics.

*Reef Size.* Detailed bathymetric maps were sketched by divers measuring depth with accurate gauges, providing a vertical reef profile referenced to a standardized (1x2 m), horizontal rope grid set over the entire reef. From these maps, the projected surface area (two-dimensional footprint of hard substrate) of each reef was estimated by summing the areas of all grid cells. Volume was estimated by multiplying the projected area increment between each two adjacent depth contours by the height of the increment above the sand at the base of the reef, and summing the products.

*Reef Complexity.* An index of reef substrate complexity, "vertical relief," was estimated for each reef following Luckhurst and Luckhurst (1978). Over each patch reef, sets of parallel horizontal lines, 1-m apart, were constructed that touched the highest point of the reef along each line. Vertical measurements were taken from these lines to the reef surface at 0.5-m intervals along each line. Vertical relief was reported as the mean of these measured distances. We also conducted Luckhurst's "substrate rugosity" chain-measured surface-contour/linear distance method to assess substrate complexity, but this measure was not used in our analysis since the interpretation was confounded for patch reefs of varying size.

*Reef Isolation.* An index of patch reef isolation was obtained by measuring distances to the nearest neighboring reefs in eight directions (one within each octant around the patch reef), taking the mean of these eight measurements, and then taking the mean of that value and the single measurement to the nearest neighboring reef. This strong weighting of the arbitrary index in favor of the closest reef seemed appropriate ecologically (e.g., may enhance fish migration via a visual stepping-stone effect) (Schroeder, 1987; 1989b).

Reef Ecological Characteristics

*Reef Fish Community Assessment.* The total-count underwater visual census method was used to quantify species composition, abundance, and temporal variability of resident fish populations on each patch reef (Schroeder and Parrish, 2005). The total number of all diurnally observable individuals of each species was recorded, separated into visually estimated size classes of fish standard length (SL), for subsequent analysis.

The patch reefs were of manageable size to permit total fish counts, as opposed to transect subsampling. Size classes were: 1-2 cm, 3-4 cm, 5-6 cm, 7-10 cm, 11-15 cm, and then each consecutively higher 5 cm class. Estimates of individual fish size were aided by reference to a calibrated 20-cm rule along the top of the underwater data form. Validation was tested periodically by comparing estimated length to actual length of individual fish speared by each observer far from the study area; estimates were highly accurate (e.g., nearly all $r^2 > 0.80$, $P<0.001$; Schroeder, 1989a). Censuses were conducted between 0800 and 1700 h during the 20 major (2-6 wk) 'survey periods' (i.e., continuous daily sampling periods) of May 1981-August 1985 (i.e., May-Jun81, Jul-Aug81, Jan82, May-Jun82, Jul-Aug82, Nov82, Dec/Jan83, Mar83, May-Jun83, Jul-Aug83, Nov83, Dec/Jan84, Mar84, Jun-Jul84, Aug84, Oct-Nov84, Jan85, Mar-Apr85, May85, Jul-Aug85). During each survey period, the census was replicated 2 to 10 times on each reef, with rare exceptions.

*Assessment of Other Reef Biota.* Common species of other resident reef biota (e.g., algae, corals, noncryptic invertebrates) at each station were visually assessed, using the standard 1x2-m grid, during the same periods (initial and final) that reef physical characteristics were measured. Data recorded included the estimated percent cover of substrate surface by each major algal and coral taxon within a grid cell, and the number of discrete, nonsessile macroinvertebrates counted per cell. The mean of values from all grid cells in a reef was used to represent the reef.

*Other Ecological Characteristics.* Mean daily frequencies for sightings of large, highly transient fishes and other marine vertebrates were recorded from May 1980 to August 1985. Taxa considered were carcharhinids (sharks), carangids (jacks), Rajiformes (rays), *Monachus schauinslandi* (Hawaiian monk seal), *Chelonia mydas* (green sea turtle), and *Stenella longirostris* (spinner dolphin). Shark and jack frequencies were calculated based on all diurnal periods per survey period during which research activities were conducted on the focal set of natural study reefs. (Observation time in the water was roughly the same for most days.) Daily records of the other large vertebrate taxa were made during any time of the day in or on the water of the Welles Harbor study area; observation time for these sightings was less standardized. Notes on behavioral patterns also were recorded for common fishes.

Fish-Physical Correlations

Spearman rank correlation analysis was used to search for associations of the major physical patch reef characteristics with the fish community. Reef characteristics used were substrate area, volume, and vertical relief (measured as described above). Characteristics of the fish community used were species richness, measured by the mean number of species censused on a reef during a survey period, the Shannon-Weaver species diversity index (H'), which incorporates both species richness and abundance (Shannon and Weaver, 1949), the numerical abundance of all (pooled) species, and the numerical abundance of several common (abundant) species, all from visual census data. (For the group of common species, the significance of the correlations was based on the experimentwise error rate [Miller, 1981].)

**RESULTS AND DISCUSSION**

Reef Physical Characteristics

*Reef Size.* Patch reef area ranged from 12-186 m² (mean 58.8 m²) and volume from 4-155 m³ (mean 52.2 m³) (Table 1). During the 4-year study, the size of some reefs changed when shifting sand either exposed or buried hard reef substrate. For example, around some reefs, water depth to the lagoon floor was reduced from 10 m to 5 m in <2-mo. time. Long, steep slopes of sand marked the transition between shallow and deep areas, somewhat analogous to wind-driven terrestrial sand dunes. During the winter of 1983-84, two study reefs ($3C_1$ and $4C_1$) were buried completely, and study sites had to be replaced with other patch reefs nearby (3C and 4C). These changes in reef size resulted from the combined effects of severe winter storms, tides, and related currents. High energy, large wave events from the NW originate during extratropical north Pacific winter storms and subject NWHI shallow-water coral reef communities to wave energy an order of magnitude greater than typical winter waves (Friedlander, et al. 2005). The

Table 1. Summary of patch reef size (area and volume), and vertical relief (mean±sd) as an estimate of substrate complexity (N= 61-183 total measurements per reef), at the beginning and end of the study.

| | Period | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Initial | | | Final | | | Change | | |
| | Area (m²) | Volume (m³) | Relief (cm) | Area (m²) | Volume (m³) | Relief (cm) | Area (%) | Volume (%) | Relief (%) |
| Station: | | | | | | | | | |
| 1C | 12.2 | 4.4 | 34.1(19.2) | 10.9 | 6.2 | 38.4(15.8) | -10.1 | 39.1[2] | 12.6 |
| 2C | 50.0 | 56.7 | 60.9(44.0) | 22.6 | 10.0 | 37.1(19.9) | -54.9 | -82.4 | -39.1 |
| 3C[1] | 39.0 | 24.0 | 67.7(46.3) | 52.2 | 66.9 | 92.3(54.9) | 34.0 | 178.8 | 36.8 |
| 4C[1] | 185.6 | 154.9 | 72.8(41.9) | 151.0 | 146.1 | 62.4(43.1) | -18.6 | -5.7 | -14.3 |

[1] Initial start times for stations 3C and 4C were later in the study, after the originally selected reefs ($3C_1$ and $4C_1$) were totally buried by progressive sand movement during winter storms.
[2] The inconsistent directions of change for area and volume may be a consequence of the small sample size compounded by the low precision of estimating volume from area maps, and by different observers.

magnitude of sand movement across lagoon floors and other shallow habitats, its effects on patch reef size and complexity, and its significance for ecological communities have been reported rarely (Yamanouchi, 1988; Mizamura et al., 2000). These changes in the sizes of patch reefs prevented straightforward analysis and comparison of different reefs on the basis of fish density.

*Reef Complexity.* The study patch reefs had roughly similar substrate, predominantly dead eroded coral (mainly *Porites lobata* and *P. compressa*), which retained much of the original colony morphology. Substrate complexity, measured as mean ($\pm$sd) vertical relief per reef, ranged from 0.34 ($\pm$0.19) m to 0.92 ($\pm$0.55) m (3 m maximum) (Table 1). These means varied spatially and temporally during the study, due to shifting sand; some stations became more complex while others became less so.

*Reef Isolation.* Sand flats surrounding our study reefs at depths of 6-10 m had little unconsolidated rubble. Inter-reef isolation (to nearest neighbor patch reef) was 123 m for reef 1C, 132 m for reef 2C, 71 m for reef $3C_1$, and 74 m for reef $4C_1$ (mean 100 [$\pm$32] m). These reefs were believed initially to be sufficiently isolated from neighboring patches that individual reefs functioned more or less as incongruous ecological communities. However, results of our subsequent experimental work at this site indicated that small, semi-resident piscivores (e.g., lizardfish) move more widely among patch reefs than had been recognized (Schroeder and Parrish, 2005).

Reef Ecological Characteristics

*Fish Communities.* Considering overall diurnal, non-cryptic fish assemblage composition of all patch reefs studied, the average minimum number (i.e., exclusive of short-lived major settlement pulses) and species richness ranged from about 15 species (50 fish) on the smallest patch reef (12 m$^2$), to about 50 species (200 fish) on the largest reef (186 m$^2$). Our values for fish species richness were similar to those found by Molles (1978) on comparable size patch reefs in the Gulf of California. They were higher than those found by Walsh (1983) on the fringing reef along the Kona coast of Hawaii (15 species [mean of 70 fish] on 25m$^2$ quadrats), and lower than those found by Jones and Chase (1975) on large, lagoonal patch reefs of Guam (67 species [1859 fish]; total transect area of 1400 m$^2$).

For each species/taxon, its percent numerical abundance (relative to the total), percent occurrence (in all censuses), and estimated size range are listed in Table 2. Consistent with studies from other geographic regions, we found that only a few species provide the bulk of the reef fish community. *Pervagor spilosoma* (Monacanthidae, filefish), *Apogon maculiferus* (Apogonidae, cardinalfish), and *Dascyllus albisella* (Pomacentridae, damselfish), which each composed ~15% of the total abundance (Table 2), were characterized by major seasonally and annually variable settlement pulses. They dominated the juvenile census counts and had the highest settlement rates of all fishes (Schroeder, 1985, 1989a). *Thalassoma duperrey* (Labridae), *Stegastes fasciolatus* (Pomacentridae), and *Chromis ovalis* (Pomacentridae) each provided an additional ~8% of the total number of fish, and also settled in considerable numbers on the patch reefs. These six common species accounted for 70% of all fish individuals visually censused on these reefs (135 total fish species/taxa). The low faunal diversity, which is characteristic of Hawaiian reefs (Randall et al., 1993), combined with strong settlement strategies by a few species (e.g., Sale, 1985; Walsh, 1985; Schroeder, 1985, 1989a), probably accentuates the numerical dominance of the fish community by several species at Midway. Similarly, Sale and Douglas (1984) found that apogonids, pomacentrids, and gobioids dominated small patch reefs of the Great Barrier Reef. Walsh (1983) found that

Table 2. Composition of the fish community as indicated by visual census, showing percent relative numerical abundance (Total N = 90,103 individuals, 135 species/taxa) and percent frequency of occurrence (in N = 20 total survey periods) for 95% of all (cumulative) fish censused, based on pooled data from four natural patch reefs from May 1981 to August 1985. (The off-reef, sand-rubble dwelling goby *Gnatholepis anjerensis* that was ubiquitous in late summer is considered separately.)

| | Abundance % | Occurrence % | Size Range (cm SL) (Min.-Max.) |
|---|---|---|---|
| Species/taxa: | | | |
| *Pervagor spilosoma* | 15.47 | 60 | 3-15 |
| *Apogon maculiferus* | 14.64 | 100 | 1-15 |
| *Dascyllus albisella* | 14.52 | 100 | 1-10 |
| *Thalassoma duperrey* | 8.14 | 100 | 1-25 |
| *Stegastes fasciolatus* | 8.05 | 100 | 1-10 |
| *Chromis ovalis* | 7.64 | 100 | 1-15 |
| Scarid spp. | 3.04 | 95 | 1-15 |
| Apogonid spp. | 2.78 | 40 | 1-20 |
| *Chaetodon miliaris* | 2.23 | 100 | 1-20 |
| *Labroides phthirophagus* | 1.96 | 100 | 1-10 |
| *Spratelloides delicatulus* | 1.78 | 5 | 3-4 |
| *Stethojulis balteata* | 1.50 | 100 | 1-30 |
| *Sebastapistes coniorta* | 1.42 | 95 | 1-20 |
| *Thalassoma ballieui* | 0.96 | 100 | 1-40 |
| *Canthigaster jactator* | 0.92 | 100 | 1-15 |
| Syndontid spp. | 0.83 | 100 | 1-35 |
| *Gymnothorax eurostus* | 0.81 | 100 | 7-100 |
| *Chromis hanui* | 0.81 | 100 | 1-10 |
| *Scorpaenodes littoralis* | 0.75 | 95 | 1-15 |
| *Mulloidichthys flavolineatus* | 0.71 | 35 | 7-25 |
| *Cirrhitops fasciatus* | 0.64 | 100 | 1-15 |
| *Plectroglyphidodon johnstonianus* | 0.60 | 95 | 1-15 |
| *Paracirrhites forsteri* | 0.59 | 100 | 1-20 |
| *Dendrochirus barberi* | 0.59 | 90 | 1-25 |
| *Mulloidichthys vanicolensis* | 0.56 | 35 | 5-15 |
| *Foa brachygramma* | 0.56 | 80 | 1-15 |
| *Chaetodon fremblii* | 0.54 | 100 | 1-15 |
| *Gymnothorax steindachneri* | 0.45 | 100 | 7-100 |
| *Bodianus bilunulatus* | 0.39 | 100 | 1-45 |

Table 2. Continued.

| | Abundance % | Occurrence % | Size Range (cm SL) (Min.-Max.) |
|---|---|---|---|
| Species/taxa: | | | |
| *Macropharyngodon geoffroy* | 0.37 | 90 | 1-20 |
| Priacanthid spp. | 0.36 | 50 | 5-25 |
| *Neoniphon sammara* | 0.33 | 100 | 1-25 |
| All others (pooled)* (103 species/taxa, below) | 5.00 | na | na |
| *Gnatholepis anjerensis* (Total separate no. of individuals = 34,541) | 100.00 | 20 | 1-6 |

*Additional fish species/taxa accounting for a total of 5% of all censused: *Anampses cuvier, Coris flavovittata, Ctenochaetus strigosus, Myripristis* sp*., Cheilinus bimaculatus, Pseudocheilinus octotaenia, Sebastapistes ballieui, Parupeneus multifasciatus, Brotula multibarbata, Coris venusta, Scarus dubius, Abudefduf abdominalis, Scorpaenopsis diabolus, Sargocentron diadema, Cirrhitus pinnulatus, Pterois sphex, Scorpaenid* sp*., Priacanthus cruentatus, Parupeneus pleurostigma, Arothron hispidus, Synodus ulae, Myripristis kuntee, Anampses chrysocephalus, Doryrhamphus melanopleura, Gobiid* spp*., Chlorurus perspicillatus, Calotomus* sp*., Enchelycore pardalis, Taenianotus triacanthus, Parupeneus porphyreus, Aulostomus chinensis, Chaetodon auriga, Zebrasoma flavescens, Zanclus cornutus, Naso unicornis, Kyphosus* sp*., Lactoria fornasini, Caracanthus maculatus, Acanthurus triostegus, Gymnothorax undulatus, Labrid* spp*., Myrichthys maculosus, Teleostei* spp*., Cheilinus unifasciatus, Paracirrhites arcatus, Chaetodon multicinctus, Cirripectes vanderbilti, Cymolutes lecluse, Cirripectes* sp*., Muraenid* spp*., Cymolutes* sp*., Priacanthus meeki, Antennariid* spp*., Saurida gracilis, Chlorurus sordidus, Priolepis eugenius, Carangoides orthogrammus, Conger cinereus, Anampses* sp*., Fistularia commersonii, Scorpaenopsis cacopsis, Bothus mancus, Calotomus zonarcha, Epinephelus quernus, Ostracion meleagris,  Sargocentron* sp*., Naso lituratus, Fusigobius neophytus, Apogon kallopterus, Amblycirrhitus bimacula, Diodon holacanthus, Bothid* spp*., Gomphosus varius, Gymnothorax hepaticus, Ophichthus polyophthalmus, Sargocentron xantherythrum, Acanthurus leucopareius, Acanthurus achilles, Caranx ignobilis, Parupeneus bifasciatus, Chaetodon ornatissimus, Forcipiger flavissimus, Diodon hystrix, Carcharhinus amblyrhynchos, Pomacentrid* spp*., Antennarius coccineus, Priolepis* sp*., Gymnothorax pictus, Caranx sexfasciatus, Caranx melampygus, Centropyge potteri, Pseudocaranx dentex, Seriola dumerili, Gymnothorax flavimarginatus, Blenniid* spp*., Gymnothorax meleagris, Gymnothorax pindae, Novaculichthys taeniourus, Pseudocheilinus* sp*., Chromis verater, Plectroglyphydodon imparipennis, Asterropteryx semipunctatus, Arothron meleagris*

two species of acanthurids and a pomacentrid predominated (>50% of total number of fish) in census counts along the Kona coast of Hawaii. Of the seven most abundant species he recorded there, only two (the wrasse *T. duperrey* and the damselfish *S. fasciolatus*) were among the six most abundant species we censused at Midway, at the opposite end of the Hawaiian Archipelago (Walsh, 1983). Similarity in species abundance rankings between the two locations was low.

Other Reef Biota

*Invertebrates.* On Midway patch reefs, visible macroinvertebrates were common. Density estimates (as grand mean number of individuals over all censuses counted/m$^2$) for all (pooled) visible, macroinvertebrate taxa varied from 18.4 $\pm$13.7 (sd) initially, to 30.4 $\pm$24.3 (sd) at the final assessment (Table 3). Six taxa (in decreasing order of abundance) provided over 90% of these numbers: *Echinometra mathaei* (urchin), *Rhynchocinetes* sp. (shrimp), *Diadema paucispinum* (urchin), *Ophiocoma pica* (brittle star), *Echinostrephus aciculatus* (urchin), and *Plakobranchus ocellatus* (sea slug). Half of all these invertebrates counted were *E. mathaei* and *D. paucispinum*. Fish predators on sea urchins include triggerfish, pufferfish, snapper, large wrasse, and porcupinefish (Ormond et al., 1973; Glynn et al., 1979; Carpenter, 1984). Sea urchin densities can greatly increase on heavily fished reefs following reductions of these predators and reduced competition from herbivores (e.g., parrotfish, surgeonfish) (Hay, 1984). Herbivorous damselfish also can exclude sea urchins from their territories (Williams, 1981).

*Corals.* More than 90% of the substrate of Midway patch reefs was dead, partially eroded coral rock (mostly from *Porites* spp.). The mean percent of total live coral cover (all species pooled) was low: 7.2% ($\pm$8.1 sd), initially, and 6.9% ($\pm$6.6), at the final assessment (Table 4). Only a few species predominated, mainly *Pocillopora meandrina* (3.2%), *P. damicornis* (1.6%), *Porites lobata* (1.4%), *Cyphastrea ocellina* (0.9%) and *Leptastrea purpurea* (0.1%). Nearly 70% of live coral was branching colonies of *Pocillopora* spp., a preferred substrate for settling postlarval damselfish *Dascyllus albisella* (Booth, 1995). On the Great Barrier Reef, the number of a related damselfish congener (*D. aruanus*) inhabiting coral heads exhibited a strong positive correlation with size (area) of the coral colony (Sale, 1972).

*Algae.* Algal cover on the Midway patch reefs was highly variable seasonally, annually, and spatially. The mean percent of total algal cover (all taxa pooled) on the patch reefs was 76.7% ($\pm$55.5 sd), during the initial summer assessment, and 32.1% ( $\pm$35.7 sd), during the final summer sampling period (Table 5). During late summer in some years, a thick, dark algal carpet covered many of the reefs, but very little algae were obvious in winter. Common taxa which collectively composed over 90% of the usual cover were (in order of decreasing abundance) Phaeophyta spp., *Centoceras clavulatum*, *Ralfsia pangoensis*, *Spyridia filamentosa*, *Dictyota* sp., *Lobophora variegata*, *Hydrolithon reinboldii*, Rhodophyta (spp.), and *Lyngbya majuscula*. Schooling herbivores (e.g., parrotfish, surgeonfish) graze reef algae heavily, and can strongly affect the community structure and standing crop of macroalgae on patch reefs (Hixon, 1997). Such activity is important for maintenance of healthy coral reefs because it opens space for settling and growth of new corals. The herbivorous damselfish, *Stegastes fasciolatus*, is common on Midway reefs, where it defends small algal territories and can affect the abundance and local species composition of reef algae (Hixon, 1997). The heavier algal mat resulting from this "gardening" inside territories increases habitat for small reef invertebrates and epiphytes (Hixon and Brostoff, 1985; Zeller, 1988).

Table 3. Grand mean density (number/m$^2$) of conspicuous invertebrates, by species, censused on undisturbed patch reefs (N=4 reefs in each period).

| Species/taxa*: | Period | | | |
| --- | --- | --- | --- | --- |
| | Initial Number/m$^2$ (SD) | | Final Number/m$^2$ (SD) | |
| *Echinometra mathaei* | 12.09 | (9.43) | 11.84 | (8.63) |
| *Rhynchocinetes* sp. | 0.42 | (0) | 8.95 | (7.53) |
| *Diadema paucispinum* | 2.98 | (1.89) | 4.57 | (3.13) |
| *Ophiocoma pica* | 0 | (0) | 1.89 | (1.75) |
| *Plakobranchus ocellatus* | 1.24 | (1.18) | 0 | (0) |
| *Echinostrephus aciculatus* | 0.89 | (0.77) | 0.50 | (0.44) |
| *Ophiocoma* sp. | 0.02 | (0) | 0.81 | (1.20) |
| *Heterocentrotus mammillatus* | 0.24 | (0.30) | 0.66 | (0.89) |
| *Coralliophila erosa* | 0 | (0) | 0.15 | (0.16) |
| *Harpiliopsis* sp. | 0 | (0) | 0.14 | (0.05) |
| Shrimp sp. | 0 | (0) | 0.12 | (0.15) |
| *Calcinus hazletti* | 0 | (0) | 0.10 | (0.14) |
| *Stenopus hispidus* | 0.07 | (0.09) | 0.09 | (0.05) |
| *Holothuria atra* | 0.04 | (0.02) | 0.08 | (0) |
| *Trapezia* sp. | 0.01 | (0) | 0.06 | (0.03) |
| *Saron* sp. | 0 | (0) | 0.05 | (0.04) |
| *Calcinus latens* | 0 | (0) | 0.04 | (0.04) |
| *Tripneustes gratilla* | 0.04 | (0) | 0 | (0) |
| *Chama* sp. | 0.01 | (0) | 0.04 | (0.00) |
| Bivalve (abalone like) | 0.04 | (0) | 0 | (0) |
| *Holothuria difficilus* | 0.04 | (0) | 0 | (0) |
| *Turbo sandwicensis* | 0.02 | (0.01) | 0.01 | (0) |
| *Domecia hispida* | 0 | (0) | 0.01 | (0) |
| *Actaea* sp. | 0 | (0) | 0.01 | (0) |
| *Stegopontonia commensalis* | 0.01 | (0) | 0.01 | (0) |
| *Tricolia variabilis* | 0 | (0) | 0.01 | (0) |
| *Eucidaris metularia* | 0.01 | (0) | 0.01 | (0) |
| *Linckia* sp. | 0.01 | (0) | 0 | (0) |
| TOTAL | 18.43 | (13.75) | 30.38 | (24.31) |

*Additional invertebrate species/taxa, each accounting for <0.1% of all censused on the four patch reefs: *Aplysia parvula, Conus leopardis, Pseudoboletia indiana, Galathea* sp., *Linckia guildingi, Conus* sp., *Pagurid* sp., *Antheopsis papillosa, Actinopyga obesa, Conus abbreviatus, Calcinus* sp., *Polyplectana kefersteinii, Euplica turturina, Dolabrifera* sp., *Conus lividus,* and *Lanice conchilega*.

Table 4. Mean percent of bottom covered by each major live coral species on undisturbed patch reefs (N=4 reefs in each period).

| | Period | | | |
| | Initial Mean | (% SD) | Final Mean | (%SD) |
|---|---|---|---|---|
| Species | | | | |
| *Pocillopora meandrina* | 2.05 | (2.03) | 4.40 | (5.30) |
| *Porites lobata* | 2.32 | (3.52) | 0.38 | (0.03) |
| *Pocillopora damicornis* | 1.85 | (1.99) | 1.26 | (0.95) |
| *Cyphastrea ocellina* | 0.83 | (0.54) | 0.91 | (0.35) |
| *Leptastrea purpurea* | 0.15 | (0) | 0 | (0) |
| *Porites compressa* | 0.04 | (0) | 0 | (0) |
| | | | | |
| TOTAL | 7.23 | (8.08) | 6.94 | (6.63) |

Table 5. Mean percent of bottom covered by each major algal taxon on undisturbed patch reefs (N=4 reefs in each period).

| Species/taxa* [TYPE]: | Period | |
|---|---|---|
| | Initial Mean % (SD) | Final Mean % (SD) |
| Red algal  [TURF] | 21.19  (9.78) | 2.79  (4.33) |
| Brown algal  [TURF] | 13.88  (2.14) | 5.76  (9.12) |
| *Spyridia filamentosa* [FRONDOSE] | 10.23 (11.55) | 1.07  (0.77) |
| *Dictyota* sp. [FRONDOSE] | 6.66  (4.78) | 2.13  (2.06) |
| *Ralfsia exponsa* [ENCRUSTING BROWN] | 6.32  (6.63) | 6.94  (2.83) |
| *Lobophora variegata* [FRONDOSE] | 3.22  (6.82) | 3.62  (6.05) |
| *Hydrolithon* (*reinboldii*?) [CRUSTOSE CORALLINE] | 3.26  (4.80) | 1.79  (1.85) |
| *Lyngbya majuscula* [BLUE-GREEN] | 2.20  (1.90) | 1.01  (1.01) |
| *Hydrolithon* (*breviclavium*?) [CRUSTOSE CORALLINE] | 2.06  (2.59) | 1.69  (1.87) |
| *Porolithon onkodes* [BRANCHED CORALLINE] | 1.16  (0.96) | 0.73  (0.94) |
| *Colpomenia sinuosa* [FRONDOSE] | 0.85  (0.92) | 0.08  (0.04) |
| *Turbinaria ornate* [FRONDOSE] | 0.84  (0.27) | 1.53  (1.98) |
| *Hormothamnion* (*enteromorphoides*?) [BLUE-GREEN] | 0.78  (0.13) | 1.49  (1.03) |
| *Lithophylum* sp. [BRANCHED CORALLINE] | 0.53  (0.38) | 0.78  (1.37) |
| *Neogoniolithon frutescens* [BRANCHED CORALLINE] | 0.40  (0.29) | 0  (0) |
| *Stypopodium flabelliforme* [FRONDOSE] | 0.31  (0) | 0  (0) |
| *Dictyosphaeria versluysi* [FRONDOSE] | 0.29  (0.23) | 0  (0) |
| *Hormothamnion* sp. [BLUE-GREEN] | 0.29  (0.29) | 0  (0) |
| *Galaxaura rugosa* [FRONDOSE] | 0.27  (0.26) | 0  (0) |
| *Codium arabicum* [FRONDOSE] | 0.25  (0.30) | 0  (0) |
| *Sporolithon* (*erythraeum*?) [CRUSTOSE CORALLINE] | 0.22  (0) | 0  (0) |
| *Halimeda opuntia* [FRONDOSE] | 0.20  (0.16) | 0.11  (0) |
| *Porolithon gardineri* [BRANCHED CORALLINE] | 0.17  (0.13) | 0.33  (0.43) |
| TOTAL | 76.69 (55.50) | 32.21 (35.67) |

*Additional algal species/taxa each accounting for <0.2% cover in either period: *Cladophora laetevivars, Laurencia nidifica, Gracilaria coronopifolia, Halymenia formosa, Dictyota acutiloba, Padina* sp.*, Sphacelaria rigidula, Peyssonnelia rubra, Codium edule, Chnoospora implexa, Grateloupia filicina,* and *Padina australis.*

Other Ecological Characteristics

*Large Transient Animals. S*hark and jack densities are reported to be relatively high in the NWHI (all major habitats pooled), except at Midway and Kure, where apex predators were significantly lower (DeMartini and Friedlander, 2004). From an independent estimate of daily sightings, we found visits by large transient fish to the natural patch reefs to be infrequent (i.e., only one shark seen every 5.6 days of underwater surveying, and only one large jack every 4.1 days; May 1981-August 1985; N=118 field dates). Rates for summer periods (May-August) were higher (i.e., one shark every 3.8 days, and one jack every 2.9 days). Whether the presence of divers had any influence on these rates or not is unknown. Estimated sizes (mean and range) are given for species of large vertebrates in Table 6. The gray reef shark (*Carcharhinus amblyrhynchos*) predominated. Tiger shark (*Galeocerdo cuvier*) were seen occasionally around the reefs during May-July, in synchrony with peak fledging by juvenile Laysan albatross (*Diomedea immutabilis*), a prey item. Dominant jacks were *Carangoides orthogrammus, Caranx melampygus, C. ignobilis,* and *Seriola dumerili.* Less frequent sightings of other large marine vertebrates in the general Welles Harbor study area were: 26 Hawaiian monk seals, 24 rays, and 10 sea turtles (May 1981-August 1985; N=221 observation dates). About 18 spinner dolphin pods (typically 35-40 individuals) were recorded (June 1984-August 1985; N=82 dates).

*Behavioral Observations.* Incidental observations throughout the study helped confirm ecological associations of resident fishes. Adult spotted cardinalfish (*Apogon maculiferus*), a nocturnal zooplanktivore, typically sheltered in holes and crevices of the reef by day. Large groups of juveniles, which settled in high densities in some summers, were also common under ledges and in small caves. Newly settled Hawaiian Dascyllus (*Dascyllus albisella*) and saddle wrasse (*Thalassoma duperrey*) sheltered in branches of live *Pocillopora meandrina* coral heads as a preferred habitat. The Pacific gregory (*Stegastes fasciolatus*) defended evenly spaced algal territories several square meters in area with variable success. Small juveniles of several common species (e.g., *A. maculiferus*, *P. spilosoma, T. duperrey*, *C. ovalis*) were found sheltering in the long spines of the sea urchin *Diadema paucispinum* during peak summer settlement periods.

Fish-Physical Correlations

Midway patch reef fish assemblages were found to be dependent upon major physical characteristics of the reef substrate. Numerical abundance and species richness for all fish (combined), and abundance for each of the six most common species, showed a strong, significant correlation with reef area (strongest correlation), volume, and vertical relief (Table 7). All correlations among the three physical reef characteristics, area, volume, and vertical relief (independent of fish), were also highly significant (Schroeder, 1989a).

Table 6. Size class estimates for large (~SL ≥50 cm, in 5-cm bins) marine vertebrates sighted in Midway lagoon from May 1980 to August 1985.

| Species/taxa: | Mean cm (SD) | Min. cm | Max. cm | N (individuals) |
|---|---|---|---|---|
| Shark: | | | | |
| *Carcharhinus amblyrhynchos* | 125 (25) | 30 | 250 | 336 |
| *Galeocerdo cuvieri* | 255 (50) | 175 | 370 | 30 |
| *Triaenodon obesus* | 150 (15) | 120 | 185 | 4 |
| *Carcharhinus melanopterus* | 135 | 135 | 135 | 1 |
| Jack: | | | | |
| *Carangoides orthogrammus* | 45 (10) | 15 | 150 | 67 |
| *Caranx melamplygus* | 50 (10) | 15 | 110 | 59 |
| *Caranx ignobilis* | 70 (25) | 5 | 180 | 30 |
| *Seriola dumerili* | 70 (20) | 15 | 110 | 27 |
| Carangid (spp.) | 60 (10) | 25 | 100 | 23 |
| *Caranx cheilio* | 40 (10) | 15 | 100 | 17 |
| *Gnathanodon speciosus* | 50 (5) | 45 | 50 | 3 |
| *Caranx lugubris* | 65 | 65 | 65 | 1 |
| *Caranx sexfasciatus* | 110 | 110 | 110 | 1 |
| Ray: | | | | |
| *Aetobatus narinari* | 100 (10) | 50 | 150 | 13 |
| Mobulid (sp.) | 55 (5) | 50 | 60 | 2 |
| *Manta birostris* | 100 | 100 | 100 | 1 |
| Turtle: | | | | |
| *Chelonia mydas* | 60 (10) | 30 | 150 | 193 |
| Seal: | | | | |
| *Monochus schauinslandi* | 170 (20) | 100 | 210 | 18 |
| Dolphin: | | | | |
| *Stenella longirostris* | 175 (25) | 100 | 300 | 18 (pods) |

Table 7. Spearman rank correlation coefficients $r_s$ relating the numerical abundance and diversity of common species visually censused with substrate physical characteristics[1] of the respective patch reefs. (N = 142 to 193 total census replicates on 10 reefs; * P < 0.05, ** P < 0.01, *** P < 0.001, ns- not significant; for the seven species the significance level designation represents the experimentwise error rate for the group of $r_s$: * P < 0.0073, ** P < 0.0014, *** P < 0.0001, ns- not significant.)

| | Reef Substrate Characteristic | | |
| Fish Parameter: | Area | Volume | Vertical Relief |
| --- | --- | --- | --- |
| DIVERSITY | | | |
| Species Richness | 0.577 *** | 0.566 *** | 0.538 *** |
| Species Diversity (N = 32 to 36) | 0.300 ns | 0.120 ns | 0.369 * |
| | | | |
| ABUNDANCE | | | |
| All species[2] | 0.758 *** | 0.731 *** | 0.677 *** |
| | | | |
| Most abundant species: | | | |
| _Pervagor spilosoma_ | 0.449 *** | 0.419 *** | 0.365 *** |
| _Apogon maculiferus_ | 0.490 *** | 0.542 *** | 0.397 *** |
| _Dascyllus albisella_ | 0.483 *** | 0.390 *** | 0.342 *** |
| _Thalassoma duperrey_ | 0.664 *** | 0.646 *** | 0.684 *** |
| _Stegastes fasciolatus_ | 0.596 *** | 0.548 *** | 0.627 *** |
| _Chromis ovalis_ | 0.304 *** | 0.240 * | 0.245 * |
| _Gnatholepis anjerensis_ | 0.256 ** | 0.201 ns | 0.091 ns |

[1] Pairwise $r_s$ correlation coefficients between substrate physical characteristics considered independent of fish abundance are: 0.976*** for Area-Volume (N = 16); 0.814*** for Area-Relief (N = 18); and 0.814*** for Volume-Relief (N = 16).

[2] All taxa pooled, excluding _Gnatholepis anjerensis_.


_Reef Size._ The size of a reef appears to be the most useful physical attribute for predicting the structure of the fish assemblage (Sale and Douglas, 1984; Ault and Johnson, 1998); in general, fish abundance and species richness increase with patch size, due to a combination of recruitment and community dynamic processes (Helfman, 1978; Luckhurst and Luckhurst, 1978; Bohnsack, 1979; Brock et al., 1979; Gladfelter et al., 1980, Anderson et al., 1981; Carpenter et al., 1981; Sale and Douglas, 1984; Clarke, 1988). In contrast, species diversity (H') did not correlate with reef size (area or volume), possibly since H' incorporates both abundance and species richness, suggesting similarity in the structure of patch reef fish communities among different size reefs. Total fish abundance decreased on Midway patch reefs experiencing major reductions in size from storm-induced shifting sand. Two common demersal species (_T. duperrey_ and _S. fasciolatus_), which had the strongest correlations between fish abundance and the three substrate variables, also were characterized by low temporal variability in numbers and had a low but steady recruitment rate over a protracted season (Schroeder, 1985, 1989a). Quantitative resource requirements (e.g., food or shelter) may contribute to higher abundances of these two demersal feeders on larger reefs. The nocturnal cardinalfish, _A._

*maculiferus*, had the strongest correlation with reef volume, suggestive of its dependence on dark shelter. Three species (*P. spilosoma*, *D. albisella* and *C. ovalis*) whose abundances correlated less strongly with the substrate factors were all characterized by heavy settlement and high temporal variability (Schroeder, 1985, 1989a). *D. albisella* and *C. ovalis*, which are primarily midwater planktivores (Hobson, 1974; Parrish *et al*., 1984), may not depend greatly on benthic substrate for food; however, the reef is probably important for their shelter. The seasonally abundant goby, *G. anjerensis*, showed low correlations with reef substrate characteristics, as it occurred primarily on the rubble-sand base around the reef.

*Reef Complexity.* Larger reefs generally offer greater habitat complexity that can enhance juvenile and adult survival. Complexity, based on vertical relief, of the Midway patch reefs correlated strongly with fish abundance and species richness, but only weakly with species diversity. Friedlander and Parrish (1998) also showed a high positive association between substrate relief and fish abundance off Kauai. In contrast, no significant correlation between fish assemblages (based on abundance or species richness) and patch reef topographic complexity was found by Sale and Douglas (1984) or by Ault and Johnson (1998) on the Great Barrier Reef, or by Roberts and Ormond (1987) in the Red Sea. The variability of substrate complexity (i.e., frequency of peaks in the vertical relief index [=sd]) also determines reef surface area and can affect fish parameters as well (Dahl, 1973; Luckhurst and Luckhurst, 1978).

*Reef Isolation.* In our study, patch reef size and isolation varied independently, while a strong size effect may have obscured any fish patterns due to isolation. Bohnsack (1979) found that numbers and species of fish on small patch reefs increased significantly with isolation, but the effect was less pronounced on large reefs. Higher juvenile fish densities found on more isolated reef patches (Schroeder, 1987, 1989b) may be due to preferential settlement (Walsh, 1985), lower predation risk (Shulman, 1985), and less interference by neighboring reef fish (Bohnsack, 1979). Settlement and post-settlement processes appear less important for more vagile fish species (e.g., lizardfish) that move among isolated reef patches, apparently guided by habitat preferences or resource availability (Ault and Johnson, 1998).

**CONCLUSION**

Coral reef communities are complex and dynamic, even at the scale of small patch reefs. In our study at Midway, major differences and changes in reef physical attributes significantly influenced fish assemblages. While most taxa of nonteleost reef biota (e.g., visible macroinvertebrates, corals, algae) exhibited considerable spatial and temporal variability, it was not obvious that any of these differences produced major variation in the fish communities. But finer-scale processes (e.g., a species' juvenile life stage affected in a particular season) may be operating and significant. It is important to supplement studies of coral reef ecosystems with detailed information on pertinent

physical, biological and ecological variables, since these factors may have the potential to mask more subtle ecological processes. Our ability to model and predict potential impacts of harvesting or other human activities, and related ecological ramifications thereof, will require a much better understanding of the structure and functional processes of these unique and valuable systems. Information presented here on ecological characteristics of coral patch reef communities should be useful as a reference for more contemporary ecosystem studies in the NWHI, as well as comparison to other patch reefs within the NWHI and in other geographic regions.

## ACKNOWLEDGEMENTS

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# DYNAMICS OF DEBRIS DENSITIES AND REMOVAL AT THE NORTHWESTERN HAWAIIAN ISLANDS CORAL REEFS

BY

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## ABSTRACT

Previous marine debris studies in the Northwestern Hawaiian Islands (NWHI) have focused on the density, type, and tonnage of debris in various reef and island habitats. Cleanup efforts have grown from a single ship working for a small amount of time to multiple vessels for extended periods. A key element to determining the effectiveness of these efforts is the decline of debris density relative to accumulation rate in these habitats. Study sites were monitored and cleaned for up to 5 years from 1999 to 2003. We measured densities, estimated accumulation rates and projected the number of days required to completely clean the atolls. Initial clean-up efforts (1999) at two atolls removed 28-63 debris items per $km^2$ with a total cleanup of the atolls estimated to require 45 years. In subsequent years, improved techniques and greater effort has resulted in an overall pattern of decreasing debris densities, projected debris levels and projected workdays to completely clean the atolls. In the final year (2003), densities at the same two atolls ranged from 6-12 debris items per $km^2$ with cleanup estimated to require 13 years. This pattern suggests the rates of debris removal within the study sites have surpassed the rate of debris accumulation and removal activities are effectively reducing debris levels. To effectively deplete the debris below current levels, an effort should be made to decrease accumulation rates by intercepting debris at sea and preventing loss and discarding of fishing gear.

## INTRODUCTION

Marine debris is one of the largest documented anthropogenic impacts in the Northwestern Hawaiian Islands (NWHI). The Pacific Islands Fisheries Science Center Marine Debris Program began in 1996 in response to the growing threat of entanglement of the endangered Hawaiian monk seal, *Monachus schauinslandi,* in derelict fishing gear (Henderson, 2001). Removal of the derelict fishing gear began with a single vessel manned by a few divers for a few weeks per year and has expanded to an extensive program with many divers working up to 5 months each year. Currently, 440 metric tons of debris has been removed from the NWHI habitats.

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Gerrodette (1985) theorized that marine debris could be modeled as a dynamic population that moved with wind and water masses and that debris density would be a function of these physical variables. Using debris densities as an index of total debris level, we used area-specific accumulation rates and debris cleanup data to extrapolate the amount of effort required to completely clean the atolls.  We define a successful cleanup as the complete removal of all debris items to a density of zero.  For this to occur, the removal rate of debris must exceed the rate at which ocean currents deposit debris at the atoll.

## METHODS

Study Sites

Nearshore study sites were established (Donohue et. al., 2001a) at three NWHI atolls: Pearl and Hermes Atoll (PHA) and Lisianski Island (LIS) in 1999, and Kure Atoll (KUR) in 2000.  Study site areas ranged between 1.0 and 1.3 km$^2$ and were 0.5 to 10.0 meters deep.  Each study site was located on the northeast side of the reef complex, between an island and the seaward barrier reef, and was directly exposed to trade winds.

Survey Procedures and Estimation of Debris Density

Study sites were surveyed annually from 1999 to 2003 to identify debris, monitor debris densities, and remove all debris found.  Support vessels ranged from 30 to 70 meters in length and conducted operations on site from 20 to 120 days.  In all cases small craft were dispatched from the support vessels to conduct the survey and removal of submerged derelict fishing gear within the study site.  All debris items in this study were large enough to be an entanglement hazard to marine life and consisted primarily of lost and discarded fishing gear such as nets and line.

Typically four craft, each with a crew of four, would work the survey site with two craft surveying and two craft removing.  Debris encountered by the survey divers was marked with a Global Positioning System (GPS) point.  This information was passed to the removal craft following the survey team.  From the survey craft two snorkel divers were towed approximately 10 m behind a small boat at a speed of 1 to 2 knots. Divers visually surveyed the water column using strip transects approximating a parallel track search pattern (Ribic et al., 1992).  During towed surveys, divers held plywood boards (90 cm x 30 cm x 2 cm) to steer themselves in an oscillating pattern from the surface to depth while serpentining from side to side.

Surveys were conducted only when divers could see the bottom clearly from the water surface, and thus we assumed a uniform vertical detection probability.  The effective swath width of transects was determined according to measured water clarity. Water clarity was visually estimated at the outset and conclusion of each transect. Visibility estimates were obtained by stationing one diver in the water and instructing the second diver to swim away from the first diver holding a piece of green trawl net of less

than 5 m² in area, suspended approximately 1 m below the surface of the water. When the net was no longer visible to the first diver, the distance of the net from the sighting diver was recorded as the visibility estimate. For each transect, the potential visible swath width was estimated at two times the mean of the initial and final water visibility estimates. The effective swath width utilized was the lesser of the potential visible swath width or 15 m, the maximum width in which we expected divers to be able to uniformly detect debris present. We assumed a uniform detection probability within the effective sampling swath. Tracks of survey transects were logged with GPS units (Garmin 12 and 76, Garmin International) and downloaded to Geographic Information System (GIS) software (ARCVIEW, ESRI Inc.) daily. The area surveyed was estimated as the product of the transect length and swath width. Debris density (debris items/ km²) was estimated by dividing the total number of debris items encountered by the size of the area surveyed.

Debris Accumulation

A GIS overlay procedure was used to compare the initial survey transects to survey transects completed the following year. The area of overlap between initial and subsequent surveys was defined as the area resurveyed. The same process was followed for consecutive years at each of the three study sites. All debris found in the resurveyed area was assumed to have accumulated since the previous year's survey and was used to estimate the annual accumulation (Boland and Donohue, 2003).

Projection of Time Required to Completely Clean the Atolls

The effort required to completely clean an atoll was defined in workdays. A workday consisted of a small craft with a crew of four either surveying or removing debris for a period of 8 hours. The eight-hour time period included transit to and from the support vessel to the study site, and all time spent surveying and removing debris.
Projections of the amount of time required to completely clean each of the atolls were made in three steps. First, the area cleaned per workday at each atoll was determined by dividing the total area cleaned within the atoll's study site by the number of workdays at the study site. Then, within each atoll, an estimate of the total area with habitat similar to the study site was determined using maps of shallow-water benthic habitat[1]. Area estimates used for this study included habitat 10m or shallower. Many areas are too deep or lack complex hard bottom that collects marine debris; such areas were excluded from the total estimated area. Types of habitat excluded included areas specified by the atlas to be deep water (>20 meters), unconsolidated sediment, and undescribed areas. Finally, estimates of the amount of time required to completely clean each of the atolls were derived by dividing the total habitat area by the area cleaned per workday.
The total weight of each boatload of debris removed was determined using a scale attached to the vessels' cranes. Cumulative weights were pooled with the weight of debris found on the beach at each of the atolls. These values were then divided by the number of workdays at the site to compute the average mass of debris removed per workday.

## RESULTS

Overall, the area surveyed at the three study sites increased over the 5 years of effort (Table 1).  Debris density (Fig. 1), accumulation (Fig. 2) and the number of debris items (Table 2) within the survey sites decreased during the 5 years of monitoring.  KUR had 4 times the accumulation rate of PHA and LIS.  Projections of debris levels for the southern atolls (PHA, LIS) increased during the early years and then precipitously declined, whereas projections for the northernmost atoll (KUR) declined every year except 2003 (Fig. 3).  Overall, the projection of workdays needed to clean up the atolls declined (Fig. 4). The number of workdays required to clean LIS started much higher than for PHA and then declined to a level consistent with PHA and KUR.  Finally, the mass of debris harvested per workday rose dramatically between 2001 and 2002, then declined slightly in 2003 (Fig. 5).

## DISCUSSION

Towboarding is an effective method for surveying benthic targets (Fernandes, 1990; Fernandes et al., 1990; Moran and De'ath, 1992).  Fernandes (1990) tested differences in the sightability of small targets (40 cm diameter) using different survey widths.  A survey width of 9 to 15 meters, consistent with our methods, had the highest correlation of sighted targets vs. true targets.  Presently there are no estimates of sighting error.  However, nearly all pieces of marine debris encountered in this study were relatively large targets (> 40 cm) that tended to float up from the seafloor, making them conspicuous and difficult to miss.

At PHA, debris density increased and then decreased while density at the other two atolls did not.  This is due to a difference in the accumulation between the first half and the second half of the study.  The accumulation rate during 2000-2001 was nearly twice the rate for 2002-2003.  Debris density and accumulation at KUR decreased except in 2003, when a rise in accumulation increased density.

Debris density and accumulation conformed to a latitudinal trend.  These variables were low at the two southernmost atolls, PHA and LIS, with the lowest densities and accumulation at LIS.

Accumulation of debris may be affected by the Subtropical Convergence Frontal Zone (STCFZ).  The STCFZ is defined by both a thermohaline front and atmospheric forcing by the North Pacific Ocean subtropical high (Roden, 1991), which create a convergence of oceanic surface waters north of the NWHI from latitude 31º N to 34º N (Roden, 1991).  The frontal zone has been proposed as a mechanism for transporting a disproportionately large amount of debris to the northern-most locations in the Hawaiian Islands (Ingraham and Ebbesneyer, 2001; Donohue et al., 2001a, b).  This mechanism

[1]National Oceanic and Atmospheric Administration. 2003. Atlas of the Shallow-Water Benthic Habitats of the Northwestern Hawaiian Islands (Draft), 160 pp.

is supported by our reported accumulation patterns at the three study sites. Kure Atoll, the northernmost study site and closest to the STCFZ, consistently had the highest accumulation, whereas LIS, the southernmost study site and furthest from the STCFZ, consistently had the lowest accumulation.

The number of projected debris items was influenced by both debris density and atoll size. Because PHA had a higher density than LIS, it had a larger projected number of debris items despite being 30 percent smaller. Because KUR is smaller than PHA, clean-up efforts reduced the density quickly at KUR, leaving PHA with the highest projected debris levels in 2001 and 2002.

Differences in the projected number of workdays were affected primarily by the total area of habitat at each atoll rather than debris density. Projected workdays decreased over time at LIS and PHA but remained higher than those for KUR. Because of its larger size, LIS required four times the number of workdays needed for PHA and KUR. It is possible that the smaller area surveyed at LIS in 1999-2001 affected the precision of the estimate, and in fact the LIS projections for the first 3 years of monitoring may have a positive bias. The high density value for LIS in 1999 (Fig. 1) may indicate the reduced precision associated with smaller survey areas. Because of its smaller size, KUR had a lower and relatively constant number of projected workdays even though it had the highest density and accumulation.

The density of debris found and removed was greater than accumulation at all sites except for KUR. Current removal efforts at PHA and LIS have effectively reduced debris levels so low that this type of survey and removal is exhibiting diminishing returns. In 2001, 8 workdays were spent surveying 57% of the study site at PHA and recorded the highest debris density and accumulation. In 2003, 6 workdays covered 96% of the area but debris density and accumulation were at their lowest. KUR has a much higher accumulation rate and current removal efforts have been insufficient there.

The rate of accumulation is an important consideration for estimating debris density, projected debris levels, and projected workdays. The focus for further work should be to decrease accumulation. Extensive effort is required to send small craft into the shallows and use divers to remove debris by hand. One way to improve the efficiency of removal efforts would be to decrease accumulation by intercepting the debris before it reaches the atoll habitats. Satellites and airborne remote sensing have been used successfully to locate debris in Alaskan waters. Once debris was located on the high seas, a ship could intercept it and haul it aboard with deck cranes. Another possibility would be a program to pay fisherman to retrieve debris they encounter on the high seas. The ideal strategy would be both a removal effort on the high seas using remote sensing and the continued removal of debris in the atoll habitats by divers.

Because our accumulation estimates, projected debris levels, and projected workdays are based on extrapolating from a single study site at each atoll, they must be regarded with caution. Atoll habitats with differing degrees of relief will snag and retain variable amounts of passing debris. Measurements of accumulation and debris densities linked to specific habitats are needed to better reflect spatial variability in debris densities and produce more comprehensive and reliable estimates of overall debris levels and the effort required to clean the atolls. It may be possible to determine debris

accumulation and densities within various habitats using the recently drafted benthic habitat maps for the NWHI.  Using the habitat atlas, a pilot effort focused on a new study site of complex, reticulated shallow reefs in the center of Pearl and Hermes Atoll and produced a preliminary annual accumulation estimate of 158 items/km², an estimated total debris level of 84,096 items, and a projection of 83,677 workdays to clean the reef (Jacob Asher, Joint Institute of Marine and Atmospheric Research, University of Hawaii, unpublished data).  These values are far higher than those determined from our study site. The differences in these estimates illustrate the difficulties and remaining uncertainties in assessing the magnitude of marine debris.

The current success at finding and removing debris at KUR, PHA, and LIS is trending downward. At LIS and PHA, removal clearly exceeds accumulation, resulting in declining estimates of debris density and projected workdays.  At these locations current marine debris survey and removal operations appear to be at a point of diminishing returns.  Alternate techniques should be explored to reduce accumulation.

Table 1. Area of the three study sites surveyed by site and year.

| | | Percent surveyed | | | | |
|---|---|---|---|---|---|---|
| Atoll | Study site (km$^2$) | 1999 | 2000 | 2001 | 2002 | 2003 |
| LIS | 1.17 | 38[a] | 27[a] | 33[a] | 60 | 58 |
| PHA | 1.00 | 66[a] | 64[a] | 57[a] | 92 | 96 |
| KUR | 1.26 | NA | 69[a] | 61[a] | 75 | 57 |

[a] From Boland and Donohue (2003).

Table 2. Atoll area 10 meters and shallower (Area), debris items on survey transect not in resurveyed area (O), debris items in resurveyed area (A) and total debris items surveyed (T).

| Atoll | Area | 1999 | | | 2000 | | | 2001 | | | 2002 | | | 2003 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | O | A | T | O | A | T | O | A | T | O | A | T | O | A | T |
| LIS | 363.2 | 28 | NA | 28 | 6 | 2 | 8 | 11 | 0 | 11 | 3 | 1 | 4 | 4 | 0 | 4 |
| PHA | 244.6 | 18 | NA | 18 | 52 | 14 | 66 | 30 | 12 | 42 | 12 | 6 | 18 | 3 | 9 | 11 |
| KUR | 69.9 | NA | NA | NA | 144 | NA | 144 | 33 | 60 | 93 | 17 | 27 | 44 | 10 | 40 | 50 |
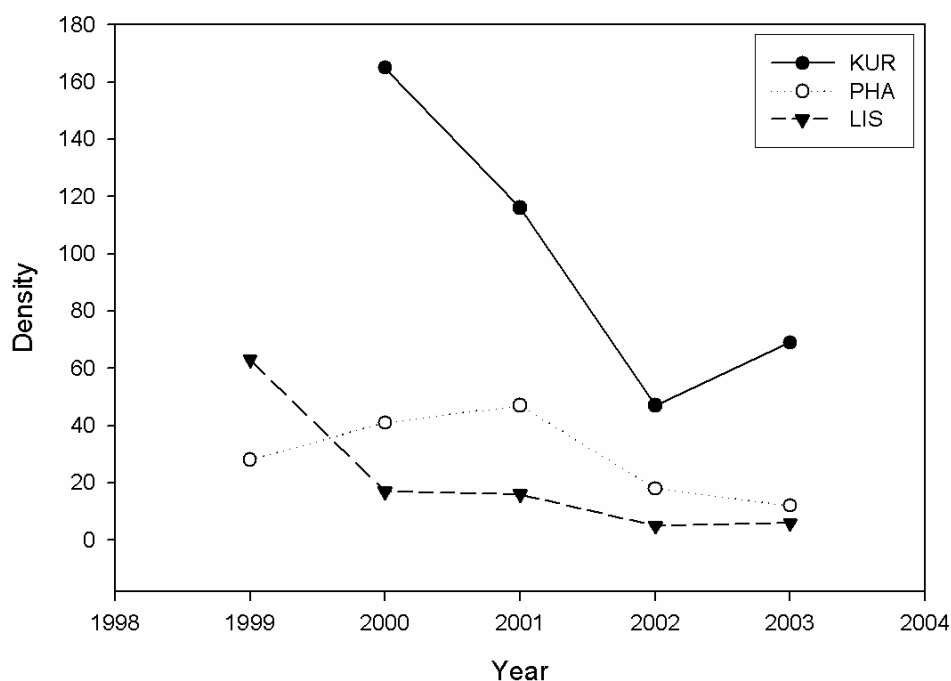


**Figure 1**. Debris density (debris items/km$^2$) by year at the three study sites: Lisianski Island (LIS), Pearl and Hermes Atoll (PHA) and Kure Atoll (KUR). All items identified in the survey were removed. Data for 1999 are from Donohue et al. (2001a).and those for 2000-2001 from Boland and Donohue (2003).

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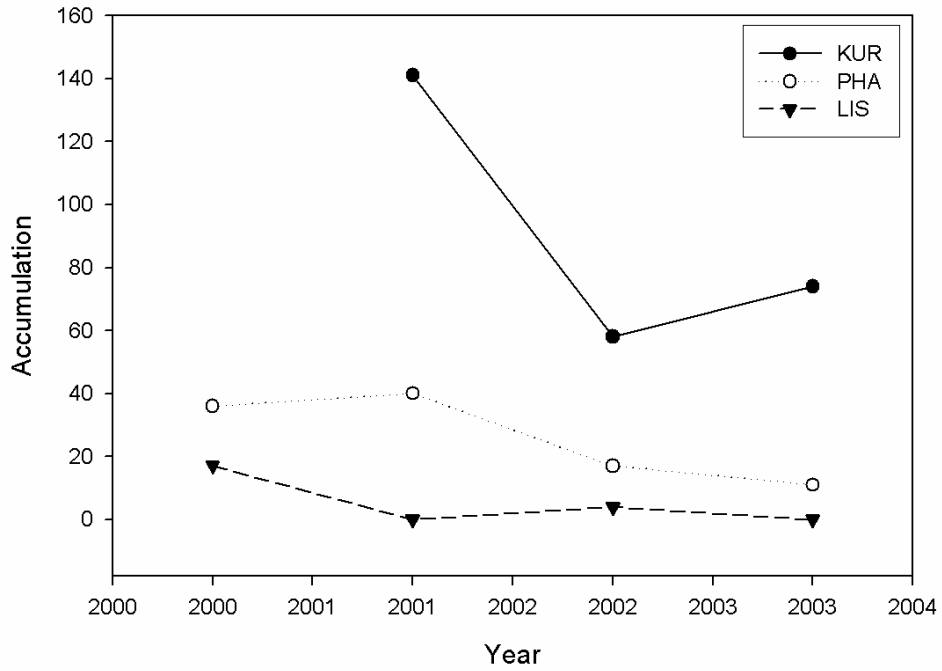


**Figure. 2**. Annual debris accumulation (debris items/km$^2$) at the three study sites: Lisianski Island (LIS), Pearl and Hermes Atoll (PHA) and Kure Atoll (KUR) . Data for 2000-2001 are from Boland and Donohue (2003).
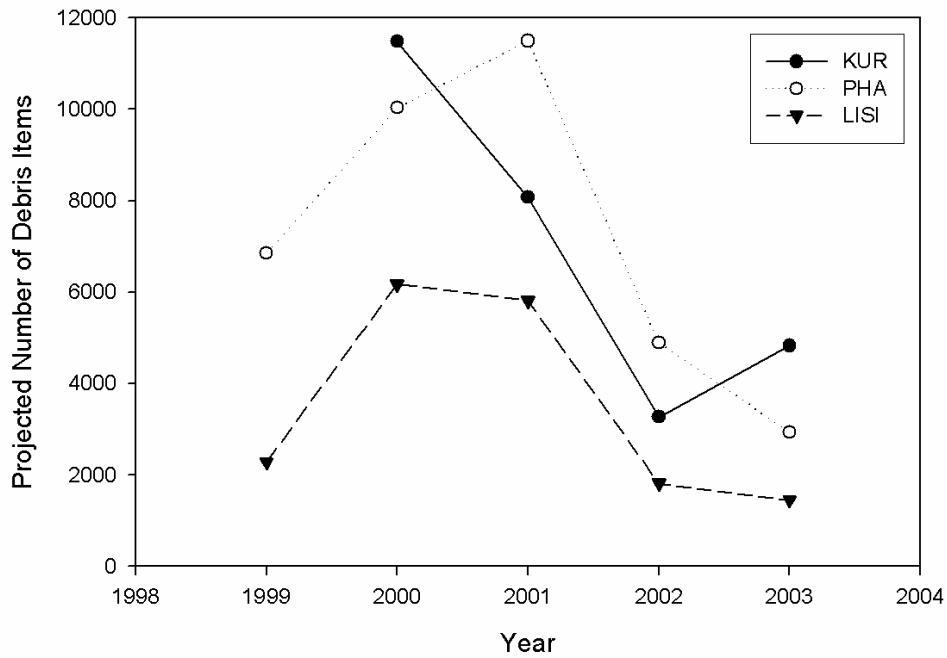


**Figure. 3**. Annual projections of total debris levels for the entire area (10-meter isobath and shallower) at the three study sites: Lisianski Island (LIS), Pearl and Hermes Atoll (PHA) and Kure Atoll (KUR).

**Figure 4**. Annual projections of the number of workdays required to completely survey and remove all debris within atolls (10-meter isobath and shallower) at the three study sites: Lisianski Island (LIS), Pearl and Hermes Atoll (PHA) and Kure Atoll (KUR).
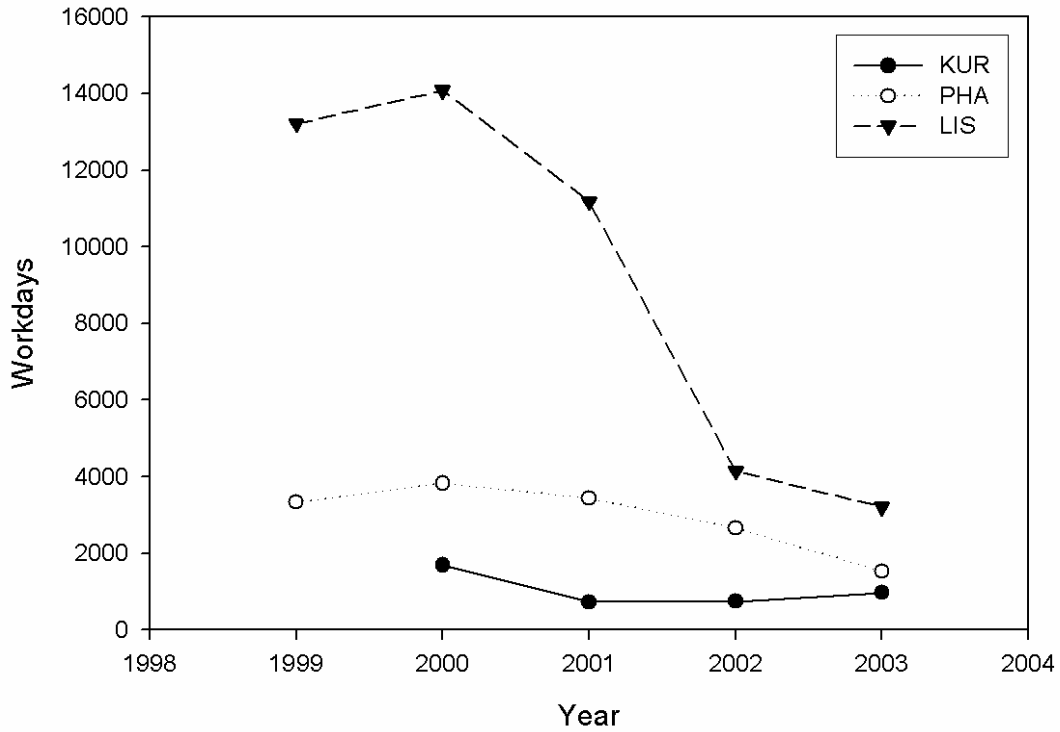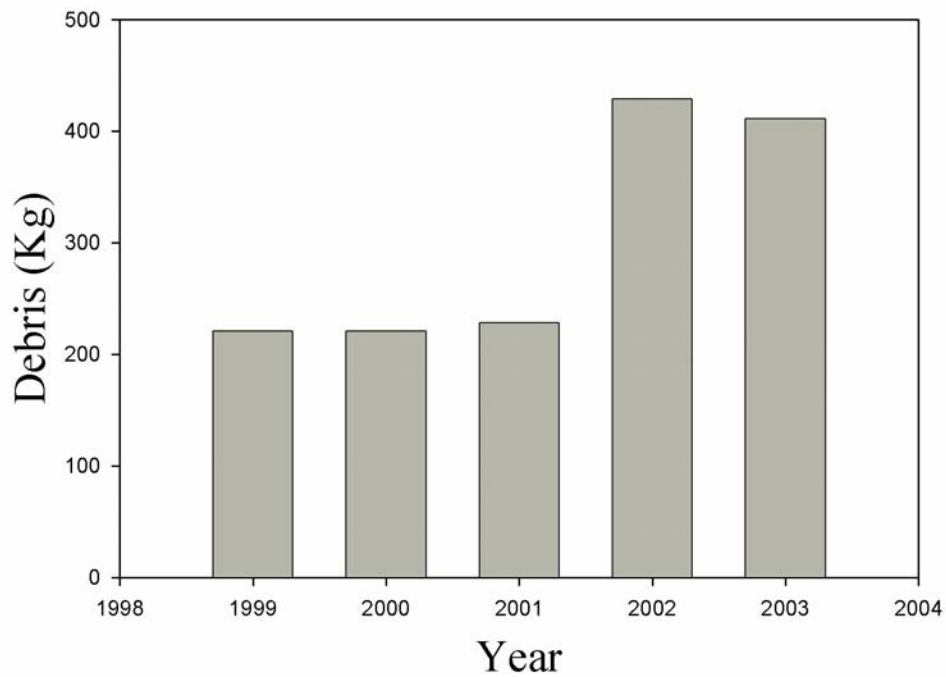


**Figure 5.** Annual estimates of the total weight (kg) of debris removed per workday from the water and beaches at all three atolls combined

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# BASELINE LEVELS OF CORAL DISEASE IN THE NORTHWESTERN HAWAIIAN ISLANDS

BY

GRETA SMITH AEBY[1]

## ABSTRACT

There has been a worldwide increase in the reports of diseases affecting marine organisms.  In the Caribbean, mass mortalities among organisms in reef ecosystems have resulted in major shifts in community structure.  However, our ability to fully understand recent disease outbreaks is hampered by the paucity of baseline and epidemiological information on the normal disease levels in the ocean.  The Northwestern Hawaiian Islands (NWHI) is considered one of the last relatively pristine coral reef ecosystems remaining in the world.  As such, it provides the unique opportunity to document the normal levels of disease in a coral reef system exposed to limited human influence.

In July 2003, baseline surveys were conducted at 73 sites throughout the NWHI to quantify and characterize coral disease.  Ten disease states were documented with the most common disease found to be *Porites* trematodiasis. This disease was widespread and is known to exclusively affect *Porites* sp. coral. Numerous other conditions were observed but at much lower levels of occurrence.  Numbers of colonies affected by *Porites* trematodiasis were not enumerated but other types of conditions were counted with the average prevalence of disease estimated at 0.5%.  Several of the observed disease states were distinct from what has been described from other coral reef systems. Coral genera exhibited differences in types of syndromes and prevalence of disease. Pocilloporids, common corals on the reefs of the NWHI, were comparatively resistant to disease.  In contrast, acroporids showed the greatest damage from disease and the highest estimated prevalence of disease.

## INTRODUCTION

Coral disease is a rising problem on coral reefs worldwide.  The numbers of diseases and coral species affected, as well as the distribution of diseases, have all increased within the last decade (Porter et al., 2001; Green and Bruckner, 2000; Sutherland et al., 2004; Weil, 2004).  Recent epizootics of coral disease have resulted in significant losses of coral cover.  An outbreak of white band disease in the 1980s killed acroporid corals all over the Caribbean substantially decreasing coral cover (Glatfelter, 1982; Aronson and Precht, 2001), and a recent outbreak of white pox disease in the Florida Keys reduced the cover of *Acropora palmata* by up to 70% (Patterson

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et al., 2002). In the Caribbean, coral disease has been implicated as a major factor contributing to the decline of coral reefs, resulting in apparent ecological phase shifts from coral- to algal-dominated ecosystems (Hughes, 1994; Aronson and Precht, 2001; Porter et al., 2001; Sutherland et al., 2004). What has changed in our oceans to produce this unprecedented increase in disease within the last decade? Increased anthropogenic stress on nearshore environments, overfishing, and environmental conditions associated with global climate change have all been implicated as contributing to increased levels of disease (Harvell et al., 1999; Barber et al., 2001). However, our ability to fully understand recent increases in coral disease is hampered by the paucity of baseline and epidemiological information on the normal disease levels in the ocean (Harvell et al., 1999). It is difficult to understand the underlying mechanisms affecting disease occurrence without knowing normal levels of disease in a healthy ecosystem.

The Hawaiian Archipelago consists of the inhabited Main Hawaiian Islands (MHI) and the more remote Northwestern Hawaiian Islands (NWHI), which span ~1,800 kilometers across more than five degrees of latitude in the northern part of the Archipelago (Fig. 1). The NWHI is a series of islands, banks, shoals, and atolls that have been under federal and state protection since 1909. Their remoteness and protected status has spared the NWHI from much of the degradation experienced by most other coral reef systems. The NWHI is considered to be one of the last relatively pristine, large-scale coral reef ecosystems remaining in the world. As such, a unique opportunity exists here to document normal levels of disease in a coral reef system exposed to only limited human influence. In 2000, the NWHI Ecosystem Reserve was established and a series of multi-agency ship-based expeditions were initiated to assess the biodiversity, status, and management needs of the shallow reefs of the NWHI. In 2002, disease assessment was added to the protocol to characterize and investigate the dynamics of coral disease on these reefs. The purpose of this study was to further characterize and quantify coral disease on the reefs of the NWHI.

**METHODS AND MATERIALS**

Study Area

The NWHI consists of ten island/banks and atolls which include from southeast to northwest: Nihoa, Necker, French Frigate Shoals, Gardner Pinnacles, Maro Reef, Laysan, Lisianski, Pearl and Hermes, Midway, and Kure (Fig. 1). Nihoa and Necker are small basalt islands, each surrounded by a shallow (<50 m) shelf. French Frigate Shoals is an open atoll with a small basaltic pinnacle in the interior. Gardner Pinnacles consists of three small rocks on an extensive submerged bank. Maro Reef is a complex of shallow reticulated reefs with no associated island. Laysan and Lisianski are low carbonate islands that crest shallow, submerged banks. Northwest of these are three atolls: Pearl and Hermes, Midway, and Kure Atolls (Maragos & Gulko, 2002).
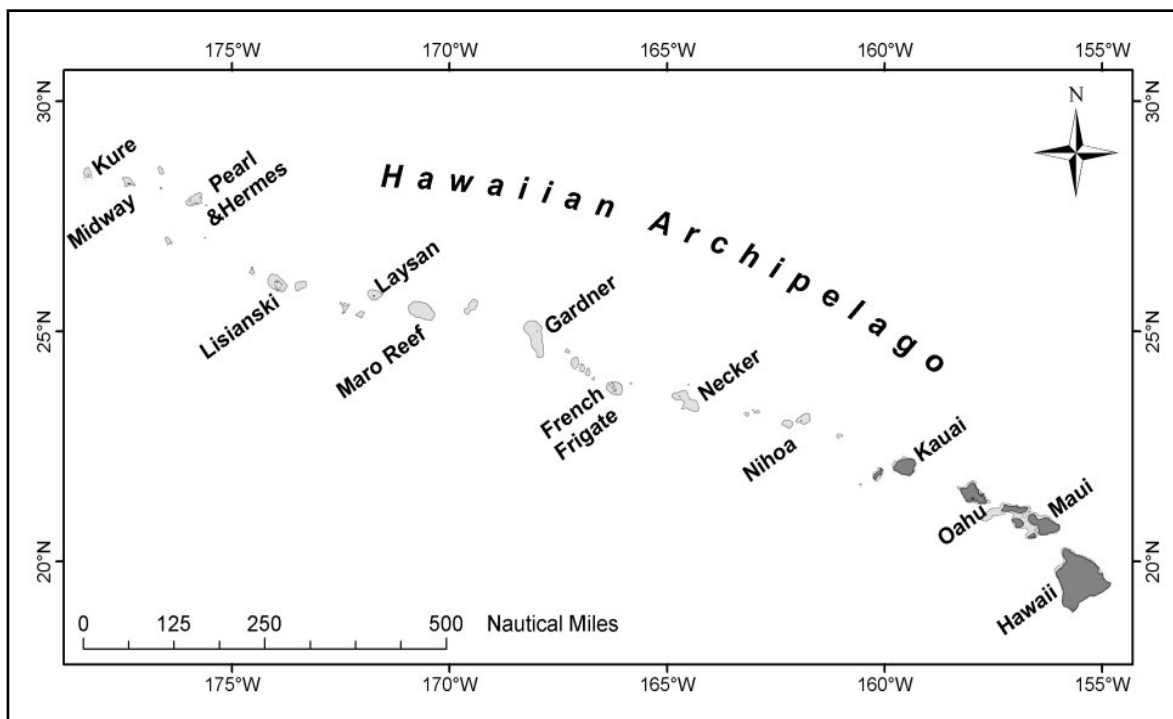
**Figure 1.** Map of the Hawaiian Archipelago.

Disease Surveys

In July 2003, 73 sites were surveyed for coral disease at nine islands/atolls across the NWHI as part of a long-term monitoring program (Table 1). The 73 sites were selected for long-term monitoring from a pool of 391 sites that had been surveyed during annual research cruises in 2000, 2001, and 2002. Criteria for selection of long-term monitoring sites included representing a range of habitats and biological communities at each location and having a high probability of being accessible to divers on annual research cruises under prevalent sea conditions. At each site, two consecutive 25-m lines, separated by approximately 5 m, were laid out along depth contours. Coral community structure was documented on the first of the two 25-m transect lines by recording coral colonies by size class. All corals, with the colony center within 1 m on either side of the transect line, were enumerated and placed into one of seven size classes: <5, 5-10, 10-20, 20-40, 40-80, 80-160, and >160 cm. These protocols have been used successfully in other studies to document coral community structure within the NWHI (Maragos et al., 2004). Disease assessment was conducted within each 25 x 2m belt transect, as well as, within a wider 25 x 6m belt transect along the 2nd line as time allowed. All coral colonies with disease signs were described, enumerated, and photographed, and samples were collected for follow-up laboratory analyses. Due to time constraints, colonies with the disease *Porites* trematodiasis were not enumerated, but presence or absence of the disease was recorded for each site.

Table 1. Number of sites surveyed for coral disease in the NWHI in July 2003. Sites are categorized by island and reef zone.

| Atoll/island | code | zone | # sites surveyed | depth range (ft) | total reef area surveyed for disease (m^2) |
|---|---|---|---|---|---|
| Necker | NEC | shelf | 3 | 38-46 | 375 |
| French Frigate Shoals | FFS | backreef | 1 | 5 | 100 |
| | | forereef | 5 | 10-38 | 500 |
| | | lagoon | 6 | 16-37 | 1500 |
| Gardner Pinnacle | GAR | shelf | 3 | 40-64 | 300 |
| Maro Reef | MAR | forereef | 6 | 35-60 | 600 |
| | | lagoon | 3 | 31-52 | 300 |
| Laysan | LAY | shelf | 3 | 40-48 | 600 |
| Lisianski | LIS | forereef | 3 | 40-51 | 600 |
| | | lagoon | 5 | 30-56 | 1000 |
| Pearl & Hermes | PHR | backreef | 6 | 3-22 | 1200 |
| | | forereef | 5 | 39-52 | 1000 |
| | | lagoon | 4 | 26-36 | 800 |
| Midway Atoll | MID | backreef | 4 | 3-5 | 800 |
| | | forereef | 4 | 38-47 | 800 |
| | | lagoon | 3 | 7-15 | 600 |
| Kure Atoll | KUR | backreef | 3 | 5-7 | 600 |
| | | forereef | 3 | 36-49 | 600 |
| | | lagoon | 3 | 11-22 | 600 |
| **total** | | | **73** | | **12,875** |

Statistical Analysis

   Time constraints underwater prevented us from enumerating 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 average number of colonies/$m^2$ found within the 25x2m belt transect using the following equation:.

number of corals examined for disease per site =
[avg. number of corals per $m^2$][X total area surveyed for disease ($m^2$)]

Prevalence of disease was then calculated as follows:

[(number of diseased colonies per site)/(number of colonies examined per site)] 100

To determine overall prevalence of disease for coral genera and disease states, data from all surveys were combined and calculated as follows:

[(number of diseased colonies (all sites combined))/(number of colonies examined (all sites combined))] 100

Overall prevalence was calculated separately for each of the four coral genera (A*cropora, Montipora, Pocillopora, Porites*). For example:

[(number of diseased A*cropora* colonies (all sites combined))/(number of A*cropora* colonies examined (all sites combined))] 100

Overall prevalence was also calculated separately for each disease state with the denominator (# colonies examined) being limited to the specific coral genera affected by that disease state.

Frequency of disease occurrence (FOC) was calculated as:

[(number of sites with disease)/(total number of sites surveyed)] 100

Disease states were categorized by coral genera. FOC of each disease state was calculated as:

[(number of sites having a particular disease state)/(total number of sites containing the affected genera)] 100

For each coral genus, FOC was calculated as:

[(number of sites having disease of each genera)/(number of sites containing that genera of coral)] 100

The data were not normally distributed, even with transformations, therefore non-parametric statistics were applied. Differences in prevalence of coral disease among islands and reef zones were tested using Kruskal-Wallis non-parametric one-way analysis of variance. Differences in overall prevalence of disease among coral genera were tested with a Chi-square test for equality of distributions.

## RESULTS

Coral Community Structure

The relative abundance of coral taxa varied by island and by zone within islands (Table 2). In atoll geomorphic systems, backreef zones at the three highest-latitude atolls (Kure, Midway, Pearl and Hermes) are dominated by montiporids and/or pocilloporids, whereas at French Frigate Shoals the backreef is dominated by massive and encrusting *Porites* and other coral (predominantly *Acropora*). At all four atolls, the forereef zone is

Table 2. Summary of colony counts within belt transect surveys conducted at each site. Data reflect the average proportion (%) of colonies within each transect belonging to each of the four dominant genera. Number in parentheses is standard error.

| Atoll/island | zone | *Acropora* | *Montipora* | *Pocillopora* | *Porites* |
|---|---|---|---|---|---|
| Necker | shelf | 0 | 2.1 (1.1) | 40.4 (8.3) | 57.5 (9.4) |
| French Frigate Shoals | backreef | 21.6 | 0 | 15.7 | 62.7 |
| | forereef | 17.1 (9.8) | 6.9 (5.5) | 27.1(14.2) | 48.9 (9.4) |
| | lagoon | 19.8 (16.3) | 3.7 (1.4) | 22.3 (11.7) | 54.2 (17.3) |
| Gardner Pinnacle | shelf | 0.33 (0.3) | 0.35 (0.18 | 9.1 (2.8) | 90.2 (3.2) |
| Maro Reef | forereef | 0.09 (0.09) | 25.2 (8.1 0 | 6.1 (1.7) | 68.6 (8.7) |
| | lagoon | 6.4 (3.3) | 22.9 (6.7) | 23.5 (9.5) | 47.1 (17.6) |
| Laysan | shelf | 0 | 3.2 (1.6) | 40.1 (30.0) | 56.7 (28.4) |
| Lisianski | forereef | 0 | 7.0 (3.0) | 7.9 (4.1) | 84.1 (3.4) |
| | lagoon | 0 | 33.0 (7.7) | 16.3 (6.3) | 50.7 (4.5) |
| Pearl & Hermes | backreef | 0 | 43.7 (19.7) | 43.8 (16.5) | 12.5 (4.7) |
| | forereef | 0 | 0 | 16.0 (11.3) | 84.0 (11.3) |
| | lagoon | 0 | 4.3 (3.0) | 27.1 (21.9) | 68.6 (21.1) |
| Midway Atoll | backreef | 0 | 47.8 (27.6) | 24.3 (12.0) | 27.9 (16.4) |
| | forereef | 0 | 0 | 13.9 (8.7) | 86.1 (8.7) |
| | lagoon | 0 | 0 | 52.9 (27.4) | 47.1 (27.4) |
| Kure Atoll | backreef | 0 | 24.5 (13.2) | 42.4 (6.5) | 33.1 (18.5) |
| | forereef | 0 | 0 | 48.6 (21.6) | 51.4 (21.6) |
| | lagoon | 0 | 0 | 61.1 (28.7) | 38.9 (28.7) |

co-dominated by pocilloporids and by massive and encrusting *Porites*. In the lagoon zone, branching *Porites compressa* dominates the coral fauna at Kure and at Pearl and Hermes, whereas massive and encrusting *Porites* along with *Porites compressa* co-dominate the lagoon zone at French Frigate Shoals. Shelf zones surrounding Necker, Gardner Pinnacle, and Laysan are sparsely populated by massive and encrusting *Porites* and by pocilloporids.

Overall Occurrence of Coral Disease

Ten different disease states were documented from the four major coral genera found in the NWHI (Table 3). Coral disease was found at 68.5% of the sites surveyed, but prevalence of disease was low, with an average of 0.5% of the colonies having signs of disease (range=0 - 7.09%). FOC of disease varied among the islands with Laysan and Lisianski having the highest (FOC=100%) and Midway having the lowest (FOC=27.3%)(Table 4).

Prevalence of disease also differed among islands with FFS and Midway having the highest prevalence of disease (Fig. 2). However, intra-island variability was also high, therefore between-island comparisons were not statistically significant (Kruskal-Wallis, $X^2$=13.2, *df*=8, P=0.1059). Disease prevalence varied among reef zones (Table

Table 3.  Description of 10 coral diseases found on the reefs of the NWHI in July 2003.
Frequency of occurrence = (# of sites with presence of the disease/# of sites containing
affected genera) X 100.

| genera | disease | characteristics | distribution | freq of occurrence (%) | host species |
|---|---|---|---|---|---|
| **Porites** | Porites trematodiasis (TRM) | 3-5mm diameter, pink to pale, swollen nodules on coral colony.  Nodules can be clustered or widely distributed on colony. | all islands | 69.8 | P. lobata, P. compressa, P. evermanni |
| | Porites tissue loss syndrome (TLS) | Irregular  patches of  tissue loss.  Patches usually bordered by a narrow, bleached, pink or mucous band.  Older exposed skeleton is algae-colonized. | FFS, MAR, PHR, MID, KUR | 15.9 | P. lobata, P. evermanni |
| | Porites discolored tissue thinning syndrome (DTTS) | Areas of tissue thinning and discoloration that are poorly defined from surrounding healthy tissue.  Polyps are reduced or absent. | FFS, MAR, LAY, LIS, PHR, KUR | 22.2 | P. lobata |
| | Porites brown necrotizing disease (BND) | Diffuse, well-defined, areas of dark brown discoloration characterized by a gelatinous texture and loss of recognizable polyp structure. | PHR | 3.2 | P. lobata |
| **Montipora** | Montipora tissue loss syndrome (TLS) | Well-defined areas of tissue loss revealing intact white skeleton.  Border between healthy and diseased tissue usually with band of mucous, bleached tissue, or thin (1 polyp deep) layer of white necrotic tissue.  Older exposed skeleton is algae-colonized. | MAR, LAY, MID | 21.1 | M. patula, M. capitata, M. turgescens, M. verrilli |
| | Montipora patchy tissue loss (PTL) | Multiple, well-defined circular areas of tissue loss revealing intact white skeleton.  Can have residual necrotic tissue in center.  Lesions usually ~ 5mm in diameter but can coalesce to form larger areas. | MAR | 2.6 | M. patula |
| | Montipora growth anomaly (GA) | Well-defined areas of excess skeletal growth.  Tissue overlying growth anomaly usually paler with calices reduced to absent. | PHR | 2.6 | M. capitata |

Table 3. Continued.

| Acropora | Acropora white syndrome (WS) | Well-defined areas of tissue loss revealing intact white skeleton. Pattern of tissue loss can be patchy or can appear as a linear pie wedged area of tissue loss extending from the center of the table coral to the outer edge. Older exposed skeleton is algae-colonized. | FFS | 9.1 | *A. cytherea* |
| | *Acropora growth anomaly (GA)* | Well-defined areas of excess skeletal growth. Anomalies can range in size from < 1cm to >35cm in diameter. Two types have been described (Work and Rameyer, 2002). One type is compact with reduced calyx structure and the other type has elongated, malformed calices. | FFS | 18.2 | *A. cytherea* |
| *Pocillopora* | white band disease (WBD) | Narrow, linear band of tissue loss revealing bare skeleton. | PHR | 1.4 | *P. meandrina* |

Table 4. Frequency of occurrence of coral disease within islands/atolls of the NWHI. Frequency of occurrence = (# sites with diseased coral/# sites surveyed) x 100.

| island/atoll | # sites surveyed | # sites w/ diseased coral | freq of occurrence (%) |
|---|---|---|---|
| | | | |
| Necker | 3 | 1 | 33.3 |
| French Frigate Shoals | 12 | 8 | 66.7 |
| Gardner Pinnacle | 3 | 2 | 66.7 |
| Maro | 9 | 8 | 88.9 |
| Laysan | 3 | 3 | 100 |
| Lisianski | 8 | 8 | 100 |
| Pearl & Hermes | 15 | 10 | 66.7 |
| Midway | 11 | 3 | 27.3 |
| Kure | 9 | 7 | 77.8 |
| | | | |
| **total** | 73 | 50 | 68.5 |
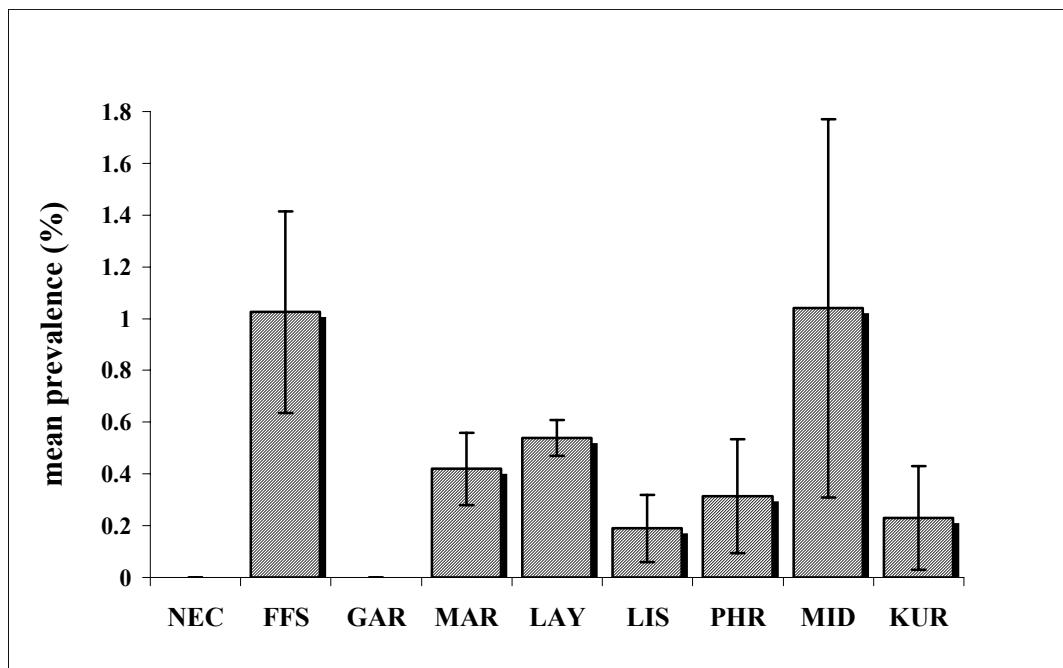
**Figure 2.** Mean prevalence (+SE) of coral disease at sites across the NWHI. Seventy-three sites were surveyed in July 2003. Prevalence = (# diseased corals/total # corals) X 100. NEC=Necker; FFS=French Frigate Shoals; GAR=Gardner; MAR=Maro; L=Laysan; LIS=Lisianski; PHR=Pearl and Hermes; MID=Midway; KUR=Kure.;

5), but again variability was high, and among-zone comparisons were not statistically significant (Kruskal-Wallis, $X^2$=4.44, $df$=3, P=0.2176). Disease prevalence varied among coral genera with *Acropora* having the highest prevalence of disease and *Pocillopora* having the lowest ($X^2$=125.1, $df$=3, P<0.0001; Fig. 3).

Distribution, Frequency of Occurrence, and Prevalence of Each Disease State

Distribution of the different coral diseases varied widely. Some diseases, such as *Porites* trematodiasis, were widespread (occurring at all islands surveyed), whereas others, such as *Pocillopora* white band disease only occurred at a single site (Table 3). The frequency of occurrence of the different diseases followed a similar pattern with some of the most widely distributed diseases such as *Porites* trematodiasis also being the most frequently encountered (69.8% of the sites containing *Porites*). Other common diseases included *Porites* discolored tissue thinning syndrome (FOC=22.2%) and *Montipora* tissue loss syndrome (FOC=21.1%). Other diseases were encountered less frequently during surveys (Table 3).

Prevalence of the different diseases varied with *Acropora* growth anomalies having the highest prevalence (1.85%) and *Porites* brown necrotizing disease having the lowest (0.012%) (Fig. 4).

Table 5. Average prevalence of disease within the different reef zones in the NWHI. Surveys were conducted in July 2003. Prevalence = (# diseased corals/total # corals) x 100. Number in parentheses is standard error.

| reef zone | Atoll/island | # sites surveyed | avg. prevalence (%) |
|---|---|---|---|
| Backreef | | | |
| | Kure | 3 | 0.62 (0.62) |
| | Midway | 4 | 2.9 (1.8) |
| | Pearl & Hermes | 6 | 0.096 (0.06) |
| | FFS | 1 | 0 |
| | **total** | **14** | **0.99 (0.57)** |
| Forereef | | | |
| | Kure | 3 | 0.074 (0.037) |
| | Midway | 4 | 0 |
| | Pearl & Hermes | 5 | 0.83 (0.64) |
| | FFS | 5 | 0.97 (0.49) |
| | Maro | 6 | 0.44 (0.17) |
| | Lisianski | 3 | 0.502 (0.27) |
| | **total** | **26** | **0.51 (0.16)** |
| Lagoon | | | |
| | KUR | 3 | 0 |
| | MID | 3 | 0 |
| | PHR | 4 | 0 |
| | LIS | 5 | 0 |
| | MAR | 3 | 0.38 (0.28) |
| | FFS | 6 | 1.2 (0.69) |
| | **total** | **24** | **0.36 (0.20)** |
| Shelf | | | |
| | LAY | 3 | 0.54 (0.069) |
| | GAR | 3 | 0 |
| | NEC | 3 | 0 |
| | **total** | **9** | **0.18 (0.09)** |
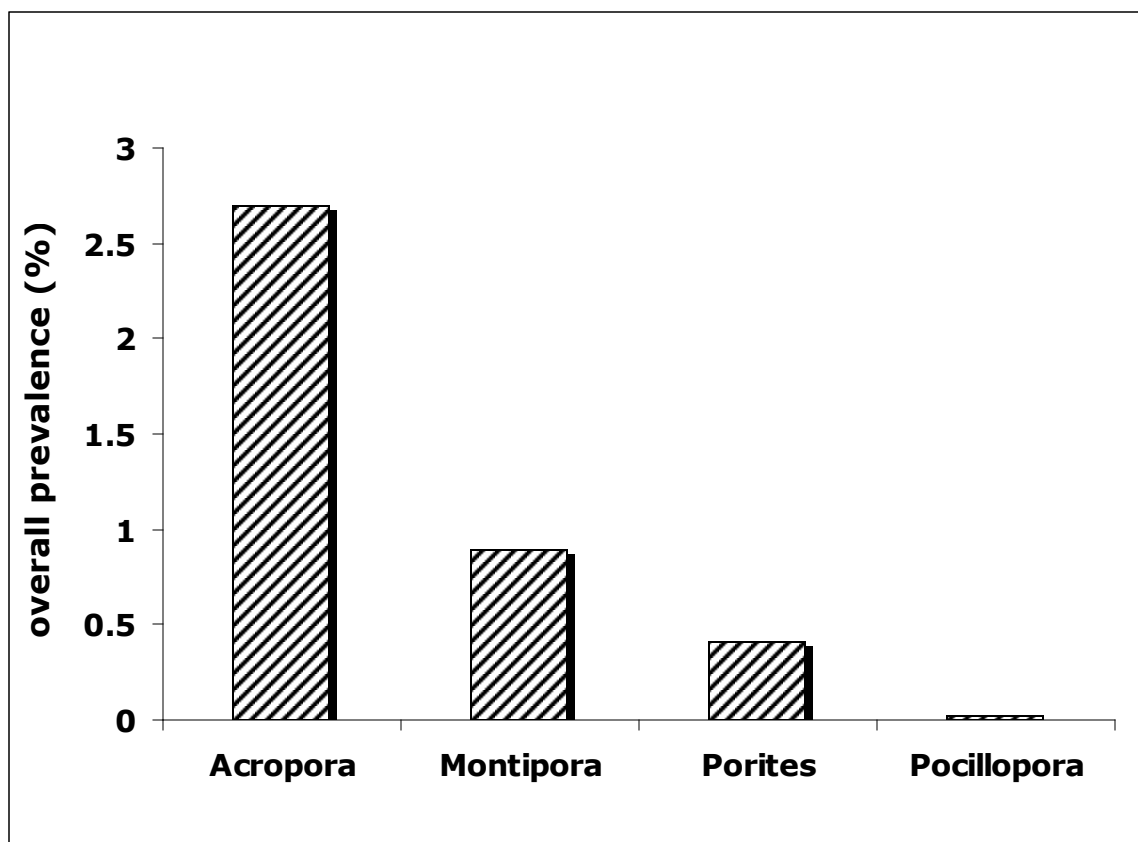
**Figure 3.** Overall prevalence of disease in the four major coral genera in the NWHI. Seventy-three sites were surveyed in July 2003. Prevalence (all surveys combined) is calculated as the number of diseased colonies per genera/total number of colonies per genera X 100.


## DISCUSSION

Approximately 0.5% of the corals examined were found to have signs of disease on the pristine reefs of the NWHI. These findings are important as they allow the level of coral disease in a healthy coral-reef ecosystem to be compared with coral reefs impacted by humans, both within the Hawaiian Archipelago and in other regions of the world. Disease levels found in the NWHI were much lower than what has been reported for other reefs, both in the Indo-Pacific and the Caribbean. Willis et al. (2004) surveyed eight sites along the Great Barrier Reef (GBR) and found the prevalence of disease in hard corals to range from 7.2-10.7%. Raymundo et al. (in press) surveyed eight sites in the Philippines and reported an overall prevalence of disease of 14.2%. In the Caribbean, Weil (2004) reported an average prevalence of 5.28% for surveys conducted at 28 sites from nine regions across the wider Caribbean. Santavy et al. (2001) assessed coral disease at 32 stations throughout the Florida Keys and found disease prevalence to range from 1.0% to 28.2% (avg. 9.6%).

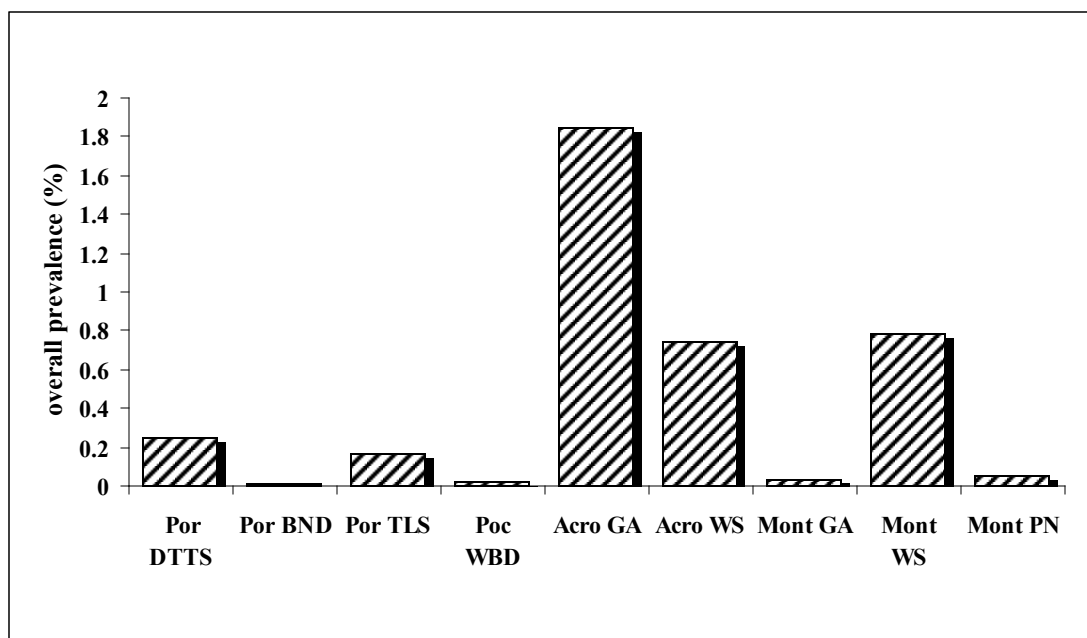**Figure 4.** Overall prevalence of each disease state in the NWHI (73 sites surveyed in July 2003). Prevalence (all surveys combined) per disease state is calculated as the number of diseased colonies/ total number of colonies of the affected genera X 100. Por DTTS=*Porites* discolored tissue thinning syndrome; Por BND=*Porites* brown necrotizing disease; Por TLS=*Porites* tissue loss syndrome; Poc WBD= *Pocillopora* white band disease; Acro GA=*Acropora* growth anomaly; Acro WS=*Acropora* white syndrome; Mont GA=*Montipora* growth anomaly; Mont TLS=*Montipora* tissue loss syndrome; Mont PTL=*Montipora* patchy tissue loss.

Ten coral disease states are described from the four major coral genera on the reefs of the NWHI. Four diseases were found to affect *Porites*, three affected *Montipora*, two affected *Acropora,* and one affected *Pocillopora*. In other areas of the Indo-Pacific, similar numbers of diseases are being reported. Six disease states were described from the Philippines (Raymundo et al., in press), and eight categories of disease have been described from the Great Barrier Reef (GBR) (Willis et al., 2004). However, on the GBR, all corals with tissue loss were classified as white syndrome regardless of coral genera or distinctive patterns of tissue loss, and thus eight categories represent a conservative number of disease states. In contrast, 22 diseases have been recorded from the Caribbean (Green and Bruckner, 2000; Sutherland et al., 2004; Weil, 2004). However, research on coral disease in the Caribbean has been ongoing for the past 30 years whereas disease research in the Indo-Pacific only recently has been initiated. For example, this study is the first quantitative disease survey ever conducted in the NWHI. The numbers of diseases described from the Indo-Pacific will no doubt increase as more areas are explored.

Disease signs similar to 7 of the 10 reported disease states within the NWHI have also been reported from other areas of the Indo-Pacific. *Porites* trematodiasis has a widespread distribution across the Indo-Pacific having been reported from Australia (Willis et al., 2004), Main Hawaiian Islands (Aeby, 1998a ), and Okinawa (Yamashiro, 2004). *Montipora* tissue loss syndrome and *Porites* tissue loss syndrome are reported

from Australia (Willis et al., 2004) and the Philippines (Raymundo et al., in press). *Acropora* white syndrome and *Pocillopora* white band disease are reported from Australia (Willis et al., 2004). Growth anomalies in both *Acropora* and *Montipora* have been recorded from Australia (Willis et al., 2004), Johnston Atoll (Work et al., 2001), American Samoa (Work and Rameyer, 2002) and Okinawa (Yamashiro et al., 2000, 2001; Yamashiro, 2004). *Pocillopora* white band disease is the only disease found in the NWHI that is similar to what has been described from the Caribbean. It must be noted that there are regional differences in names assigned each set of field disease signs. For example, swollen pink spots on *Porites* are called *Porites* trematodiasis in Hawaii, pink spot in Australia, and *Porites* pink block disease in Okinawa. It is hoped that through the efforts of the Coral Disease and Health Consortium (CDHC) (www.coral.noaa.gov/ coral_disease/cdhc.shtml) that this nomenclature problem will eventually be resolved. It should also be noted that any similarities in field signs of disease between regions does not necessarily imply the diseases have the same etiology.

Three of the disease states found in the NWHI have not yet been described from elsewhere in the world. They include *Montipora* patchy tissue loss (although this may have been reported as white syndrome in Australia), *Porites* tissue thinning syndrome, and *Porites* brown necrotizing disease. Whether these diseases are specific to Hawaii or not remains to be seen, as studies elsewhere in the Indo-Pacific are still very limited. Much more work is needed to document the occurrence, distribution, etiology, and transmission of diseases across the Indo-Pacific.

The distribution and frequency of occurrence of the different coral diseases varied widely within the nine islands/atolls of the NWHI. Some diseases were both widespread and encountered frequently while other disease states were quite rare. One factor affecting disease occurrence is the distribution of their host populations. Acroporids are limited to five islands/atolls within the NWHI (Necker, French Frigate Shoals, Gardner Pinnacle, Maro, Laysan). The abundance and diversity of *Acropora* is highest on the reefs at French Frigate Shoals (Grigg, 1981; Grigg et al., 1981; Maragos et al., 2004) which is also the only place acroporid disease was found. In contrast, *Porites* is the dominant coral on the reefs of the NWHI comprising 63.5% of the overall coral community within our transects and found at all islands. Accordingly, poritid diseases had both a wider distribution and higher frequency of occurrence than did acroporid diseases. In fact, the most common and widespread disease was *Porites* trematodiasis. In other reef systems where *Porites* is less common, *Porites* trematodiasis is also less common (Willis et al., 2004). However, host distribution is not the only factor controlling disease occurrence, as some poritid diseases, such as *Porites* brown necrotizing disease, were found to be quite rare (FOC=2.7%).

Other factors associated with a pathogen's life history also are important in determining its relative success. Where its coral host is abundant, *Porites* trematodiasis is quite successful, and this can be explained by the attributes of its life history. *Porites* trematodiasis is caused by the encystment of the larval stage of a digenetic trematode in the coral host (Cheng and Wong, 1974; Aeby, 1998a). Completion of the parasite's life cycle occurs when coral-feeding fish ingest the infected polyp, with the adult worm subsequently residing in the guts of fish (Aeby, 1998b). The encysted stage of

the parasite within the coral host can last for several months before senescence of the parasite (Aeby, 1998a). The pink, swollen appearance of the infected polyp attracts fish that preferentially feed on the infected polyps (Aeby, 1992 and 2002). Both of these attributes, the ability to stay viable for long periods of time awaiting transmission and the altered appearance of the coral host, result in an increased probability of successful transmission into the final fish host. Fecal release of the parasite's eggs into the environment from the fish host facilitates transmission of this disease across the reef. Little is known about the etiology or ecology of other diseases, but when more information is available, a clearer picture of the proximate factors controlling disease occurrence should emerge.

Patterns in disease prevalence among the coral genera suggest *Acropora* is the most susceptible to disease and *Pocillopora* is the most resistant. *Acropora* comprised only 2.2% of the overall coral community along our transects. Yet, acroporids showed the highest overall prevalence of disease with *Acropora* growth anomalies having the highest prevalence of all described diseases. *Acropora* white syndrome also resulted in the greatest amount of damage of any of the diseases. An outbreak of *Acropora* white syndrome at one site at FFS resulted in massive tissue loss from numerous large table corals (*A. cytherea*). Tissue loss was visually estimated as ranging from 10-60% of the affected colonies (Aeby, in press). Acroporids have also been greatly affected by disease in Australia (Willis et al., 2004) and have been decimated by disease in the Caribbean (Green and Bruckner, 2000; Porter et al., 2001; Patterson et al., 2004; Weil, 2004). Acroporids were one of the major frame-building corals in the Florida Keys, but losses of acroporids are now averaging 87% or greater (Miller et al., 2002; Patterson et al., 2002; Sutherland et al., 2004).

Hawaii differs from other regions in the exceptionally low occurrence of disease in pocilloporids. In Australia, Willis et al. (2004) found pocilloporids to have the highest prevalence of disease among all coral families surveyed despite pocilloporids having the lowest coral cover. In contrast, pocilloporids are a common coral in the NWHI (21.1% of the overall coral community along our transects) yet seldom showed signs of disease. In fact, an estimated 6,081 pocilloporid colonies were examined during our surveys with only a single colony exhibiting any signs of disease. This suggests that pathogens do not necessarily affect the most common or abundant corals. It also raises the question as to why pocilloporids within the NWHI are so disease free. It could be that the pocilloporids within the NWHI possess inherent mechanisms of defense against disease not found in corals from other regions. Alternatively, since the studies in Australia were conducted on more impacted reefs than found in the NWHI, it may suggest that pocilloporids could be sensitive to certain stressors which makes them more susceptible to disease. Future surveys planned for the impacted reefs of the inhabited Main Hawaiian Islands may shed light on this question.

The distribution and levels of overall disease differed among the nine islands/atolls surveyed. The occurrence of disease would depend on a number of factors, such as host density, host susceptibility, environmental conditions, or mode of transmission, among others. The NWHI encompasses a variety of reef habitats including shallow backreefs, deeper forereefs, and protected lagoonal reefs. Each reef zone has a unique

set of environmental conditions that influence both coral community structure and overall coral cover. These differences in coral community among reef zones could explain variability in coral disease found among islands. For example, Nihoa, Necker, and Gardner are all high islands surrounded by deeper, forereef environments. These islands experience high wave energy in the winter months, therefore their coral communities are low density encrusting *Porites lobata* and scattered colonies of *Pocillopora meandrina* (Maragos et al, 2004). Accordingly, these sites have few disease states and a low overall prevalence of disease. In contrast, the atoll environments encompass forereef, backreef, and lagoonal reef environments. The number of coral species and colony densities are greater, as well as the number of disease states and prevalence of disease.

Differences in coral community also varied within reef zones and thus affected the level of disease found within zones. For example, at Midway Atoll some backreefs are dominated by montiporids that are more susceptible to disease as compared to other backreefs dominated by the more disease resistant pocilloporids. It is the taxon of corals found on a reef, regardless of which island or reef zone, that primarily affects the types and levels of disease that will occur.

Levels of disease also were also affected by disease outbreaks at two of the atolls (French Frigate Shoals and Midway). At French Frigate Shoals, there was an outbreak of white syndrome on acroporids at one site (prevalence =4.1%), and at Midway there was a high prevalence of *Montipora* tissue loss syndrome at one site (prevalence=7.1%). Interestingly, the montiporids at the site at Midway had experienced a severe bleaching event the year prior (2002) (Aeby et al., 2003; Kenyon et al., in press). The relationship between bleaching stress and disease susceptibility is one that should be investigated more thoroughly especially in light of the predicted increases in bleaching events associated with global climate change (Hughes et al., 2003)

With increased human populations, the scale of human impacts on reefs has grown exponentially. Compounding these anthropogenic stressors are the impacts of global climate change, predicted to result in more frequent bleaching episodes and higher levels of disease (Hughes et al., 2003). Although disease is a natural component of all ecosystems, levels of disease that are higher than expected or changes in levels of disease through time could be indicative of underlying problems. This study of coral disease on the pristine reefs of the NWHI provides an estimate of the normal levels of disease expected on a healthy reef with minimal impact from anthropogenic stress. In this study, colonies with *Porites* trematodiasis were not enumerated; therefore, the prevalence of disease reported here is quite conservative. However, this study combined with further work in the NWHI, which includes enumeration of *Porites* trematodiasis, will serve as an important baseline for comparison with other regions and for monitoring disease levels through time. From these studies, a clearer picture should emerge of the underlying mechanisms that may be influencing the levels of disease found on coral-reef ecosystems throughout the world.

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# THE ROLE OF OCEANOGRAPHIC CONDITIONS AND REEF MORPHOLOGY IN THE 2002 CORAL BLEACHING EVENT IN THE NORTHWESTERN HAWAIIAN ISLANDS

BY

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## ABSTRACT

Researchers on two research cruises to the Northwestern Hawaiian Islands (NWHI) in September 2002 recorded widespread massive coral bleaching, particularly at Kure, Midway, and Pearl and Hermes atolls at the northern end of the Hawaiian Archipelago. While details of the coral bleaching and biological impacts are presented by Kenyon et al. (in review), this work is focused on the contributions of broad-scale meteorological and oceanographic conditions, as well as the local effects of reef morphology, to the severity and distribution of the observed coral bleaching.

Anomalously high regional sea surface temperature (SST), identified as the primary proximate factor in the bleaching event, was related to a band of quiescent winds and high insolation intersecting the northern end of the Hawaiian Archipelago. These conditions were in turn related to a variable ridge of high atmospheric surface pressure present both immediately preceding and during the event. Atoll/reef morphology and circulation patterns inferred from *in situ* observations are used to explain localized elevation of SST within the three northernmost atolls which increased the severity of bleaching within lagoon and backreef habitats.

A method of predicting overall differences in bleaching between adjacent reef groups in the absence of detailed *in situ* temperature data is presented. This method relies on regression of lagoon and backreef volumes and satellite SST to describe observed coral bleaching.

## INTRODUCTION

Mass coral reef bleaching events, when significant numbers of corals in a reef system expel their symbiotic zooxanthellae, often lead to major coral mortality and decreased coral cover. Although many other local stressors to coral reefs worldwide also have been documented, coral bleaching has been identified as globally significant and arguably the major worldwide threat to coral reefs (Hoegh-Guldberg, 1999). Determining

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an area's susceptibility to bleaching through identification of causal factors in the context of climate change is a key to designing successful refugia for coral reefs (West and Salm, 2003).

High water temperatures and high insolation have been found to be the primary proximate factors in mass bleaching events (Lesser, 2004; Hoegh-Guldberg, 1999). A number of researchers have used 1ºC, or a similar threshold, over the maximum value in a monthly long-term sea surface temperature (SST) climatology (sometimes referred to as the maximum monthly climatological mean) as a proxy for bleaching conditions (Hughes et al., 2003). These thresholds have been used successfully in several cases to predict both the onset of coral bleaching and overall bleaching intensity (Strong et al., 1997; Berkelmans et al., 2004).

The Northwestern Hawaiian Islands (NWHI), part of the Hawaiian Archipelago, stretch 1,200 nautical miles (2,200 km) northwest of the northernmost of the Main Hawaiian Islands (MHI) (Fig. 1). By Executive Orders in 2000 and 2001, the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve was designated, making the NWHI the second largest coral reef reserve in the world, second only to Australia's Great Barrier Reef Marine Park. The Islands are also unique in their extreme remoteness; the area is one of very few coral reef ecosystems largely free from significant fishing impacts and other local anthropogenic stressors. Several researchers have suggested further that the central Pacific location and high latitude of the Archipelago (Kure, the northernmost reef area, is centered at 28.5º N latitude) would make it one of the last places in the world to experience a massive bleaching event (Turgeon et al., 2002; Hoegh-Guldberg, 1999). These unique characteristics of the NWHI support the supposition that the NWHI provide important refugia for coral ecosystems from both localized anthropogenic stressors and degradation due to forecasted climate change.

Beginning in late July 2002, the U.S. National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch program identified elevated SST by both satellite and *in situ* observations near Midway in the NWHI. Based on these alerts, the focus of an annual interdisciplinary NOAA-led NWHI Reef Assessment and Monitoring Program expedition in September was modified to better investigate the predicted bleaching. Extensive data from these cruises were used to confirm that widespread massive coral bleaching had occurred, particularly at Kure, Midway, and Pearl and Hermes atolls at the northwestern end of the Hawaiian Archipelago (Aeby et al., 2003; Kenyon et al., in review).

In this paper, reasons for the gross distribution and severity of coral bleaching in the NWHI in 2002 are examined. Observed bleaching patterns are attributed to both large-scale regional oceanographic and meteorological conditions and to the local influences of reef and atoll morphology. Large differences between insular water temperatures and regional conditions have been noted in the Hawaiian Islands, especially during bleaching conditions (Jokiel and Brown, 2004). An empirical method of predicting overall differences in the amount of bleaching among reefs, based on lagoon and backreef containment volume, is discussed. For specific detail of the spatial and taxonomic distribution of bleaching severity, the reader is referred to Kenyon et al., in review.
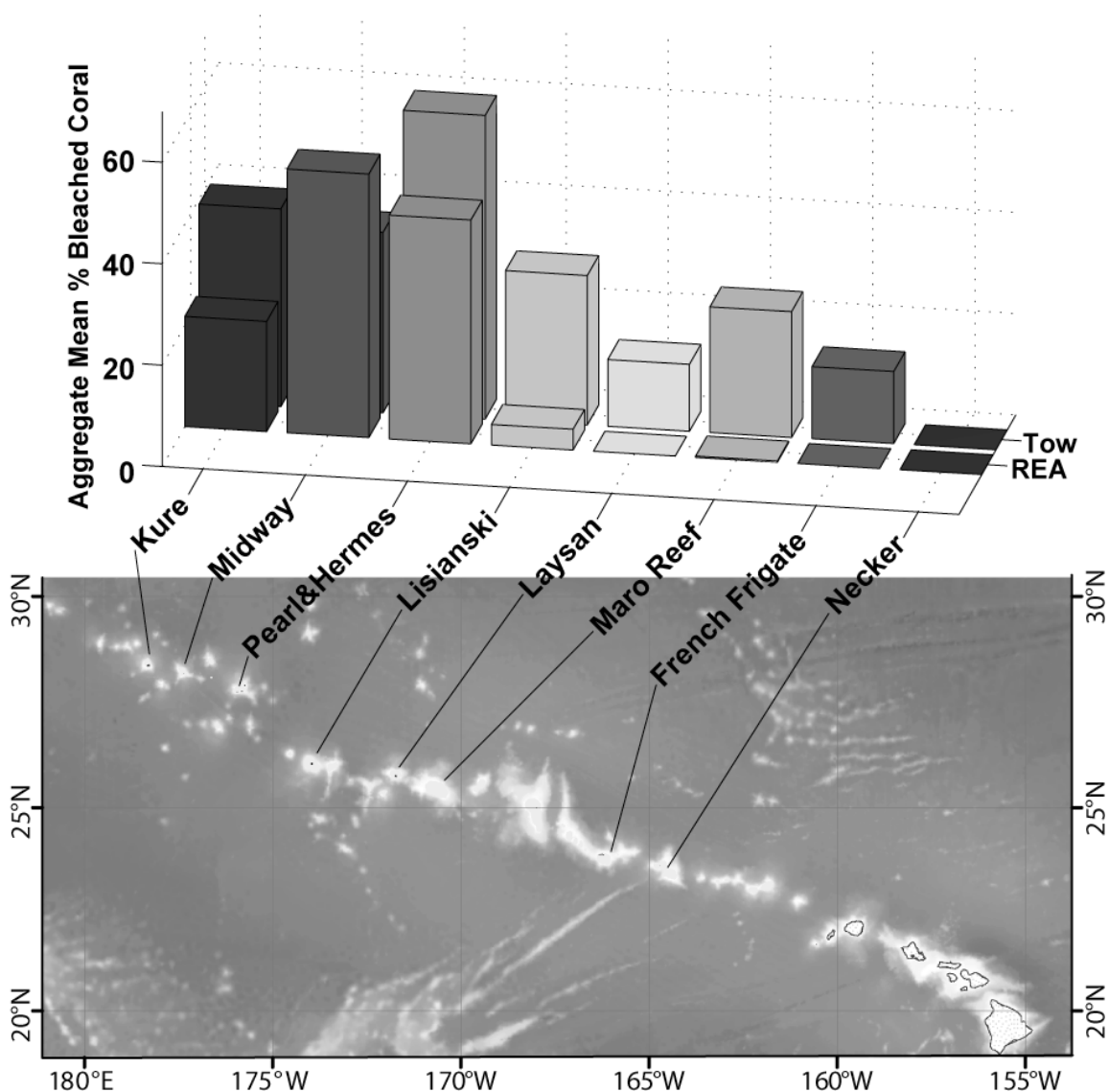
**Figure 1.** The Hawaiian Archipelago and gross distribution of coral bleaching observations from the 2002 Northwestern Hawaiian Islands mass bleaching event. Percent bleaching values presented in the bar graph above were generated by taking the mean observed percent bleached coral at all survey locations at each reef group location listed. Two survey techniques were used: rapid ecological assessments at fixed transects (REA) and towed-diver benthic survey video analysis (TOW). No bleaching was observed in the Main Hawaiian Islands in 2002.

## METHODS

Three gridded data products were used to identify and describe the larger scale conditions implicated in the bleaching event. NOAA Pathfinder 9-km SST, a stable, well-documented satellite sea surface temperature data product (Vazquez et al., 2002) was used to establish a chronology of the elevated SST event and study overall SST distribution patterns. One degree latitude by one degree longitude location boxes were

constructed around each island/reef group area in the Hawaiian Archipelago; the mean temperature for each spatial dataset was calculated for each location box to provide a time series. Maximum SST anomaly and degree heating weeks (DHW), a useful metric of heat exposures (Strong et al., 1997; Wellington et al., 2001), were calculated from this time series using the following equation:

$$DHW = \sum [SSTA > (Max. \ Monthly \ Mean)]$$

In other words, the value of DHW used here is simply the sum of SST Anomalies (SSTA) greater than the maximum monthly climatological mean SST for the particular location in question, over some time period, usually a year or less. For instance, 1 week of SST 1.5ºC above the maximum monthly climatological mean would result in a DHW value of 1.5.

NASA/JPL QuikSCAT SeaWinds, a satellite scatterometer surface level wind product (Piolle, 2002), was used to identify spatial and temporal correlations between wind patterns and SST. The same boxes defined for Pathfinder SST were used for the wind time series.

NOAA NCEP/NCAR Reanalysis 1 (Kalnay et al., 1996) was used to qualitatively examine a number of surface variables, including: atmospheric pressure gradients, cloud cover, and incoming short-wave radiation levels.

The NOAA-led interdisciplinary Pacific Reef Assessment and Monitoring Program (Pacific RAMP) routinely collects *in situ* oceanographic data at the coral reef ecosystems in the U.S.-affiliated Pacific islands. These data include intensive sampling of temperature and salinity at different depths, performed concurrently with ecological assessments, as well as long-term temperature, salinity, current, wind, atmospheric pressure, and solar radiation measurements from instrument moorings (Brainard et al., 2004). Although intensive sampling of temperature and salinity was performed approximately 1 month after the end of the period of elevated SST, only data from instrument moorings was collected during the period of highly elevated regional SST indicated from the Pathfinder data. Temperature and salinity data from other time periods and other locations have been investigated to provide insights into small-scale circulation patterns during similar conditions. These data then were used to infer the existence of similar small-scale circulations and water properties in the NWHI during the 2002 event as have been observed elsewhere (see Results and Discussion section).

Estimates of coral bleaching used in this paper are derived from two methods of reef assessment utilized by NOAA Pacific RAMP: 1) Rapid Ecological Assessments (REA) belt transects, and 2) towed-diver benthic survey videos. Details of these methods are given in Kenyon et al.(in review). All quantitative bleaching estimates given in this paper are mean values for each of the assessment methods at each NWHI reef location (Fig. 1, Table 1).

Lagoon and backreef volumes were determined by digitizing the location of the reef crest at all NWHI reefs using IKONOS satellite imagery. The reef crest was identified generally as the interior limit of breakers visible in the imagery. This delimiter was easily defined in atoll morphologies such as French Frigate Shoals or Midway; areas of extremely complex morphology, such as Maro Reef or the Lisianski/Neva Shoals complex, sometimes required highly subjective estimations. Backreef/lagoon volumes

Table 1. Data summary table. REA and Towboard bleaching columns represent the mean fraction of bleached coral to total coral of all samples at each reef (after Kenyon et al., in review). SSTA and DHW represent the Pathfinder maximum SST anomalies and degree heating weeks, respectively. Area and volume columns represent lagoon and backreef planimetric areas and volumes derived from IKONOS satellite imagery.

| | REA | | Towboard | | | | | |
| | sites | bleaching | tows | bleaching analysis | SSTA | DHW | Area | Volume |
|---|---|---|---|---|---|---|---|---|
| Kure | 9 | 0.217 | 11 | 0.390 | 1.967 | 7.13 | 4.61E+07 | 1.41E+08 |
| Midway | 9 | 0.520 | 15 | 0.356 | 1.603 | 6.89 | 6.65E+07 | 2.13E+08 |
| Pearl& Hermes | 14 | 0.442 | 22 | 0.599 | 1.496 | 5.87 | 3.60E+08 | 2.93E+09 |
| Lisianski | 7 | 0.041 | 10 | 0.295 | 0.752 | 2.85 | 5.06E+07 | 2.42E+08 |
| Laysan | 3 | 0.000 | 4 | 0.132 | 0.405 | 1.72 | 1.69E+06 | 3.60E+06 |
| Maro | 5 | 0.003 | 6 | 0.248 | 0.233 | 1.45 | 6.41E+07 | 6.11E+08 |
| French Frigate | 11 | 0.000 | 15 | 0.142 | 0.016 | 0.06 | 2.45E+08 | 1.91E+09 |
| Necker | 1 | 0.000 | 0 | 0.000 | -0.112 | 0.00 | 1.60E+04 | 6.42E+04 |
| Nihoa | - | - | - | - | -0.467 | 0.10 | - | - |
| Kauai | - | - | - | - | 0.168 | 0.78 | - | - |
| Oahu | - | - | - | - | 0.298 | 0.44 | - | - |

were then estimated by integrating depth values within the digitized reef crest; depths were calculated from IKONOS imagery using a method provided by Stumpf et al.(2003). Multiple regression analysis was used to establish relationships between DHW, lagoon and backreef volumes, and coral bleaching. A numerical algorithm was used to identify the relationship of the regression variables and associated coefficients.

## RESULTS AND DISCUSSION

Large-Scale Regional Conditions

Reviewing the Pathfinder SST time series at selected locations, a rapid rise in sea surface temperatures followed by approximately 4 weeks of elevated temperatures is readily apparent at the northern end of the chain (Fig. 2). Pathfinder temperatures were well over 1 degree above the maximum monthly climatological mean at Midway, Kure, and Pearl and Hermes atolls during this event; temperatures of this magnitude often are associated with coral bleaching (Strong et al., 1997; Wellington et al., 2001). Reef groups towards the southeast experienced progressively smaller positive temperature anomalies and DHWs with distance from these northern atolls (Fig. 2). The spatial extent of this high temperature anomaly can be seen as a broad band across the northern end of the Hawaiian Archipelago, while the Main Hawaiian Islands experienced near normal or even slightly cooler than normal surface water temperatures (Fig. 3a).
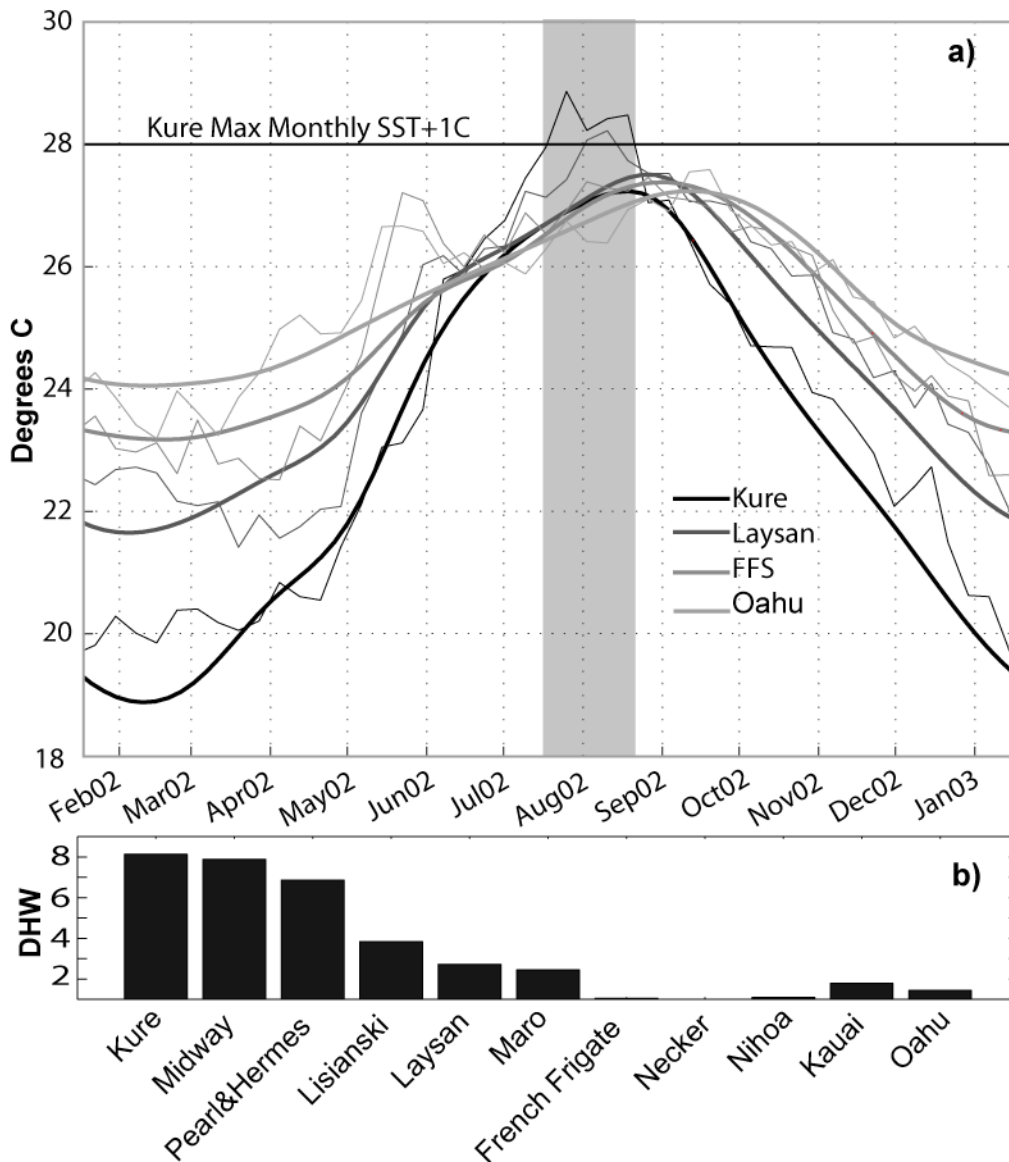
**Figure 2.** a) NOAA Pathfinder SST time series at four locations in the Hawaiian Island Chain centered on the summer of 2002. The thicker smooth lines represent interpolated monthly climatological Pathfinder SST; the finer lines represent the 2002 time series; both were constructed from 1°x1° boxes surrounding each region above. The approximately four-week period of highly elevated Pathfinder SST (July 28 – August 29) is highlighted with a grey bar in the center of the plot. b) Degree Heating Weeks (DHW) for 2002 constructed from the same 1°x1° boxes.

**Figure 3**. a) NOAA Pathfinder SST anomaly composite during summer 2002 period of NWHI elevated temperatures, July 28 – August 29.  b) NASA/JPL Quikscat winds (wind stress overlayed by wind vector arrows) composite during summer 2002 period of increasing SSTs, July 16 − August 13.  c) Mean NCEP Sea Level Pressure Reanalysis, July 16 − August 16.  d) Mean NCEP Surface Short Wave Radiation Reanalysis, July 16 − August 16.  In each graphic above, the Hawai'i Exclusive Economic Zone (EEZ) is indicated with a heavy black line; all island shorelines in the archipelago are also plotted.
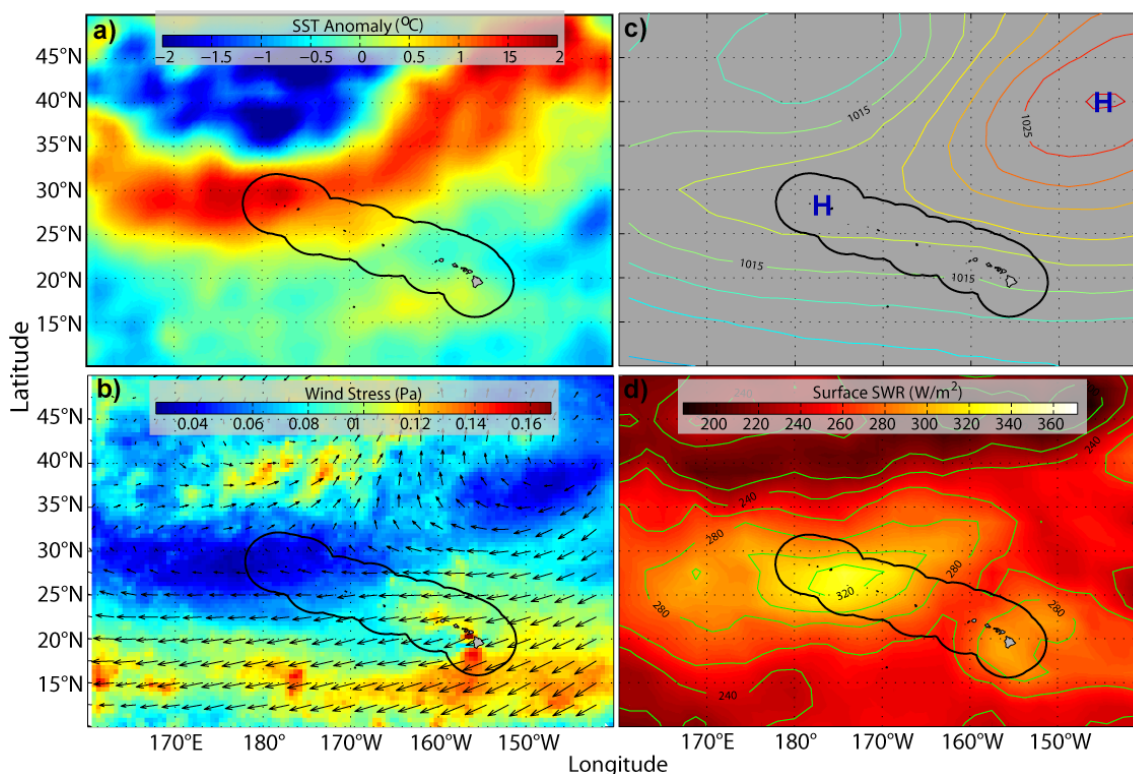
The distribution of high temperatures appears to be linked directly to exceptionally quiescent winds preceding and during the event; good correspondence exists between low wind speeds and rapid increase in SST during this period (Fig. 3b). In turn, these light winds were linked with a variable, but persistent high-pressure ridge associated with the North Pacific Subtropical High (Fig. 3c). The axis of the ridge generally intersected the northern end of the Hawaiian Archipelago for much of the summer, coinciding with the light winds, very low cloud cover, and high surface insolation (Fig. 3d). In the MHI, by contrast, wind speeds remained consistently much higher, with trade winds driven by the atmospheric pressure gradient south of the high-pressure ridge.

## Small-Scale Morphological Effects

While synoptic weather features describe the gross distribution of both SST and observed bleaching at the archipelago scale, they do not explain relatively large differences in the overall extent and severity of bleaching observed among adjacent reef groups. These differences are most evident at Laysan Island, where significantly less

overall bleaching was recorded than at neighboring Maro Reef or Lisianski/Neva Shoals (Kenyon et al. in review). Less overall bleaching also was documented at Kure Atoll than at neighboring Midway Atoll, despite Kure experiencing slightly higher Pathfinder SSTs. While these differences are partially due to differences in coral species compositions and distributions at the different locations (Kenyon et al., in review), they are likely also due in large part to differences in water circulation connected to differing reef morphologies.

During a Pacific RAMP assessment at Rose Atoll in American Samoa, researchers documented the formation of a lens of highly stratified water within the atoll's lagoon and inner reef flat that was up to 3ºC warmer than surrounding water temperatures (Hoeke, 2002, unpublished data). The meteorological conditions during this visit (light winds and high atmospheric surface pressure) were similar to those of the NWHI 2002 bleaching event. The formation of such a warm water lens can be attributed to surface gravity wave setup across the forereef, which mechanically mixes water over the forereef, but causes surface convergence within the lagoon and backreef (Krains et al., 1998; Prager, 1991). In light wind conditions, wave setup across the forereef would tend to balance baroclinic forcing (horizontal density gradients), heating surface waters trapped within the atoll throughout the day, with little or no mixing (Andrews et al., 1984).

*In situ* measurements of SST support the supposition that similar features occurred within the northern atolls in the NWHI at the time of bleaching in 2002. During the warming period preceding the bleaching event, average *in situ* SST measured near the center of Pearl and Hermes' lagoon was 0.7ºC warmer than Pathfinder SST of the surrounding area, and diurnal maxima were up to 2.6ºC warmer (Fig. 4).

Local water circulations are highly dependent on reef morphology (Atkinson et al., 1981). Atolls, with narrow forereefs and large protected lagoons, likely are prone to these lens-like stratified features during low wind conditions, while it is unlikely that such features occur at islands with fringing reef systems. The residence time of water in lagoon and backreef areas is related to water volume (Delesalle and Sournia, 1992), and therefore might serve as one of the primary factors controlling the extent and temperature maxima of these features in the Northwestern Hawaiian Islands, where tidal mixing is low compared to gravity wave mixing at shallow reef depths (Andrews et al., 1984; Atkinson et al., 1981). These hypotheses explain why Laysan Island, with its fringing reef and very little backreef area, experienced less overall coral bleaching than neighboring reefs on either side, and why Pearl and Hermes Atoll, with its complex, large, deep lagoon and narrow encircling forereef, experienced the most. Lisianski Island and its associated Neva Shoals complex of both fringing reef and backreef areas may represent an intermediate case (Fig. 1, Table 1).

Kenyon et al. (in review) describe significant differences in overall bleaching within the atolls' different morphological zones and inverse correlation of bleaching severity with depth. Bleaching was greatest within shallow backreef and lagoon areas, and least on the forereefs. These observations are consistent with the inference that highly stratified waters with surface layers significantly warmer than surrounding open ocean conditions occurred in lagoon and backreef areas, while forereef areas remained relatively cool as turbulence due to surface gravity waves rapidly mixed surface layers heated by daytime insolation.
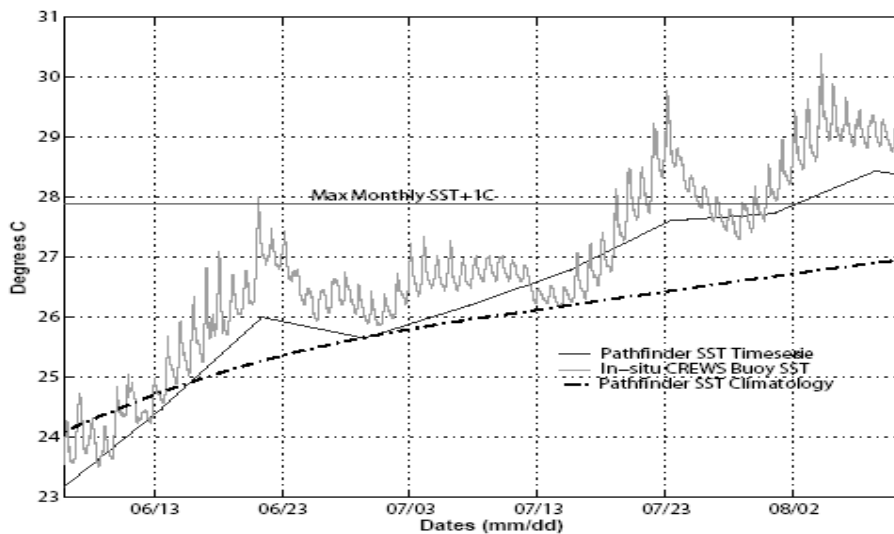
**Figure 4**. Comparison of Pathfinder SST in the area of Pearl and Hermes Atoll and in situ water temperatures measured near the center of the Atoll at a depth of approximately 1 m. Maximum departure of in situ temperatures from Pathfinder SST is +2.6ºC.

Prediction of Differences in Bleaching Among Adjacent Reefs

Several researchers have developed indices of bleaching severity using DHWs (Strong et al., 1997; Wellington et al., 2001), such as those provided by NOAA's Oceanic Research and Applications Division (ORAD) products. Regression of DHW alone describes between 60-80% of the variability seen in overall mean coral bleaching observations among reefs (Fig. 5, Table 2). As outlined above, such satellite SST-derived products help describe and predict gross, archipelago-scale bleaching, but cannot account for differences among adjacent reefs due to local circulation patterns and mixing. These

**Figure 5.** Comparison of mean bleaching variance described by DHW versus DHW·V$^{1/5}$ at NWHI locations. REA obs and TOW obs in the upper panel indicate observations from the rapid ecological assessments at fixed transects and towed-diver benthic survey video analysis, respectively; Obs in the lower panel represents mean of all observations of all methods at each location. Predictions based on regression of D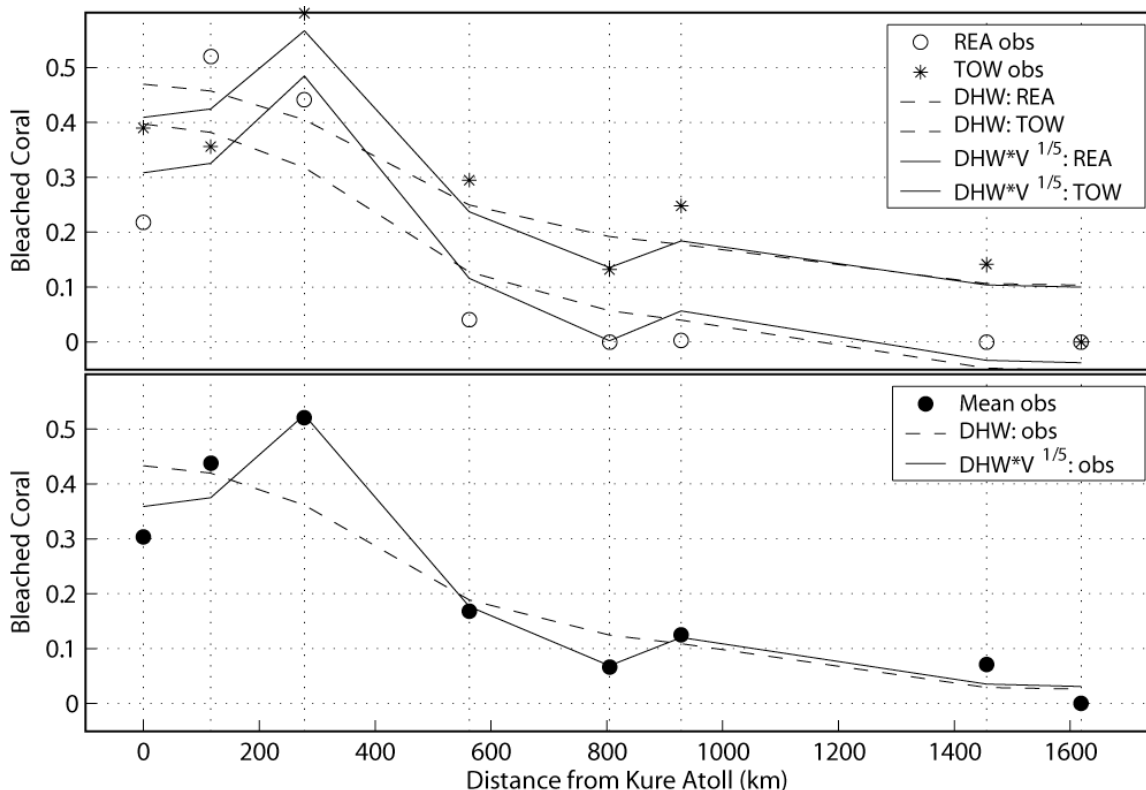HW are given with dashed lines. Predictions based on regression of DHW and fifth root of lagoon and backreef volume (V$^{1/5}$) are given with solid lines.

Table 2. Variance, F-, and p-statistics for the regression analysis of mean bleaching observations for each reef in the NWHI from Necker to Kure. REA and TOW indicate observations from the rapid ecological assessments at fixed transects and towed-diver benthic survey video analysis, respectively; mean represents mean of all observations of all methods at each location. The upper portion is regression statistics using DHW alone; the lower is multiple regression of DHW and the fifth root of lagoon and backreef volume, as explained in the text.

| Degree Heating Weeks (DHW) | | | |
|---|---|---|---|
| | $r^2$ | F | p |
| REA | 0.7443 | 17.4643 | 0.0058 |
| TOW | 0.6791 | 12.6996 | 0.0119 |
| Mean | 0.80431 | 24.6612 | 0.0025 |

| DHW·V$^{1/5}$ | | | |
|---|---|---|---|
| | $r^2$ | F | p |
| REA | 0.8195 | 27.2407 | 0.0020 |
| TOW | 0.8959 | 51.6156 | 0.0004 |
| Mean | 0.9624 | 153.894 | 0.0000 |

differences are reflected in the local heat budgets of the adjacent reefs as changes to the advective heat flux and turbulent diffusive (mixing) heat flux terms (Dong and Kelly, 2003). Temperature changes for reservoirs and estuaries often are estimated using bulk formulations (Beck et al., 2001; Fischer et al., 1979). If lagoons and backreefs are considered a reservoir, than changes in temperature can be estimated by the following bulk formula:

$$\frac{dT}{dt} = \underbrace{\frac{Q_{net}}{C_p \rho V}}_{1} - \underbrace{\frac{(U_{in} T_{ocean} - U_{out} T_{lagoon})}{V}}_{2}$$

In term 1, on the right side of the equation, $Q_{net}$ is the total net heat flux through the air-sea interface of the lagoon and backreef surface area; $C_p$ is the specific heat of the water; and $\rho$ is the density of the water. Term 2 represents a bulk estimation of heat advection and mixing between the ocean and the lagoon: $U_{in}$ and $U_{out}$ are the total volume flux of the water coming into and out of the lagoon/backreef; $T_{ocean}$ and $T_{lagoon}$ represent the temperature of the surrounding oceanic water and the mean temperature of the lagoon. In both terms, $V$ is the volume of the lagoon/backreef reservoir. Thus, for neighboring reefs experiencing similar meteorological conditions, it is primarily the ratio of total volume flux to V that defines differences in temperature among reefs. Residence time is defined as $R = V/U_{total}$ (Delesalle and Sournia, 1992), where $U_{total}$ is the total volume flux of the lagoon/backreef. Reefs with longer lagoon/backreef residence times exchange less heat per unit volume with the relatively cooler forereefs and open ocean.

Unfortunately, accurate estimation of the total volume flux ($U_{total}$) is extremely difficult, and generally requires intensive measurements and/or complex numerical modeling. It is possible, however, that volume flux is linked to volume, especially in areas with similarities in small-scale morphological features. If volume flux per unit width across the forereef barrier is the same among reefs, then volume flux will increase in a nonlinear fashion with volume for basins with roughly the same geometry. Based on this assumption, regression analysis of bleaching to DHW multiplied by the additional factor of the volume to a constant power was investigated, e.g.:

$$Bleaching = a \cdot DHW \cdot V^k + b$$

where $a$, $b$, and $k$ are regression constants. In this case, the best-fit value of the nonlinear coefficient, $k$, was 1.5. This method, while relying on admittedly tenuous assumptions, describes approximately 80-90% of the variability of the observed coral bleaching, and represents a statistically significant improvement over the relationship to DHW alone (Table 2). Figure 5 shows the ability of the empirical relationship to account for large differences in observed overall bleaching among adjacent reefs not accounted for by SST anomaly or DHW alone. This suggests that such empirical relationships between DHW and lagoon/backreef volumes are potentially useful to better describe heat stress to corals.

# CONCLUSIONS

High water temperatures and high ultraviolet (UV) radiation have been identified as the primary stressors leading to coral bleaching (Hoegh-Guldberg, 1999). Although UV radiation probably played a large role in bleaching severity during the 2002 NWHI event, as observations of greater bleaching on the upper surfaces of individual coral colonies suggest (Kenyon et al., in review), overall spatial patterns of bleaching can be described by measured and inferred distributions of water temperatures alone. SST anomalies associated with archipelago-scale bleaching patterns appear to be directly connected to a series of atmospheric high-pressure ridges present shortly before and during the onset of elevated temperatures. These atmospheric features, extensions of the North Pacific Subtropical High, were centered over the northwestern end of the Island chain, where the greatest SST anomalies occurred. In contrast, atmospheric pressure gradients to the southeast maintained trade winds, mixing the surface layer and keeping SSTs relatively cooler. Circulation patterns influenced by reef morphology coupled with light winds further elevated water temperatures (up to 3°C) at some locations, particularly at the three northernmost atolls: Kure, Midway, and Pearl and Hermes.

Based on the ~20 year Pathfinder dataset, SSTs at the northwestern end of the Hawaiian chain reached higher temperatures and remained elevated (>1°C over climatological means) for longer than any other warming episodes in the entire Archipelago. Although gross patterns of SST anomaly associated with the bleaching event are linkable to synoptic weather patterns near the time of the event, the magnitude of the anomaly is probably at least partially due to longer-term processes. While SST anomalies at the northern end of the Hawaiian Archipelago were not significant during the springtime preceding the summer of 2002, wintertime SSTs over the 3 years preceding the event have been noticeably elevated (~>1°C ) over climatological means. Higher wintertime SSTs over several years point to large-scale climate oscillations such as the Pacific Decadal Oscillation (PDO) (Schneider et al., 2002). It is also of note that all episodes of elevated SST in the NWHI occurred during periods of a positive El Nino/ Southern Oscillation phase (ENSO), although the magnitude of SST anomaly does not correspond with the magnitude of ENSO. It is beyond the scope of this work to identify links between large-scale climate oscillations and bleaching conditions, but they appear to play a major role.

Mean summertime SST (June 15 – September 15) maxima (based on Pathfinder data) are 0.4°C warmer at Midway than at Oahu, and summertime SSTs have higher standard deviation toward the northern end of the chain. The higher variability and higher maximum temperatures suggest that more frequent episodes of high surface water temperatures coupled with light and variable winds, conditions associated with mass bleaching, occur at the northwestern end of the Hawaiian Archipelago than in the MHI; although notable exceptions occur such as a bleaching event in the MHI in 1996 (Jokiel and Brown, 2004). These temperature characteristics, along with the hypothesized circulation patterns of atolls in low wind conditions, strongly suggest that the northern atolls of Kure, Midway, and especially Pearl and Hermes are at the greatest risk of future mass bleaching episodes of all reef ecosystems within the Hawaiian Archipelago.

Based on the NWHI 2002 bleaching observations, the overall bleaching a particular reef experiences appears to be well parameterized by an empirical relationship to satellite-derived heat exposure (DHW) and the lagoon/backreef volume. Although local flushing and mixing in the NWHI's reefs are very complex and largely unknown, using a nonlinear factor of the lagoon/backreef volumes appears to capture the effect of localized heating in a statistically significant fashion (Table 2). Until these circulations are better understood, which probably requires fine-scale hydrodynamic modeling, the propensity of a particular reef to experience bleaching may be described from this simple relationship. Pearl and Hermes Atoll, with its vast lagoon and backreef area, would have the highest likelihood of experiencing the greatest amount of coral bleaching. It is unlikely that a similar relationship exists for the MHI, where freshwater input, turbidity, and other orographic effects associated with high islands have been shown to influence bleaching patterns (Jokiel and Brown, 2004). More investigation into relationships among local heat stress, residence times, and reef morphology is warranted.

## ACKNOWLEDGEMENTS

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# SECOND RECORDED EPISODE OF MASS CORAL BLEACHING IN THE NORTHWESTERN HAWAIIAN ISLANDS

BY

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## ABSTRACT

Mass coral bleaching involves multiple species over large areas. A second known episode of mass bleaching was documented in the Northwestern Hawaiian Islands (NWHI) during September/October 2004. Bleaching was observed in 10 species of the three dominant genera (*Porites, Pocillopora, Montipora*). Spatial and taxonomic patterns of bleaching in 2004 bore many similarities to a 2002 bleaching event, the first ever recorded from this region. The incidence of bleaching was higher at the three northern atolls (Pearl and Hermes, Midway, Kure) than at Lisianski and reefs farther south in the NWHI. At these northern atolls, the incidence of bleaching was higher in shallow backreef and patch reef habitats than on the deeper forereef. In both years, the combined influence of depth and the relative abundance/differential susceptibility of coral taxa underlay the salient spatial patterns of bleaching. In both years, the backreef habitat at Pearl and Hermes Atoll experienced the highest levels of bleaching. *Montipora*, among the genera most susceptible to bleaching, experienced extensive mortality and algal overgrowth in backreef habitats at the three northern atolls following the 2002 event. *In situ* subsurface temperature recorders, which registered water temperatures at 22 shallow backreef and lagoon sites, indicate corals experienced temperatures exceeding local bleaching thresholds for substantially longer periods of time in 2004 than in 2003, when only low levels of bleaching were observed. The occurrence of two episodes of mass bleaching over a period of three calendar years lends credence to predictions that the frequency of bleaching events will increase.

## INTRODUCTION

The prevalence of mass coral bleaching events, in which multiple coral species are affected over large areas, has increased worldwide during the past 25 years (Hoegh-Guldberg, 1999; Wilkinson, 2002). These large-scale events are associated with heightened sea-surface temperatures (SSTs), which in turn have been linked to climate change driven by increased atmospheric concentrations of greenhouse gases (Wellington et al., 2001; Hughes et al., 2003; Bellwood et al., 2004; Jokiel and Brown, 2004). The aftermath of bleaching can range from nearly complete recovery of affected corals (Jokiel

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and Brown, 2004) to widespread mortality (Aronson et al., 2002), algal overgrowth (McClanahan et al., 2001), and phase shifts (Ostrander et al., 2000).

Despite predictions that reefs in the central Pacific would be among the last in the world to bleach (Hoegh-Guldberg, 1999; Turgeon et al., 2002), reefs throughout the Northwestern Hawaiian Islands (NWHI) experienced a mass coral bleaching event in late summer 2002 (Aeby et al., 2003; Kenyon et al., 2004; Kenyon et al., in press). This event, in which the three northern atolls (Pearl and Hermes, Midway, and Kure) were more severely affected than reefs farther south in the NWHI, was the first ever recorded from this remote area (reviewed in Kenyon et al., in press). At these northern atolls, shallow backreef and patch reef habitats were more severely affected than deeper forereefs; the spatial patterns of bleaching were related to the combined factors of depth and the relative abundance of the dominant coral genera (*Montipora, Pocillopora, Porites*) in different atoll habitats, coupled with their differential susceptibility to bleaching (Kenyon et al., 2004; Kenyon et al., in press). Bleaching coincided with a period of prolonged, elevated SST, detected by satellite remote sensing and *in situ* moorings, which was particularly intense at the three northern atolls (Hoeke et al., 2004).

Resurveys of backreef sites at Midway Atoll in December 2002 revealed that colonies of *Montipora capitata*, a dominant component of the northern backreef, were still bleached or were becoming overgrown with turf and macroalgae; in contrast, pocilloporids, which predominate along other backreef exposures, had experienced low mortality and were recovering normal pigmentation (Kenyon and Aeby, unpublished data). Surveys in July/August 2003 further revealed the decline through mortality and algal overgrowth of *Montipora capitata* and the comparatively high recovery of pocilloporids at Midway as well as other northern atoll sites (G. Aeby, personal communication). In preparing for 2004 survey activities, scientists were alerted to the probability of again encountering substantial bleaching by a bleaching warning issued by National Oceanic and Atmospheric Administration's (NOAA) Coral Reef Watch for Pearl and Hermes Atoll, as well as by reports from NOAA personnel engaged in marine debris removal activities at Pearl and Hermes Atoll of widespread bleaching along the southwest backreef (J. Asher, personal communication). This paper is focused on the spatial and taxonomic patterns of coral bleaching documented throughout much of the NWHI using quantitative surveys conducted in September/October 2004. We show that this episode, while of more moderate intensity than the 2002 event, was of sufficient magnitude and spatial extent to be considered the second mass bleaching event to affect this region within three years. This second documented episode of mass bleaching corresponded to another period of prolonged, elevated SSTs in shallow waters, which were registered using *in situ* temperature recorders during deployments that included the warmest months in both 2003 and 2004. In both 2002 and 2004, bleaching was most intense on the backreef at Pearl and Hermes Atoll, a finding that may warrant special research and management attention to this habitat as the NWHI move through a sanctuary designation process for possible inclusion in the U.S. National Marine Sanctuary system.

## METHODS AND MATERIALS

Study Area

The NWHI consist of ten island/banks and atolls, as well as numerous deeper submerged banks. From southeast to northwest the shallow-water reefs include: Nihoa, Necker, French Frigate Shoals, Gardner Pinnacles, Maro Reef, Laysan, Lisianski, Pearl and Hermes, Midway, and Kure (Fig. 1). Nihoa and Necker are small basalt islands, each surrounded by a shallow (<50 m) shelf. French Frigate Shoals (FFS) is an open atoll with a small basaltic pinnacle in the interior. Gardner Pinnacles constitutes the last basaltic outcrop in the Hawaiian Archipelago, consisting of three small rocks on an extensive submerged bank. Maro Reef is a complex of shallow reticulated reefs with no associated island. Laysan and Lisianski are low carbonate islands that crest shallow, submerged banks. Northwest of these are three atolls: Pearl and Hermes, Midway, and Kure Atolls (NOAA, 2003). Surveys spanned a latitudinal/longitudinal range between 23°63' N latitude, 166°14' W longitude (French Frigate Shoals), and 28°45' N latitude, 178°38' W longitude (Kure Atoll).

Benthic Surveys

In 2003, 73 sites were selected for long-term monitoring by a group of biologists experienced in surveys of fish, algae, corals, and other macro-invertebrates in the NWHI. These long-term monitoring sites were selected from a pool of 391 sites that had been surveyed during annual research cruises in 2000, 2001, and 2002. Criteria for selection of long-term monitoring sites included representation of a range of habitats and biological communities at each location and a high probability of accessibility to divers on annual research cruises under prevalent sea conditions. Belt-transect (25 m x 2 m) surveys were conducted at 66 of these 73 long-term monitoring sites (Table 1) between 16 September and 11 October 2004 according to the methods described by Maragos et al. (2004) for 2002 Rapid Ecological Assessments (REA). The species and size class of each coral colony whose center fell within 1 m of each side of the transect line were recorded as well as the number of bleached colonies of each species. A colony was tallied as "bleached" if more than half of its live tissue had lost an estimated 75% or more of its normal pigmentation (Cook et al., 1990; Bruno et al., 2001; Cumming et al., 2002). For species in which clonal propagation (e.g. *Porites compressa*) or fissioning (e.g. *Porites lobata*) is an important part of the life history pattern, consideration was given to tissue color, interfaces with neighboring conspecifics, and distance between conspecifics in determining the number of colonies. Either 50 m$^2$ or 100 m$^2$ was surveyed at each site. Identical protocols were used as during 2002 surveys (Kenyon et al., in press), with the exception that most corals were tallied at the genus level in 2002.

Temperature Recorders

In order to monitor *in situ* temperature regimes at the major reef systems between French Frigate Shoals and Kure, inclusive, 12 subsurface temperature recorders (STRs)

(SBE 39; SeaBird Electronics, Inc.) were fastened to the benthos between 12 September and 3 December 2002. Between 15 July and 3 August 2003, these were retrieved and replaced with fresh STRs; nine more STRs were fastened to the benthos at additional sites, and one STR was attached to the cable of a moored buoy in the central lagoon at Kure Atoll (Table 2). Benthic STR deployments at the atoll locations targeted backreef and lagoon patch reef habitats, which had experienced the highest levels of bleaching in 2002. Depths of STR sites (n = 22) ranged from 0.5 to 10.4 m. Temperature ($^o$C) was electronically recorded at 15- or 30-minute intervals (17 and 5 STRs, respectively). Recorders deployed in 2003 were retrieved from 19 September to 9 October 2004, and replaced with fresh STRs.

Data Analysis

Incidence of bleaching by site, habitat, or taxon was calculated as the percentage of colonies with bleached tissue. Non-parametric tests were used for statistical analyses in which data sets were not normally distributed or had unequal variances. Statistical analyses were conducted using SigmaStat® software. The Mann-Whitney rank sum test and one-way analysis of variance (ANOVA) were used to examine spatial and habitat differences in bleaching incidence; one-way ANOVA was used to examine differences among coral taxa in bleaching incidence; and the Bonferroni t-test was used for multiple group comparisons. The relationship between incidence of bleaching and depth at each location was examined using Pearson or Spearman rank correlation methods; at each site the percentage of colonies with bleached tissue was paired with that site's depth. In comparing the incidence of bleaching in 2002 and 2004, data for the three dominant genera (*Montipora, Pocillopora, Porites*) were pooled for each location and habitat within location, and the differences between years were examined with t-tests.

For each location, the maximum monthly climatological mean (MMM) temperature over the years 1985-2001 was calculated using a single 4-km pixel from the Pathfinder version 5.0 SST dataset that best overlapped each location. MMM + 1$^o$C is considered the bleaching threshold, above which thermal stress to corals accumulates (Strong et al., 1997; Skirving et al., 2004). Temperature records downloaded from each STR were inspected to determine, for 2003 and 2004, the date on which SST first exceeded the bleaching threshold, the maximum temperature, and the date of maximum temperature. As a comparative indicator of accumulated thermal stress (ATS), the number of temperature observations at each STR site that exceeded MMM + 1 was tallied and normalized by the number of data points per day to yield ATS in days.

A Spearman rank correlation coefficient was calculated to examine the relationship between ATS in the backreef habitat at the three northern atolls and incidence of bleaching; for each STR within close proximity (≤ 2.5 km) of a backreef REA site, ATS was paired with the percentage of colonies bleached at the corresponding site.

## RESULTS

Belt-transect Surveys

Sixty-six surveys totaling 3,900 m$^2$ were conducted at French Frigate Shoals, Gardner Pinnacles, Maro Reef, Laysan, Lisianski, Pearl and Hermes Atoll, Midway Atoll, and Kure Atoll, ranging in depth from 0.6 to 15.5 m. Nihoa and Necker were not surveyed due to foul weather. A total of 9,499 colonies belonging to 25 species within ten genera (*Pocillopora, Acropora, Montipora, Porites, Leptastrea*, *Cyphastrea, Fungi, Cycloseris, Pavona*, *Psammacora*) were counted within the belt transects. Bleaching was not observed at any location in *Acropora* (n = 257), *Leptastrea* (n = 229), *Cyphastrea* (n = 448), *Fungia* (n = 130), *Cycloseris* (n = 3), *Pavona* (n = 180), or *Psammacora* (n = 176). Bleaching was observed in ten of the 25 species recorded (Table 3), belonging to three genera (*Montipora, Pocillopora, Porites*; Fig. 2).

A low level of bleaching (< 20% of colonies) was seen in pocilloporids in shallow patch reef habitats at French Frigate Shoals. No bleaching was seen at Gardner Pinnacles. *Montipora patula* was the most frequently affected species at Maro, Laysan, and Lisianski, with bleaching recorded in 68.8%, 35.5%, and 56.3% of the colonies, respectively. More than a quarter of the colonies of *Porites evermanni* and *Pocillopora damicornis* were bleached at both Maro and Lisianski, with lesser incidences in *Porites lobata, P. compressa, Pocillopora meandrina*, and *Montipora capitata* (Table 3).

There was a significant difference between the incidence of bleaching on the northern atoll reefs ($n_1$ = 32) and on reefs at Lisianski and farther south ($n_2$ = 34)(Mann-Whitney rank sum test, T = 1225.5, p = 0.050). At the three northern atolls, differences existed among the three habitats surveyed (forereef, backreef, patch reef) in the overall incidence of bleaching (one-way ANOVA, F = 8.332 p = 0.001), though only the backreef-forereef comparison was significant (Bonferroni t-test, t = 4.049, p = 0.001). On the backreef at Pearl and Hermes Atoll, more than half the colonies of *Montipora capitata, M. patula, M. turgescens*, and *Pocillopora meandrina* were bleached, while more than half the colonies of *Montipora capitata* and *M. turgescens* on the Midway backreef were bleached (Table 3). At Kure Atoll, *Montipora capitata* in the backreef habitat was again the most severely affected species (Table 3), although the incidence of bleaching (61.5% of colonies) at Kure was less than at Pearl and Hermes and at Midway Atolls (75.5% and 100%, respectively). There was a significant difference among the backreefs at the three northern atolls in the incidence of bleaching (one-way ANOVA, F = 15.098, p <0.001), with the severity of bleaching significantly greater at Pearl and Hermes Atoll than at Midway (Bonferroni t-test, t = 3.425, p = 0.017) or Kure Atolls (Bonferroni t-test, t = 5.308, p = 0.001).

Pocilloporids on patch reef sites at the three northern atolls also sustained moderate to high levels of bleaching. More than two-thirds of the pocilloporids recorded on patch reefs at Pearl & Hermes Atoll (*P. meandrina* and *P. damicornis*) were bleached, while more than a quarter of *P. meandrina* colonies were bleached at the Midway Atoll and Kure Atoll patch reef sites surveyed (Table 3). *Pocillopora ligulata*, recorded within belt transects only on patch reefs at Kure Atoll, also sustained moderately high levels of bleaching (40% of colonies, Table 3).

Within the range of locations most affected by bleaching (Maro to Kure Atoll, inclusive) differences existed among the three dominant genera (*Montipora, Pocillopora, Porites*) in their incidence of bleaching (one-way ANOVA, F = 4.65, p = 0.027), though only the *Montipora-Porites* comparison was significant (Bonferroni t-test, t = 3.050, p = 0.024). A significant correlation between depth and the percent of coral colonies that were bleached was found at Pearl and Hermes and at Midway Atolls, but the correlation was not significant at other locations where bleaching was observed (Table 4).

Comparison to 2002 Bleaching Patterns

The incidence of bleaching at the three northern atolls is presented in Figure 3; however, the difference in bleaching incidence between the two events was not statistically significant (t-test, t = 1.777, p = 0.095). The difference in bleaching incidence between 2004 and 2002 at Maro, Laysan, and Lisianski also was not statistically significant ($|t| = 0.681$, p = 0.570).

Temperature Records

The maximum monthly climatological mean (MMM) temperature at the eight reef systems between French Frigate Shoals and Kure ranges from 26.9 to 27.5°C (Table 5). Of the 12 STRs deployed in 2002, only one (Lisianski) registered temperatures above the bleaching threshold (MMM + 1°C) before being retrieved and replaced with a fresh STR in late July 2003.  Because of the shallow depth of this STR, the high accumulated thermal stress (ATS) relative to other sites, and the low ATS registered prior to its replacement (1.6 of the total 21.3 days), it is assumed that sites where STRs were initially deployed in 2003 did not experience temperatures exceeding their bleaching threshold until after their STRs were deployed, i.e., the values calculated for these sites in 2003 accurately reflect rather than underestimate the ATS. Most STRs first registered temperatures above the bleaching threshold several days to several weeks earlier in 2004 than in 2003. All 22 STRs registered maximum temperatures in 2004 that exceeded those in 2003, with the exception of a brief, isolated spike registered at the southeast corner of Laysan in 2003 (Table 5). Differences in maximum temperature between years ranged from 0.1°C at a Kure backreef location to 1.6°C at a Midway backreef location. Except for Gardner Pinnacles, where the STR never registered temperatures exceeding this location's threshold in either year, all locations experienced higher ATS in 2004 than in 2003 (Table 5). ATS exceeding 30 days in 2004 was recorded at Lisianski, Pearl and Hermes Atoll, and Kure Atoll. The highest ATS in 2004 (49.1 days) was documented in the central lagoon at Pearl and Hermes Atoll (Table 3). There was a significant correlation ($r_s$ = 0.80, p = 0.006) between ATS and bleaching incidence in shallow ($\leq$ 3 m) backreef habitats at the three northern atolls where STRs and REA sites were in close proximity (i.e., within 2.5 km of each other) (Table 6).

## DISCUSSION

Coral bleachings documented in the NWHI in late summer 2002 and 2004 shared numerous spatial and taxonomic features. In both years, the incidence of bleaching was greater at the three northern atolls (Pearl and Hermes, Midway, Kure) than at Lisianski and farther south (Kenyon et al., in press). Minimal or no bleaching was observed in either year at French Frigate Shoals and Gardner Pinnacles, respectively. At the three northern atolls, bleaching was most severe in shallow backreef and lagoon habitats. While studies from other regions have noted more severe bleaching in shallow than in deep habitats (Fisk and Done, 1985; Oliver, 1985), checkered patterns of statistical correlation between depth and the incidence of bleaching in 2002 (Kenyon et al., in press) and 2004 (Table 4) suggest that factors other than those associated with depth *per se* (e.g., thermal stratification, penetration of UV radiation) contributed to the observed spatial patterns in the NWHI. In both years, significant differences existed among the three dominant coral genera (*Montipora, Pocillopora, Porites*) in their incidences of bleaching, and the average incidence of coral bleaching experienced in different reef systems and habitats closely corresponded to the composition of the dominant coral fauna coupled with its susceptibility to bleaching (Kenyon et al., in press; Fig. 2). Hence, the combined influences of depth and the relative abundance/susceptibility of coral taxa underlie salient spatial patterns. The lack of statistically significant differences in bleaching incidence between the two years throughout the range of affected reefs (Maro to Kure, inclusive) supports the conclusion that bleaching in 2004 may be of sufficient spatial extent, intensity, and taxonomic diversity to be called a mass coral bleaching event.

In both years, colonies in the genus *Montipora* sustained the highest levels of bleaching (Kenyon et al., in press; Fig. 2). At Maro, Laysan, and Lisianski, *Montipora patula* consistently showed the highest incidence of bleaching, with almost 70% of colonies affected at Maro (Table 3). *Montipora capitata* and *M. turgescens*, which along with *M. flabellata* dominate many backreef locations at the three northern atolls, showed the greatest differential susceptibility to bleaching in both years, with up to 100% of the colonies bleached (Kenyon, unpublished data; Table 3). Preliminary quantification of coral mortality from the 2002 bleaching event, as assessed through analysis of photo quadrats (Preskitt, 2004) recorded along the same lines as those used for belt transects in 2002 and 2004, indicates reduction of live *Montipora* cover by as much as 30% at backreef sites at Midway and Pearl and Hermes Atolls (Vroom and Kenyon, unpublished data). Consequently, bleaching was not as visually dramatic in 2004 as in 2002, as there was less surviving coral remaining to bleach in 2004. The shallow (1-2 m) crest of a large central patch reef system at Kure Atoll, known previous to 2002 as "the coral gardens" due to its luxuriant growth of montiporids and pocilloporids, was heavily bleached in 2002 (77.0% of colonies, n = 177; Kenyon, unpublished data); in 2004, only a few branches of *Porites compressa* remained alive, and the dead coral skeletons were thickly covered in turf and macroalgae. Live coral cover was reduced from 58.2% in 2001 to 7.3% in 2004, with a corresponding increase in algal cover from 40.4% to 91.6% (Kenyon, unpublished data). A phase shift (Done, 1992) from a system dominated by coral to a system dominated by algae occurred on this shallow reef during this interval;

such a rapid shift from coral to algae has been considered a sign of reef degradation (Done, 1992; Hughes, 1994; McCook, 1999; Nyström et al., 2000; Bellwood et al., 2004), and has been documented in the aftermath of mass bleaching in other regions (Ostrander et al., 2000).

Skirving et al. (2004) show that accumulation of thermal stress to corals exceeding four Degree Heating Weeks (DHW, in which one DHW represents 1°C above the bleaching threshold for one week) is frequently accompanied by bleaching. In 2002, regional SST around the three northern atolls reached warmer temperatures than any observed in the last 20 years, for a time period that lasted longer than any previously observed warm-water events; at Kure Atoll, regional temperatures that exceeded the bleaching threshold persisted for four weeks (Hoeke et al., in review). In 2003, surveys were conducted in July/early August, before the time of maximum temperatures (Table 5), and low levels of bleaching (< 5% of colonies) were noted at most locations (G. Aeby, personal communication). Although the extent to which bleaching increased in response to continued warming in late summer 2003 is not known, the low number of cumulative days above the bleaching threshold in 2003 determined from *in situ* temperature recorders (Table 5) suggests that bleaching was neither widespread nor severe, with the possible exception of very shallow (< 1 m) reefs off Lisianski. In 2004, all locations experienced substantially greater ATS than in 2003. The greatest ATS in 2004 was recorded at Pearl and Hermes Atoll, which experienced the highest level of bleaching in backreef and patch reef habitats during both years' bleaching events (Fig. 3). In backreef habitats at the three northern atolls, the significant positive correlation between ATS and the incidence of bleaching at REA sites within close proximity of corresponding STRs (Table 6) further demonstrates the connection between bleaching and elevated water temperatures.

Barton and Casey (2005) provide evidence from analysis of three historical SST data sets that conditions for thermally induced large-scale bleaching may have existed in the NWHI during the late 1960s. They suggest, however, that bleaching actually did not occur and that some other coral stressor acting synergistically with elevated SSTs may have brought about the large-scale bleaching observed in this region in 2002. Jokiel and Brown (2004), using one of the same data sets (HadISST) as Barton and Casey (2005), also note the absence of bleaching reports in Hawaii despite hind-cast indications that thermally-induced bleaching should have occurred during 1968 and 1974. However, rather than invoke the advent of additional, synergistic stressors as possible triggers of mass coral bleaching in the Main Hawaiian Islands and NWHI, these authors suggest the use of caution in interpreting hind-casting results on coral bleaching events. Both sets of authors, however, show an SST warming trend in the Hawaiian Archipelago that is most pronounced at the northern end of the NWHI, and other investigators (Brainard et al., 2004) have noted that maximum SSTs in the Hawaiian Archipelago are generally found at the three northern atolls. Further accounts of earlier bleaching events are documented by Kenyon et al. (in press). While contemporary methods of investigation have not provided conclusive evidence as to whether mass coral bleaching events occurred in the NWHI before 2002, the occurrence of two documented episodes of mass bleaching within a period of three calendar years lends credence to predictions of other authors that the frequency and severity of bleaching events is increasing both world-wide (Hoegh-Guldberg, 1999) and in the Hawaii region (Jokiel and Brown, 2004).

**ACKNOWLEDGEMENTS**

Table 1. Position, transect depth, zone, and 2004 survey date of long-term monitoring sites in the Northwestern Hawaiian Islands. Position coordinates are given in decimal degree units. Sites are categorized by zone according to a benthic habitat classification scheme developed for the NWHI (NOAA, 2003): B = backreef, F = forereef, L = lagoon, LP = La Perouse Pinnacles, S = shelf. Within each location, sites are listed in chronological order of 2004 surveys. NS = not surveyed.

| Site # | Latitude (N) | Longitude (W) | Transect depth, m | Zone | Survey date, 2004 |
|---|---|---|---|---|---|
| **Necker** | | | | | |
| R6 | 23.5752 | 164.7058 | 13.7 | S | NS |
| 4 | 23.5740 | 164.7038 | 12.2 | S | NS |
| 2 | 23.5782 | 164.7064 | 12.2 | S | NS |
| **French Frigate Shoals** | | | | | |
| H6 | 23.8805 | 166.2737 | 11.3 | F | 9/16 |
| 21 | 23.8479 | 166.3264 | 10.7 | B | 9/16 |
| 23 | 23.8669 | 166.2418 | 1.5 | L | 9/16 |
| R46 | 23.7694 | 166.2612 | 6.1 | L (LP) | 9/17 |
| 32 | 23.8063 | 166.2309 | 8.4 | L | 9/17 |
| 33 | 23.8358 | 166.2660 | 7.6 | L | 9/17 |
| R30 | 23.8666 | 166.2145 | 1.5 | B | 9/18 |
| 30 | 23.8496 | 166.2973 | 5.8 | L | 9/18 |
| 34 | 23.6278 | 166.1358 | 10.7 | F | 9/19 |
| 12 | 23.6378 | 166.1800 | 10.7 | B | 9/19 |
| R29 | 23.6785 | 166.1464 | 6.9 | L | 9/19 |
| 22 | 23.8659 | 166.2554 | 2.7 | L | NS |
| **Gardner Pinnacles** | | | | | |
| R6 | 25.0006 | 168.0015 | 17.4 | S | 9/20 |
| R3 | 24.9969 | 167.9987 | 16.5 | S | 9/20 |
| R5 | 24.9984 | 168.0000 | 15.2 | S | 9/20 |
| **Maro Reef** | | | | | |
| R8 | 25.3342 | 170.5252 | 13.7 | S | 9/21 |
| R6 | 25.3406 | 170.5005 | 11.6 | S | 9/21 |
| R5 | 25.3684 | 170.5021 | 7.3 | S | 9/21 |
| R9 | 25.4713 | 170.6434 | 10.7 | S | 9/22 |
| R12 | 25.4615 | 170.6836 | 16.8 | S | 9/22 |
| R3 | 25.4192 | 170.6694 | 18.3 | S | 9/22 |
| 22 | 25.3782 | 170.5675 | 14.3 | S | 9/23 |
| 6 | 25.3982 | 170.5747 | 6.1 | S | 9/23 |
| 8 | 25.4171 | 170.5841 | 12.8 | S | 9/23 |
| **Laysan** | | | | | |
| R12 | 25.778 | 171.7471 | 12.2 | S | 9/24 |
| R9 | 25.754 | 171.7414 | 9.6 | S | 9/24 |
| R11 | 25.766 | 171.7442 | 9.8 | S | 9/24 |
| **Lisianski** | | | | | |
| R14 | 26.0781 | 173.9971 | 14.6 | S | 10/9 |
| 12 | 26.0658 | 174.0017 | 7.9 | S | 10/9 |
| R9 | 26.0396 | 174.0126 | 7.9 | S | 10/9 |
| 10 | 25.9409 | 173.9222 | 9.0 | S | 10/10 |
| R10 | 25.9445 | 173.9535 | 12.6 | S | 10/10 |
| R7 | 25.9538 | 173.9708 | 11.0 | S | 10/10 |
| 18 | 26.0042 | 173.9943 | 7.5 | S | 10/11 |
| 16 | 25.9869 | 173.9945 | 12.2 | S | 10/11 |
| 17 | 25.9707 | 173.9642 | 10.8 | S | 10/11 |

Table 1 (Con'td)

| Site # | Latitude (N) | Longitude (W) | Transect depth, m | Zone | Survey date, 2004 |
|--------|--------------|---------------|-------------------|------|-------------------|
| **Pearl and Hermes Atoll** | | | | | |
| R26 | 27.7858 | 175.7803 | 12.2 | F | 9/26 |
| R32 | 27.8391 | 175.7528 | 2.0 | B | 9/26 |
| R31 | 27.8267 | 175.7922 | 10.4 | L | 9/26 |
| R39 | 27.9405 | 175.8616 | 13.6 | F | 9/27 |
| 26 | 27.9578 | 175.8024 | 2.4 | B | 9/27 |
| 24 | 27.9198 | 175.8617 | 8.8 | L | 9/27 |
| 33 | 27.7857 | 175.8238 | 12.2 | F | 9/28 |
| 22 | 27.7954 | 175.8666 | 1.8 | B | 9/28 |
| 30 | 27.7794 | 175.8953 | 2.7 | B | 9/28 |
| R42 | 27.7534 | 175.9488 | 13.7 | F | 9/29 |
| 31 | 27.7759 | 175.9733 | 2.4 | B | 9/29 |
| 32 | 27.7729 | 175.9392 | 5.5 | L | 9/29 |
| R44 | 27.9109 | 175.9047 | 13.4 | F | 9/30 |
| R22 | 27.8993 | 175.9148 | 4.1 | B | 9/30 |
| 23 | 27.8811 | 175.9328 | 7.6 | L | NS |
| **Midway Atoll** | | | | | |
| R15 | 28.2374 | 177.3951 | 2.1 | L | 10/1 |
| 1 | 28.2693 | 177.3862 | 0.9 | B | 10/1 |
| H21 | 28.2774 | 177.3661 | 1.1 | B | 10/1 |
| H10 | 28.2140 | 177.4259 | 13.0 | F | 10/2 |
| R25 | 28.1938 | 177.4021 | 2.1 | B | 10/2 |
| R20 | 28.2319 | 177.3184 | 1.1 | B | 10/3 |
| R3 | 28.1906 | 177.3999 | 13.3 | F | 10/4 |
| R7 | 28.1965 | 177.3752 | 14.5 | F | 10/4 |
| 2 | 28.1976 | 177.3462 | 12.3 | F | 10/4 |
| 3 | 28.2180 | 177.3439 | 7.6 | L | NS |
| H11 | 28.2178 | 177.4033 | 7.6 | L | NS |
| **Kure Atoll** | | | | | |
| R33 | 28.4167 | 178.3786 | 14.3 | F | 10/5 |
| 2 | 28.4535 | 178.3443 | 12.2 | F | 10/5 |
| R36 | 28.4204 | 178.3711 | 2.4 | B | 10/5 |
| 12 | 28.3826 | 178.3248 | 10.1 | F | 10/6 |
| 9 | 28.4058 | 178.3427 | 4.9 | L | 10/6 |
| R35 | 28.3931 | 178.3495 | 4.1 | B | 10/6 |
| 18 | 28.4187 | 178.3450 | 6.4 | L | 10/7 |
| 17 | 28.4321 | 178.3662 | 3.0 | B | 10/7 |
| 14 | 28.4537 | 178.3283 | 1.1 | B | 10/7 |

Table 2. Position of subsurface temperature recorders (STRs) in the Northwestern Hawaiian Islands. Position coordinates are given in decimal degree units. *STR initially deployed in 2002; STRs at other sites initially deployed in 2003.

| Location/habitat | Latitude (N) | Longitude (W) |
|---|---|---|
| **French Frigate Shoals** | | |
| Northeast backreef* | 23.8661 | 166.2197 |
| South backreef | 23.6448 | 166.1735 |
| La Perouse* | 23.7689 | 166.2614 |
| Central lagoon | 23.7382 | 166.1669 |
| **Gardner** | | |
| West central | 24.9988 | 167.9995 |
| **Maro** | | |
| South central* | 25.3842 | 170.5397 |
| South | 25.3670 | 170.5137 |
| **Laysan** | | |
| Northwest | 25.7795 | 171.7389 |
| Southeast | 25.7589 | 171.7294 |
| **Lisianski** | | |
| East of island* | 26.0634 | 173.9610 |
| **Pearl & Hermes** | | |
| Northwest backreef* | 27.9119 | 175.8943 |
| North backreef* | 27.9577 | 175.7808 |
| Southeast backreef | 27.8027 | 175.7793 |
| Southwest backreef* | 27.7747 | 175.9787 |
| Central lagoon | 27.8980 | 175.8313 |
| **Midway** | | |
| North backreef* | 28.2777 | 177.3679 |
| North backreef* | 28.2711 | 177.3860 |
| East backreef* | 28.2445 | 177.3234 |
| Southwest backreef | 28.1936 | 177.4018 |
| **Kure** | | |
| Northeast backreef* | 28.4474 | 178.3060 |
| West backreef* | 28.4293 | 178.3685 |
| Central lagoon | 28.4186 | 178.3446 |

Table 3. Frequency of bleaching in affected species throughout the NWHI, September/October 2004. n = number of colonies tallied within belt transects; % = percentage of colonies bleached; NT = not tallied.

| Species | FFS | | | | | | | | Gardner | |
| | Forereef | | Backreef | | Patch reef | | La Perouse | | | |
| | n | % | n | % | n | % | n | % | # | % |
| *Montipora patula* | 14 | 0.0 | 4 | 0.0 | 11 | 0.0 | 19 | 0.0 | 0 | |
| *Montipora capitata* | 9 | 0.0 | 3 | 0.0 | 26 | NT | 0 | | 14 | 0.0 |
| *Montipora flabellata* | 3 | 0.0 | 0 | | 0 | | 3 | 0.0 | 0 | |
| *Montipora turgescens* | 0 | | 0 | | 0 | | 0 | | 0 | |
| *Porites evermanni* | 3 | 0.0 | 12 | 0.0 | 35 | 0.0 | 0 | | 0 | |
| *Porites compressa* | 5 | 0.0 | 8 | 0.0 | 80 | 0.0 | 0 | | 0 | |
| *Porites lobata* | 176 | 0.0 | 67 | 0.0 | 198 | 0.0 | 40 | 0.0 | 906 | |
| *Pocillopora damicornis* | 0 | | 13 | NT | 106 | 23.6 | 2 | 0.0 | 1 | 0.0 |
| *Pocillopora ligulata* | 13 | 0.0 | 7 | NT | 26 | 0.0 | 0 | | 0 | |
| *Pocillopora meandrina* | 49 | 0.0 | 4 | NT | 21 | 9.5 | 45 | 0.0 | 222 | 0.0 |

| Species | Maro | | Laysan | | Lisianski | |
| | n | % | n | % | n | % |
| *Montipora patula* | 93 | 68.8 | 20 | 35.5 | 190 | 56.3 |
| *Montipora capitata* | 193 | 6.2 | 38 | 13.2 | 205 | 2.4 |
| *Montipora flabellata* | 0 | | 0 | | 0 | |
| *Montipora turgescens* | 0 | | 0 | | 0 | |
| *Porites evermanni* | 32 | 35.2 | 10 | 0.0 | 154 | 52.6 |
| *Porites compressa* | 92 | 6.5 | 11 | 0.0 | 77 | 9.1 |
| *Porites lobata* | 227 | NT | 146 | NT | 91 | 23.1 |
| *Pocillopora damicornis* | 40 | 27.5 | 2 | 0.0 | 172 | 27.3 |
| *Pocillopora ligulata* | 2 | 0.0 | 1 | 0.0 | 3 | 0.0 |
| *Pocillopora meandrina* | 87 | 8.0 | 13 | 0.0 | 15 | 20.0 |

| Species | Pearl and Hermes Atoll | | | | | | Midway Atoll | | | | | |
| | Forereef | | Backreef | | Patch reef | | Forereef | | Backreef | | Patch reef | |
| | n | % | n | % | n | % | n | % | n | % | n | % |
| *Montipora patula* | 1 | 0.0 | 1 | 100.0 | 0 | | | | 0 | | 0 | |
| *Montipora capitata* | 2 | 0.0 | 237 | 75.5 | 1 | 100.0 | 2 | 50.0 | 18 | 100.0 | 0 | |
| *Montipora flabellata* | 0 | | 81 | 1.2 | 0 | | 0 | | 68 | 7.4 | 0 | |
| *Montipora turgescens* | 0 | | 31 | 83.9 | 0 | | 0 | | 15 | 66.7 | 0 | |
| *Porites evermanni* | 2 | 0.0 | 1 | 0.0 | 0 | | | | 3 | 33.3 | 0 | |
| *Porites compressa* | 3 | 0.0 | 1 | 0.0 | 96 | 9.4 | | | 0 | | 0 | |
| *Porites lobata* | 540 | 0.0 | 91 | 1.1 | 0 | | 456 | 0.0 | 52 | 1.9 | 25 | 0.0 |
| *Pocillopora damicornis* | 5 | 0.0 | 98 | 43.9 | 6 | 66.7 | | | 16 | 18.8 | 33 | 9.1 |
| *Pocillopora ligulata* | 0 | | 0 | | 0 | | 0 | | 0 | | 0 | |
| *Pocillopora meandrina* | 145 | 4.1 | 279 | 60.2 | 123 | 74.8 | 73 | 0.0 | 9 | 11.1 | 16 | 31.3 |

| Species | Kure Atoll | | | | | |
| | Forereef | | Backreef | | Patch reef | |
| | n | % | n | % | n | % |
| *Montipora patula* | 0 | | 0 | | 0 | |
| *Montipora capitata* | 0 | | 91 | 61.5 | 0 | |
| *Montipora flabellata* | 0 | | 73 | 1.4 | 0 | |
| *Montipora turgescens* | 0 | | 7 | 0.0 | 0 | |
| *Porites evermanni* | 0 | | 0 | | 0 | |
| *Porites compressa* | 0 | | 0 | | 24 | 0.0 |
| *Porites lobata* | 169 | 0.0 | 18 | 0.0 | 0 | |
| *Pocillopora damicornis* | 2 | 0.0 | 80 | 3.7 | 7 | 6.7 |
| *Pocillopora ligulata* | 0 | | 2 | 0.0 | 5 | 40.0 |
| *Pocillopora meandrina* | 253 | 4.1 | 258 | 6.2 | 35 | 42.9 |

Table 4. Correlation between depth and incidence of bleaching. FFS = French Frigate Shoals; P & H = Pearl and Hermes Atoll; NB = no bleaching observed

| Location | # sites | r | p |
|---|---|---|---|
| FFS | 11 | -0.10 | 0.76 |
| Gardner | 3 | NB | - |
| Maro | 8 | 0.42 | 0.30 |
| Laysan | 3 | -0.41 | 0.74 |
| Lisianski | 9 | -0.44 | 0.24 |
| P&H | 14 | -0.68 | 0.01 |
| Midway | 9 | -0.88 | 0.00 |
| Kure | 9 | -0.40 | 0.24 |

Table 5. Summary of data extracted or calculated from subsurface temperature recorder (STR) data. *STR initially deployed in 2002; STRs at other sites initially deployed in 2003. ATS = accumulated thermal stress. See Methods for details.

| Location/habitat | Depth, m | MMM | 2003 | | | | 2004 | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | First date >MMM+1 | Max. temp. $^oC$ | Date of max. temp. | ATS (days) | First date >MMM+1 | Max. temp. $^oC$ | Date of max. temp. | ATS (days) |
| **French Frigate Shoals** | | 27.2 | | | | | | | | |
| Northeast backreef* | 2.1 | | 7/29 | 28.6 | 9/27 | 1.1 | 7/10 | 29.3 | 8/21 | 6.0 |
| South backreef | 2.1 | | 9/13 | 28.6 | 9/21 | 0.8 | 7/26 | 28.7 | 9/3 | 2.7 |
| La Perouse* | 4.0 | | 9/20 | 28.2 | 9/20 | 0.0 | 8/16 | 28.6 | 8/18 | 2.0 |
| Central lagoon | 2.1 | | 7/29 | 28.6 | 9/20 | 3.0 | 7/10 | 29.5 | 9/5 | 13.5 |
| **Gardner** | | 26.9 | | | | | | | | |
| West central | 10.4 | | -- | 27.4 | 9/21 | 0 | -- | 27.9 | 8/22 | 0 |
| **Maro** | | 27.3 | | | | | | | | |
| South central* | 1.5 | | 9/17 | 28.5 | 9/18 | 1.6 | 8/18 | 29.1 | 9/7 | 28.9 |
| South | 4.3 | | 9/17 | 28.4 | 9/22 | 0.8 | 8/20 | 28.9 | 9/7 | 25.0 |
| **Laysan** | | 27.1 | | | | | | | | |
| Northwest | 1.2 | | 8/5 | 29.0 | 9/21 | 12.8 | 8/6 | 29.4 | 8/21 | 21.2 |
| Southeast | 1.0 | | 8/6 | 30.2 | 9/14 | 5.3 | 8/18 | 29.0 | 9/21 | 16.2 |
| **Lisianski** | | 27.5 | | | | | | | | |
| East of island* | 0.6 | | 7/17 | 31.0 | 8/1 | 21.3 | 7/1 | 31.2 | 8/23 | 35.9 |
| **Pearl & Hermes** | | 26.9 | | | | | | | | |
| Northwest backreef* | 2.4 | | 8/6 | 28.4 | 8/10 | 2.5 | 7/28 | 29.5 | 9/3 | 37.8 |
| North backreef* | 0.5 | | 8/3 | 29.4 | 8/10 | 6.0 | 7/10 | 30.0 | 8/20 | 34.8 |
| Southeast backreef | 1.5 | | 8/1 | 28.0 | 8/10 | 0.1 | 8/12 | 28.9 | 9/2 | 28.3 |
| Southwest backreef* | 1.5 | | -- | 27.8 | 9/5 | 0 | 8/12 | 28.7 | 9/3 | 18.4 |
| Central lagoon | 2.0 | | 8/3 | 29.1 | 8/12 | 16.9 | 7/10 | 30.1 | 8/23 | 49.1 |
| **Midway** | | 27.0 | | | | | | | | |
| North backreef* | 0.9 | | 8/9 | 29.0 | 9/7 | 3.4 | 8/8 | 30.4 | 8/16 | 22.1 |
| North backreef* | 1.5 | | 8/3 | 29.1 | 8/15 | 2.9 | 7/13 | 30.6 | 8/17 | 24.6 |
| East backreef* | 0.9 | | 8/11 | 28.7 | 9/16 | 0.6 | 8/12 | 30.3 | 8/20 | 16.5 |
| Southwest backreef | 0.9 | | -- | 27.9 | 9/18 | 0 | 8/15 | 28.8 | 9/2 | 13.4 |
| **Kure** | | 26.9 | | | | | | | | |
| Northeast backreef* | 0.8 | | 8/3 | 28.4 | 8/31 | 1.5 | 7/30 | 29.5 | 8/19 | 7 |
| West backreef* | 0.6 | | 7/30 | 29.2 | 9/2 | 5.3 | 7/14 | 29.3 | 8/19 | 11.8 |
| Central lagoon | 1.2 | | 8/10 | 29.3 | 8/11 | 14.4 | 7/11 | 30.6 | 8/17 | 30.7 |

Table 6. Summary of accumulated thermal stress (ATS) calculated from subsurface temperature recorders (STRs) and bleaching incidence (% of colonies bleached) at REA sites within 2.5 km of STR, in backreef habitats at the three northern atolls, NWHI.

| STR location | Site #, closest REA site | Distance (km) between STR and REA site | STR depth, m | REA transect depth, m | ATS (days), 2004 | Bleaching incidence at REA site |
|---|---|---|---|---|---|---|
| **Pearl & Hermes** | | | | | | |
| Northwest backreef | R22 | 2.5 | 2.4 | 4.1 | 37.8 | 55.6 |
| North backreef | 26 | 2.0 | 0.5 | 2.4 | 34.8 | 45.7 |
| Southwest backreef | 31 | 0.5 | 1.5 | 2.4 | 18.4 | 56.2 |
| **Midway** | | | | | | |
| North backreef | 1 | 0.2 | 0.9 | 0.9 | 22.1 | 24.0 |
| North backreef | H21 | 0.2 | 1.5 | 1.1 | 24.6 | 35.1 |
| East backreef | R20 | 1.5 | 0.9 | 1.1 | 16.5 | 26.7 |
| Southwest backreef | R25 | 0.0 | 0.9 | 2.1 | 13.4 | 7.4 |
| **Kure** | | | | | | |
| Northeast backreef | 14 | 2.2 | 0.8 | 1.1 | 7 | 0.9 |
| West backreef | 17 | 0.3 | 0.6 | 3.0 | 11.8 | 6.5 |
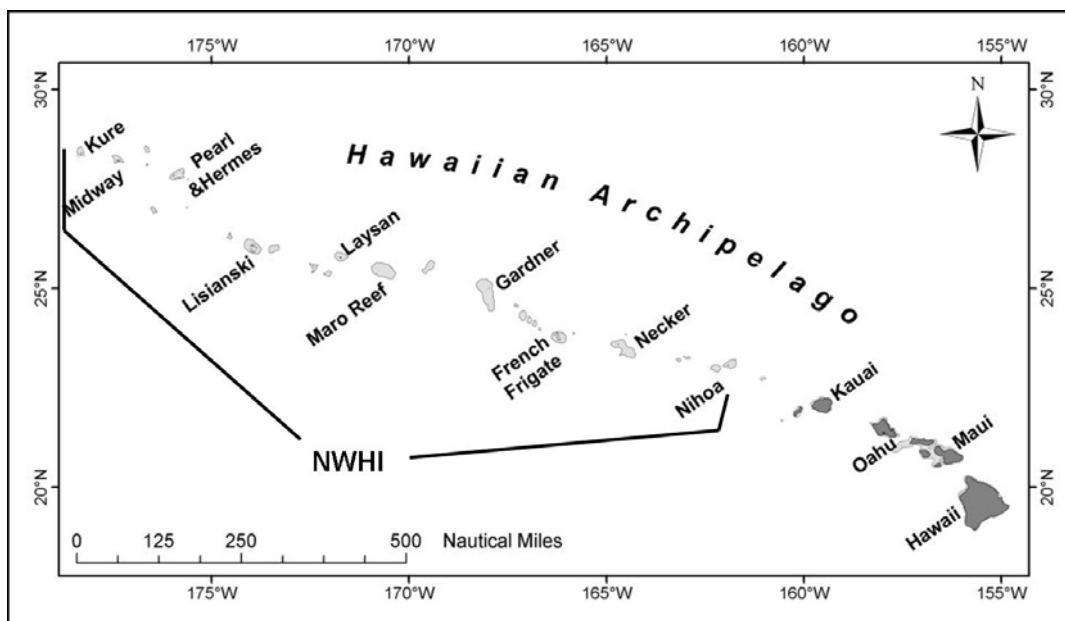


**Figure 1**. The Hawaiian Archipelago. Lightly shaded areas represent 100-fathom isobaths. The NWHI extend northwestward from Nihoa Island to Kure Atoll.
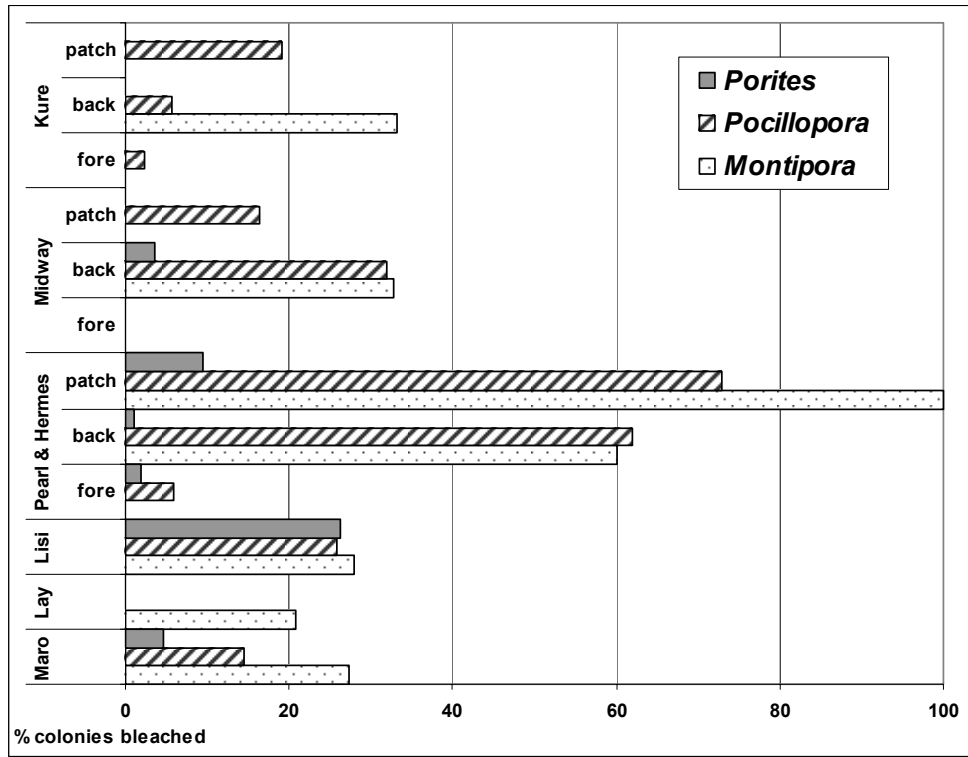
**Figure 2.** Incidence of bleaching within belt transects by location, habitat, and genus, September/October 2004.  Lay = Laysan; Lisi = Lisianski. Gardner Pinnacles and French Frigate Shoals are not shown to reduce the complexity of the figure.
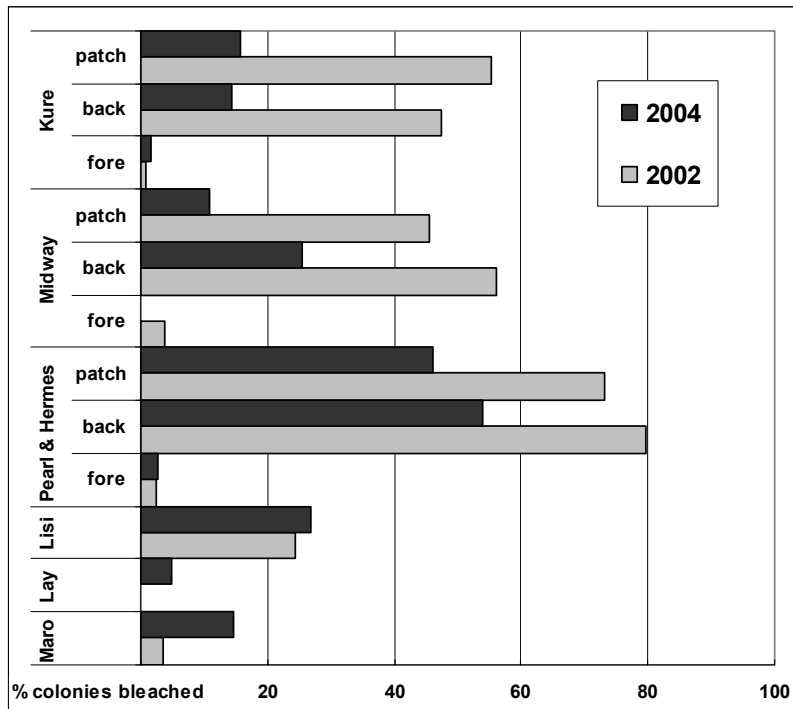


**Figure 3.** Incidence of bleaching in 2002 and 2004. Colony count data for the three dominant genera (Montipora, Pocillopora, Porites) are pooled for each location and habitat within location. Lay = Laysan; Lisi = Lisianski. Gardner Pinnacles and French Frigate Shoals are not shown to reduce the complexity of the figure.

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# DEEP SUBTIDAL MARINE PLANTS FROM THE NORTHWESTERN HAWAIIAN ISLANDS: NEW PERSPECTIVES ON BIOGEOGRAPHY

BY

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## ABSTRACT

In the past 15 years, scientific focus on the marine flora of the Northwestern Hawaiian Islands (NWHI) has intensified, resulting in a doubling of the total number of known species. In 1989, 205 species were recorded; as of January 2005, 353 species have been published for the NWHI. Over 5,100 specimens collected from Midway Atoll and other atolls, reefs, islands, and deep-water sites in the NWHI have shown a marine flora with geographic distribution patterns different from any known similar-sized area in the Pacific. Several new species of macroalgae have been described, including *Dudresnaya babbittiana* (Rhodophyta), *Kallymenia thompsonii* (Rhodophyta), *Hydroclathrus tumulis* (Phaeophyta), *Padina moffittiana* (Phaeophyta), and *Codium hawaiiense* (Chlorophyta). Since 1989, numerous macroalgal and two seagrass species have been documented as records of species new to the NWHI, including *Kallymenia sessilis, Desmarestia ligulata, Nereia intricata, Sporochnus moorei, Caulerpa antoensis, C. cupressoides, C. elongata, C. microphysa, Halophila decipiens,* and *H. hawaiiana.* Although the Hawaiian Archipelago is considered part of the Tropical Indo-West Pacific phytogeographic region, the NWHI's mixture of tropical species, cold-temperate species, species with disjunct distributions, and endemic species suggests alternative biogeographic patterns and dispersal routes.

## INTRODUCTION

While the bulk of the Hawaiian marine flora contains species that are found throughout the tropical Pacific, as is true of the marine floras of other warm Pacific areas (i.e., Fiji and Tahiti), the occurrence of subtropical and cool water entities marks the Hawaiian marine flora as different from most other locations. Collections of marine plants in the Northwestern Hawaiian Islands (NWHI) since 1978 have yielded numerous new species; some appear to be NWHI endemics, and others are new records from these atolls, islands and reefs north of the main Hawaiian Islands (MHI) (Brostoff, 1984; Abbott, 1989; Abbott, 1999; DeFelice, 1999; Abbott and McDermid, 2001; McDermid et al., 2001; Abbott and McDermid, 2002; Abbott and Huisman, 2003; Kraft and Abbott,

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2003; Abbott and Huisman, 2004; Vroom and Abbott, 2004 a, b). In the last 4 years, deep subtidal (10 - 100 m in depth) collections from the National Oceanic and Atmospheric Administration (NOAA) cruises to the NWHI in connection with National Marine Fisheries Service (NMFS) lobster monitoring, and recent National Ocean Service (NOS) and NMFS biological surveys conducted by the Northwestern Hawaiian Islands Rapid Ecological Assessment and Monitoring Program (NOWRAMP, 2000 and 2002), have shown a marine flora with geographic distribution patterns different from any known similar-sized area in the Pacific. For instance, some recently discovered species in the NWHI previously were known only from Japan (i.e., *Kallymenia sessilis* Okamura and *Nereia intricata* Yamada), or Australia (i.e., *Distromium flabellatum* Womersley and *Sporochnus moorei* Harvey), or only from cool temperate to polar regions (*Desmarestia ligulata* (Lightfoot) Lamouroux) (Abbott and Huisman, 2004). The geographic isolation of the Hawaiian Archipelago, whose nearest neighbor is Johnston Atoll over 600 km to the southwest, and whose closest continental land mass is over 5,000 km away, makes species with disjunct distributions of special significance to our understanding of biogeography. The purpose of this paper is to take stock of the many new species of deep subtidal marine plants recently recorded from the NWHI, and for the first time to evaluate their biogeographic affinities, and examine possible oceanographic explanations for these patterns.

## METHODS AND MATERIALS

Pressed herbarium specimens and microscope slides of marine plants, preserved according to methods outlined by Tsuda and Abbott (1985), that had been hand-collected using SCUBA or recovered from lobster traps from the NWHI during various NOS and NMFS research expeditions (1978-2002), were examined. Distribution records of previously reported genera and specific species were compared (Abbott, 1999; Guiry and Nic Dhonncha, 2002; Abbott and Huisman, 2004).

## RESULTS

Approximately 300 species of marine macroalgae and 2 species of seagrasses are known from the NWHI (Abbott, 1999; McDermid et al., 2001, 2003; Abbott and Huisman, 2004). Many species, either new to science or newly reported for the area, have been discovered in recent NWHI collections (Table 1). Many of the macroalgal and both seagrass species belong to characteristically tropical genera known from the warm Indo-West Pacific, such as *Caulerpa*, *Dictyota*, *Dudresnaya*, *Halophila*, *Hydroclathrus*, and *Padina*. The calcified green seaweed genus, *Halimeda,* also has a warm tropical distribution, but several species found in the NWHI (*H. copiosa* Goreau et Graham, *H. macroloba* Decaisne, and *H. velasquezii* Taylor) have no published records in the MHI.

Some NWHI species have unusually disjunct distributions. Species with Japanese affinities include *Crouania mageshimensis* Itono collected from a depth of 10-70 m in the NWHI (Abbott, 1989), *Nereia intricata* from 32-94 m Maro Reef (Abbott and Huisman 2003), and *Kallymenia sessilis* found subtidally in the NWHI and the Island of Hawai'i

Table 1. New species** and new records* from NWHI, 1984 to 2004.

| Name | Distribution | Reference |
|---|---|---|
| CHLOROPHYTA | | |
| *Caulerpa antoensis* | NWHI (Gardner, Necker), Ant Atoll, Bikini Atoll, Tanzania | Abbott & Huisman (2004) |
| *Caulerpa cupressoides* | NWHI (FFS), circumtropical | Abbott & Huisman (2004) |
| *Caulerpa elongata* | NWHI (Lisianski), Indo-West Pacific | Abbott & Huisman (2004) |
| *Caulerpa microphysa* | NWHI (Midway), Indian Ocean, Fiji | Abbott & Huisman (2004) |
| **Codium campanulatum* | NWHI & MHI endemic | Silva & Chacana in Abbott & Huisman (2004) |
| **Codium desultorum* | NWHI & MHI endemic | Silva & Chacana in Abbott & Huisman (2004) |
| **Codium hawaiiense* | NWHI endemic | Silva & Chacana in Abbott & Huisman (2004) |
| **Codium intermedium* | NWHI endemic | Silva & Chacana in Abbott & Huisman (2004) |
| *Codium subtubulosum* | NWHI, MHI, Japan, Pakistan | Abbott & Huisman (2004) |
| *Halimeda copiosa* | NWHI, Caribbean, Australia, Micronesia | Abbott (1989) |
| *Halimeda macroloba* | NWHI (Midway), Indo-West Pacific | Abbott & Huisman (2004) |
| *Halimeda velasquezii* | NWHI, Philippines, China, Japan, Indian Ocean | Abbott (1989) |
| PHAEOPHYTA | | |
| *Desmarestia ligulata* | NWHI (Necker), Alaska, California, Chile, Australia, Antarctica, Scotland | Abbott & Huisman (2003) |
| *Dictyota stolonifera* | NWHI, MHI, Nicaragua, Kenya | Abbott & Huisman (2003) |
| *Distromium flabellatum* | NWHI, MHI, southern Australia, New Caledonia | Abbott & Huisman (2003) |
| **Hydroclathrus tumulis* | NWHI endemic | Kraft & Abbott (2003) |
| *Nemacystus decipiens* | NWHI, MHI, Japan, Indian Ocean, Arabian Sea | Abbott (1989) |
| *Nereia intricata* | NWHI (Maro), Japan | Abbott & Huisman (2003) |
| **Padina moffittiana* | NWHI endemic | Abbott & Huisman (2003) |
| *Sporochnus dotyi* | NWHI & MHI endemic | Brostoff (1984), Abbott & Huisman (2004) |
| *Sporochnus moorei* | NWHI, southern Australia, New Zealand | Abbott & Huisman (2003) |

Table 1. Continued.

RHODOPHYTA

| | | |
|---|---|---|
| **_Acrosymphyton brainardii_ | NWHI (FFS) endemic | Vroom & Abbott (2004a) |
| *_Crouania mageshimensis_ | NWHI, Japan, Caroline Is. | Abbott (1989) |
| **_Dudresnaya babbittiana_ | NWHI (Midway) endemic | Abbott & McDermid (2001) |
| *_Kallymenia sessilis_ | NWHI, MHI, Japan | Abbott & McDermid (2002) |
| **_Kallymenia thompsonii_ | NWHI endemic | Abbott & McDermid (2002) |
| **_Scinaia huismanii_ | NWHI endemic | Vroom & Abbott (2004b) |

MAGNOLIOPHYTA

| | | |
|---|---|---|
| *_Halophila decipiens_ | NWHI (Midway), MHI, circumtropical | McDermid et al. (2001) |
| *_Halophila hawaiiana_ | NWHI (Pearl & Hermes, Midway) & MHI endemic | DeFelice (1999) McDermid et al. 2003) |

(Abbott and McDermid, 2002). Taxa with Australian affinities include _Acrosymphyton, Distromium_, and _Sporochnus_. _Distromium flabellatum_ is found only in southern Australia, the NWHI, and the MHI, and all other species in this genus are restricted to Japan and the Juan Fernandez Islands off Chile. _Sporochnus moorei_ is known only from southern Australia, New Zealand, and Necker Island at 38-72 m (Abbott and Huisman, 2003), and Midway Atoll at 20 m (collected Sept. 23, 2002, specimen number KM7992).

Other members of the NWHI marine flora have cold-temperate water biogeographic affinities, including _Desmarestia, Sporochnus_ and _Kallymenia_. _Desmarestia ligulata_, a species frequently occurring with kelps from Alaska to Antarctica, and often in California, was found alive on Necker Island at a depth of 30-56 m (Abbott and Huisman, 2003). Most members of _Sporochnus_, except the Hawaiian endemic, _S. dotyi_ Brostoff, are cool water species from Japan, China, Australia, Scandinavia, California, and the Galapagos Islands. _Kallymenia_ species "are unusual occurrences in the tropics" (Abbott, 1999), since most species in this genus are cool-temperate water species of North and South America and Japan.

In addition, several recently reported new species probably are endemic to the NWHI, including _Acrosymphyton brainardii_ Vroom et Abbott, _Codium hawaiiense_ Silva et Chacana, _Codium intermedium_ Silva et Chacana, _Dudresnaya babbittiana_ Abbott et McDermid, _Hydroclathrus tumulis_ Kraft et Abbott, _Kallymenia thompsonii_ Abbott et McDermid, _Padina moffittiana_ Abbott et Huisman, and _Scinaia huismanii_ Vroom et Abbott.

Often in the NWHI, cold-temperate species are collected sympatrically with tropical species; for instance, _Sporochnus_ (Phaeophyta) entangled on the same lobster trap as _Caulerpa_ (Chlorophyta), and _Kallymenia_ (Rhodophyta) found within the same 0.25 $m^2$ quadrat as _Halimeda_ (Chlorophyta). Such observations call for investigation of species' actual temperature requirements, as well as measurement of localized thermal fluxes that might allow these species to co-exist.

# DISCUSSION

The geographic distributions of marine plants are attributed primarily to water temperature and the temperature thresholds governing growth, reproduction, and survival of each species (Breeman, 1988; Lüning, 1990; Bolton, 1994; Lobban and Harrison, 1994). The large-scale phytogeographic regions for benthic marine plants are based on water temperature according to van den Hoek (1984). The marine floras of oceanic Pacific islands, including the Hawaiian Archipelago, have been lumped within a huge phytogeographic region: the Tropical Indo-West Pacific Region, which stretches 22,000 km from East Africa to the Tuamotus in French Polynesia. Warm water is the defining character used to unite this vast region of diverse landmasses and complex oceanographic conditions. Adey and Steneck (2001) proposed a temperature/space/time integrated model for marine biogeographic regions, which compiles rocky, sublittoral, photic zone temperature regimens and coastal area over time since the last glacial period 18,000 years before present (BP). The model defines 20 thermogeographic regions, including an Indo-Pacific region to which the Hawaiian Islands are assigned. However, the use of temperature alone as the critical factor in distribution or in delineating phytogeographic regions is debatable.

It has been assumed that "in general, the stock of seaweed species of central Pacific oceanic islands is relatively small and consists mainly of immigrated, widely distributed species accompanied by few endemics" (Lüning, 1990, p. 232). This assumption does not hold true for the Hawaiian Islands, which are home to over 500 species of marine macroalgae, perhaps because of the Archipelago's extreme isolation, geologic time frame, and variety of habitats. Even within the island chain, the NWHI differ from the MHI in terms of substratum, habitat variety, age, size, intertidal area, water temperature, current patterns, day length, and exposure to short-term climate events (e.g. El Niño Southern Oscillations) (Abbott, 1989; Silva, 1992).

With another theory, known as vicariance biogeography, scientists explain the geographic distribution of marine algae based primarily on patterns of dispersal and barriers to dispersal (Hommersand, 2001). Barriers to dispersal to the Hawaiian Islands include open-ocean distance, ocean depth, current patterns, and open-ocean sea temperatures. The sea surface temperatures in the north Pacific in the vicinity of the Hawaiian-Emperor Chain were above 20°C in the early Tertiary, about 65 to 40 million years ago (mya), then ranged between 16°C and 20°C during the Oligocene and Early Miocene (40-15 mya), then rose above 20°C again, and have remained nearly stable in the central gyres of the subtropical north Pacific since the last glacial period (18,000 years BP) (Grigg, 1988). In addition, cores from the Emperor Seamounts contain tropical, shallow, marine fossils (Grigg, 1988). However, Grigg (1988) hypothesized that prior to 34 mya, the Hawaiian Archipelago was isolated from the Indo-West Pacific because of the dominant equatorial circulation patterns before the closure of the Tethys Sea. The ancient marine flora of the Hawaiian-Emperor Chain may have been very different from today. Subsequent to the Tethys Sea closure, north-south circulation patterns (gyres) were enhanced, and currents in the north Pacific may have been strengthened sufficiently to transport organisms from the Indo-West Pacific to the Hawaiian Archipelago.

Xie et al. (2001) suggested the existence of a subsurface, eastward ocean current, the Hawaiian Lee Counter Current located at 19° N latitude and driven by the wind wake that trails westward behind the Hawaiian Islands. The Hawaiian Lee Counter Current draws warm water at nearly 0.2 m/s from the Asian coast 8,000 km from the Hawaiian Archipelago. At this rate it would take approximately 400 days for a propagule to travel from the Philippines to Hawai'i in this current. The role of this current in spore dispersal and vegetative fragment transport is unknown.

The deployment and tracking of 6 floats and 22 drifters in the NWHI from 2001-2003 (Firing et al., 2004) have shown various patterns of surface-water (0-35 m) movement, including "lingering" of drifters around the northernmost atolls, long distance travel of drifters among central atolls, limited connections between southern NWHI and northern MHI, movement of two floats from the NWHI westward to Johnston and Wake Atolls, and even a round-trip voyage by one drifter from the NWHI to the coast of Japan and back. These circulation patterns suggest several possible dispersal routes for algal spores, seagrass seeds, and marine plant fragments to and from the NWHI, and may provide a mechanism for the retention of endemic species within the NWHI.

Kuroshio Current eddies and meanders, and the Kuroshio Extension in the north Pacific may be responsible for the presence of macroalgae in the Hawaiian Islands with Japanese affinities. *Desmarestia ligulata* populations in the NWHI may be the result of microscopic gametophytes (whose gametes fuse to form macroscopic sporophytes) rafting in the California Current as it turns southwest (Abbott and Huisman, 2004). Species shared by southern Australia and the Hawaiian Islands perhaps traveled via a long route in the West Wind Drift to South America and northward. While many studies have tracked the movement of large fishes, such as tuna, or macroalgae floating in the Sargasso Sea, in connection with oceanographic currents, no Pacific studies, to our knowledge, have used marine plants of *Sargassum*-size or smaller to test hypotheses that might explain their occurrences in isolated locations.

Our present concepts about large-scale phytogeographic regions are focused on water temperature. Other factors also may be responsible for marine plant distributions in the Pacific, such as circulation patterns, seasonal, localized, deep subtidal temperature fluxes or upwellings, short-term climate events, and the presence of suitable substrata for hitchhiking epiphytes, e.g. logs, nets, or other floating plant material. Although the Hawaiian Archipelago is considered part of the Tropical Indo-West Pacific phytogeographic region, the NWHI's mixture of tropical species, cold-temperate species, species with disjunct distributions, and endemic species confounds current biogeographic regional boundaries, and suggests alternate patterns and dispersal routes. In the future, molecular methods, in combination with phylogenetic systematics and paleo- and modern oceanographic data, may help identify ancestral taxa, ancestral areas, and dispersal pathways.

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# RELATIVE ABUNDANCE OF MACROALGAE (RAM) ON NORTHWESTERN HAWAIIAN ISLAND REEFS[1]

BY

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## ABSTRACT

The Northwestern Hawaiian Islands (NWHI) represent one of the last relatively intact tropical reef ecosystems in existence, yet macroalgal community dynamics of the 10 atolls, islands, and reefs situated in the NWHI Coral Reef Ecosystem Reserve remain virtually unknown. This manuscript is the first to provide distributional maps of six common species along the NWHI chain, statistically compare sites from differing habitats and islands based on relative abundance of macroalgae (RAM), and look for temporal differences in macroalgal populations. Our findings reveal that the abundance of most macroalgal species is low, but that members of *Halimeda* and *Microdictyon* can be extremely common and in some cases form dense monotypic meadows on the reef. Other genera, such as *Stypopodium*, *Lobophora*, and *Laurencia*, become increasingly prevalent in northwesterly atolls of the Hawaiian Archipelago. The RAM across the NWHI chain as a whole remained relatively static for the years surveyed. However, slight changes occurred at Kure and Midway atolls where coral bleaching events were documented in 2002 and 2004.

## INTRODUCTION

Qualitative understanding of the marine algal flora of the Northwestern Hawaiian Islands (NWHI) has improved dramatically since 2000 as the National Oceanic and Atmospheric Administration (NOAA) Pacific Island Fisheries Science Center's Coral Reef Ecosystem Division (CRED) and multi-agency Northwestern Hawaiian Islands Reef Assessment and Monitoring Program (NOWRAMP) began conducting annual research expeditions to these remote reefs. Comprehensive lists of reported algal species have been compiled (Abbott, 1989 and 1999; Abbott and Huisman, 2003), several algal species new to science described (Abbott and McDermid, 2001 and 2002; Vroom and Abbott, 2004a and b; Vroom, 2005), and reproductive processes for some algal species reported for the first time (Vroom and Smith, 2003). Yet despite this dramatic increase in phycological activity, very little quantitative research has been published to provide

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an understanding of baseline community structure on reefs surrounding these relatively unpolluted islands (Maragos and Gulko, 2002; Friedlander et al., 2004).  In order to protect and conserve these valuable ecosystems in times of potential environmental change, scientists need knowledge of algal abundance and distribution in conjunction with algal diversity.

In 2002, CRED began quantitative algal monitoring of the NWHI (Fig. 1) using a rapid ecological assessment (REA) protocol developed specifically for remote island ecosystems (Preskitt et al., 2004).  The species-level percent cover analyses possible through the Preskitt method (Preskitt et al., 2004) were used to successfully complete a detailed analysis of benthic cover at the French Frigate Shoals (FFS), NWHI (Vroom et al., 2005 and 2006); however photoquadrat and voucher specimen analyses proved time-consuming.  An expedited method of analysis relying on the field note component of the Preskitt method was desired to quickly give a coarse-level understanding of distribution and relative abundance of macroalgae (RAM) over the entire NWHI Archipelago within a short time of returning from the field.  The objectives of this study were to: (1) assess the effectiveness of field collected data for rapid post-cruise analysis (~ 1 month) of macroalgal assemblages across an entire archipelago; (2) create distributional maps of common macroalgal species; (3) determine if RAM differed significantly among sites from different habitats; (4) determine if RAM differed significantly among sites from different islands/latitudes; and (5) determine if significant differences in RAM at specific sites occurred between sampling years.

## MATERIALS AND METHODS

Field Work

Benthic REA data from three research expeditions (10 September - 4 October, 2002; 14 July - 8 August, 2003; 13 September - 17 October, 2004) to the NWHI (Fig. 1) visited 59, 71, and 67 sites, respectively.  The 2002 cruise marked the end of the CRED random multi-site reef assessment era, while the 2003 and 2004 cruises established and revisited long-term monitoring sites.  Long-term monitoring sites were selected by a multidisciplinary group of researchers to represent a variety of habitat types at each island that could be accessed on an annual basis regardless of prevailing weather or oceanographic conditions.  At each site, phycologists worked along two 25-m transect lines set in a single-file row, with each transect separated by ~10 m.  With the exception of some shallower back reef and lagoonal sites, most transects were placed at a standard 10 -15 m depth.  Macroalgae were identified to species in the field when possible, and rankings of macroalgal genera were observed in each quadrat (1 being the most abundant, 2 being the next most abundant, etc., with 10 being the maximum number of genera found in a single quadrat) to determine RAM.  Six quadrats were located at randomly selected points along the transects (three per transect), and six quadrats were located at points 3 m perpendicular from each random point in the direction of shallower water (Vroom et al., in press).  Because of difficulties with identification in the field,

macroalgae that fell within the functional groups of cyanophytes, branched coralline algae, and crustose coralline algae were lumped into their respective categories. All ranked data were collected by the same individual during each sampling year (P. Vroom 2002, 2004; K. Page 2003) to minimize the effects of observer bias.

Data Analysis

The percentage of quadrats in which each species occurred was determined for each site sampled in 2004 and used to create distributional maps of algal abundance (Figs. 2, 3). Because ratios of major algal lineages (red, brown, and green algae) have been used historically to categorize tropical and temperate ecosystems (Cheney, 1977; Schils and Coppejans, 2003), macroalgal genera also were characterized by evolutionary group, and trends among the percentage of quadrats in which each evolutionary group occurred at each island were illustrated using SigmaPlot (Fig. 4).

To test whether significant differences of RAM existed among habitats and among islands, genus ranks from quadrats surveyed in 2002 and 2003 were treated as individual replicates within a site (n = 12), and a Bray-Curtis similarity matrix of quadrats was created using PRIMER-E (Clarke and Warwick, 2001). Two rigorous analyses using two-way nested analysis of similarity (ANOSIM; 5,000 permutations) were conducted: one nesting sites within habitat type, the other nesting sites within island. Relationships among sites from different habitat types based on RAM were visually depicted using multidimensional scaling (MDS; 30 restarts). Additionally, to depict relationships among islands (latitudes) based on RAM, data within the matrices were averaged by island, and a Bray-Curtis similarity matrix of this averaged data was generated. Ordinations of relationships were created via MDS and these relationships visually compared to geographic maps of the Archipelago (Figs. 1, 5).

To determine if RAM in the NWHI changed over time, several two-way crossed ANOSIMs were conducted (Factor A = year, Factor B = site; 5,000 permutations). In the first analysis, 17 sites from across the NWHI that were sampled in 2002, 2003, and 2004 were compared. In the second analysis, 55 sites from across the chain with data for 2003 and 2004 were compared. Finally, analyses for the 17 sites with 3 years of data were conducted by island (FFS, Lisianski, Pearl and Hermes Atoll (PHR), Midway, and Kure) to determine if particular islands in the NWHI were changing more than others.

**RESULTS**

Distribution and Abundance

During the 2004 sampling season, 65 species of macroalgae were identified in the field (22 chlorophytes, 34 rhodophytes, 9 phaeophytes) along with branched coralline, crustose coralline, cyanophyte, and turf algal functional categories. Most species occurred in only 1-5% of the quadrats sampled. However, species of the green algal genus *Halimeda* (particularly *H. velasquezii* Taylor and *H. opuntia* Lamouroux) were

found in over 70% of quadrats at numerous islands and were major substrate occupiers across broad geographic regions and habitat types (Figs. 2, 3).  Other prevalent species such as the brown algae *Lobophora variegata* Agardh, *Stypopodium flabelliforme* Weber-van Bosse, and the red alga *Laurencia galtsoffii* Howe were locally abundant across several habitat types, but on only one to several islands in the northwestern part of the NWHI chain (Figs. 2, 3).  Yet other species such as the green alga *Microdictyon setchellianum* Howe were found throughout the chain, but were abundant only in forereef to backreef regions (Figs. 2, 3).

When macroalgal distributional trends were considered based on evolutionary lineage, a lower prevalence (defined as the percentage of photoquadrats at a given site in which a genus or evolutionary group occurred) of green algae was observed at Midway Atoll than other islands in the NWHI (Fig. 4a).  Gardner Pinnacles exhibited a lower prevalence of red algae when compared to Maro Reef, Laysan and Lisianksi Islands, and a higher prevalence of cyanophytes than any other island in the NWHI chain (Fig. 4b, d).  The French Frigate Shoals also showed a lower prevalence of red algae than Maro Reef.  Midway and Kure Atolls, located at the extreme northwest end of the Hawaiian Archipelago, revealed a higher prevalence of brown algae from all other islands except Gardner Pinnacles and the French Frigate Shoals (Fig. 4c).

Relative Abundance

A two-way nested ANOSIM of ranked data from 107 sites at nine islands found a moderately low global *r*-value between sites, indicating slight differences between RAM when sites from all habitats were compared simultaneously (Table 1).  However, a negative global *r*-value for tests between habitats revealed that more algal variability existed among sites within a habitat type than between habitats (Chapman and Underwood, 1999).  Pairwise comparisons among the three habitat types surveyed confirmed this finding (Table 1).

A similar two-way nested ANOSIM examining RAM among latitudinally distinct islands/atolls revealed a relatively low global *r*-value between sites, indicating negligible to slight differences between RAM when sites from all islands were compared simultaneously (Table 2).  However, a negative global *r*-value for tests between islands revealed that more algal variability existed among reefs within an island ecosystem than between islands as a whole (Chapman and Underwood, 1999).  Pairwise comparisons between individual islands confirmed this finding, with over 80% of the *r*-values generated being negative (Table 2).  The remaining island comparisons exhibited *r*-values below 0.250 (Table 2), indicating that essentially no differences existed in algal genus abundance between these islands.  However, a moderate difference was revealed between Necker Island and Gardner Pinnacles ecosystems with a mid-range *r*-value.

Relationships among habitats and islands based on RAM were illustrated using MDS (Fig. 5).  Clearly, sites did not segregate into distinct clusters based on habitat type (Figure 5A), and a stress value above 0.20 indicated that the relationship of sites in the MDS ordination is close to arbitrary (Clarke and Warwick, 2001).  However, relationships among islands as revealed through MDS were remarkably similar to a

physical map of the NWHI island chain (Figs. 1, 5B) even though ANOSIM was not particularly successful in defining differences between islands based on rank (Table 2). Necker Island, at the southeastern end of the island chain, was located at one end of the MDS plot, while Pearl and Hermes, Midway, and Kure atolls, located at the northwestern end of the island chain, were located at the opposite corner (Figure 5B). Additionally, Lisianski Island, Laysan Island, and Maro Reef, three mid-archipelago, non-atoll-like islands and reefs, appeared clustered together in the MDS plot about halfway between Necker Island and Kure Atoll. The French Frigate Shoals, a true atoll system, appeared to be the only ecosystem whose geographic location was not accurately reflected in the MDS ordination (Figs. 1, 5B).

Comparisons BetweenYears

$R$-statistics around or below 0.250 from two-way crossed ANOSIMs using ranked data indicate no major difference in RAM between years at sites located in the eastern end of the NWHI chain (Table 3). However, $r$-statistics above 0.300 at both Midway and Kure atoll indicate slight to moderate differences in RAM (Clarke and Warwick, 2001) among sites located in these high latitude reefs (Table 3) and suggest that changes in the reef environment may be occurring in these areas. $R$-statistics close to 0.250 indicate that RAM has not changed significantly when the NWHI are compared as a whole.


**DISCUSSION**

This study provides the first quantitative data for algal genera across the entire NWHI chain and lays the groundwork for continued macroalgal monitoring studies. Field data collected via the Preskitt method (Preskitt et al., 2004) proved sufficient to create distributional species maps (Figs. 2, 3) and conduct multivariate statistical analyses of RAM among habitats, islands, and sampling periods. ANOSIM analyses revealed that percent cover data (Vroom et al., 2005) is better at detecting differences between islands than ranked abundance data. However, the field-assigned macroalgal ranks (this study) provided critical data useful for quickly interpolating seasonal or yearly differences in RAM. If a particular species "blooms" at certain times of the year, its abundance will increase in relation to other species. Similarly, if environmental changes or anthropogenic activities favor the growth of certain species over others, RAM will change over time, and these changes may be detectable through basic statistical and multivariate analyses.

Distributional maps of six common macroalgal species demonstrated a necessary leeward sampling bias in long-term monitoring sites because of weather/oceanographic constraints (Figs. 2, 3). Despite this bias, important observational trends were evident. Green algae are the most abundant macroalgal group in terms of biomass and spatial coverage in the NWHI, and calcified species play an important role in sand production (P. Vroom, personal observation). *Halimeda velasquezii*, a species that has never been recorded in the Main Hawaiian Islands (Abbott and Huisman, 2003), is the single-most

ubiquitous alga, occurring in relatively high numbers in most habitats on all islands (Figs. 2, 3). *Microdictyon setchellianum* is most abundant in terms of percent cover, especially in forereef regions on the windward sides of atolls (Vroom et al., 2005). *Halimeda opuntia* forms dense three-dimensional mats on leeward reefs and in calm lagoonal waters. Although the brown algae *Lobophora variegata* and *Stypopodium flabelliforme* are found across the entire Hawaiian island chain, distributional maps clearly show these species to be more abundant in the northwestern-most atolls (Figs. 2, 3), a phenomenon also observed by Walsh et al. (2002) in their study of shallow lagoonal reef communities at Kure Atoll. While *S. flabelliforme* was a major component of shallow-reef systems at Kure Atoll, it was a minor component of reefs at most other islands and atolls in the NWHI. Because brown algae are known to predominate over other algal lineages in cool, temperate environments (Cheney, 1977), it is possible that the cooler sea-surface temperatures found at Kure and Midway atolls during winter months (Friedlander et al., 2005) may favor a higher abundance of brown algal species (Fig. 4).

Multivariate Primer analyses testing for differences in RAM among habitats (forereef, backreef, lagoonal reefs) revealed significant variation to occur within habitat type (Table 1), a phenomenon also observed in Vroom et al. (2005) during a detailed study of benthic cover at French Frigate Shoals. Considering the amount of environmental variation present within single habitats (e.g., water motion, turbidity, light, and nutrient availability), such findings are not surprising. More revealing than significant site differences within habitats was that multivariate analyses showed no major differences among islands as a whole (Table 2) despite known temperature variation over latitude (Friedlander et al., 2005). Algal diversity appears similar across the NWHI chain even though brown algae tend to be more abundant at Midway and Kure atolls than most other islands (Fig. 4). The lower abundance of green algae at Midway may be tied to lower apex predator biomass and higher herbivorous fish densities at this atoll system, suggesting possible top-down control of the benthic habitat (DeMartini and Friedlander, 2004; E. DeMartini, personal communication).

It is remarkable that the orientation of islands based on RAM mimics the spatial patterns and geographic relationships of these island ecosystems (Figs. 1, 5B). An MDS ordination of islands based on RAM closely resembles a geographic map of the NWHI and suggests that detectable (although not significant) differences in RAM exist among islands that mirror physical distance and latitude. The placement of French Frigate Shoals away from its closest geographical neighbors and close to the three northwestern-most islands suggests similarities in RAM between these four true atoll systems (Fig. 5B). Laysan, Lisianski, and Maro, three non-atoll reefs and islands, lack broad lagoonal regions and likely exhibit a different suite of habitat types than found in true atolls. The corresponding difference in RAM is shown through MDS by these islands clustering together a slight distance away from the atolls (Fig. 5B). Gardner and Necker, the only basaltic islands, are distant from the other seven islands depicted (Fig. 5B).

Although no significant temporal differences in RAM were observed when the NWHI were compared as a whole (Table 3), slight to moderate differences in RAM at Midway and Kure may result from mass coral-bleaching events that occurred in these high-latitude reefs during 2002 and 2004 (Aeby et al., 2003; Kenyon and Brainard,

2006). Although most dead coral were anecdotally observed to be overgrown with turf algae (P. Vroom, personal observation), increased substrate availability may also affect macroalgal community dynamics by clearing space for certain species to settle and grow. Although RAM may have increased because of this additional substrate availability, it is important to consider that algae are among the fastest growing organisms in reef systems, so seasonal or oceanographic differences (e.g., El Niño events) could rapidly alter RAM for short periods. Therefore, the slight differences observed at Midway and Kure atolls in this study do not necessarily indicate permanent changes.

Overall, reefs in the NWHI are healthy, top-predator-dominated ecosystems that naturally contain a diverse and abundant algal community. Although the mix of macroalgal species is relatively similar throughout the NWHI chain, certain species (e.g., *Stypopodium flabelliforme*, *Laurencia galtsoffii*) are more abundant in the northwestern-most atolls where sea surface temperatures experience the greatest annual fluctuation (Friedlander et al., 2005). The majority of macroalgal species in the shallow (<15 m) reef habitats surveyed exhibit relatively low abundances and occurred in 1-5% of quadrats sampled for a particular island. However, species of the green algal genera *Halimeda* and *Microdictyon* often formed dense meadows with up to 100% cover in some areas. Dense meadows of algae have also been documented in deeper bank habitats not considered in this manuscript (Parrish and Boland, 2004). Future annual or biennial monitoring at established long-term sites will continue to provide understanding of normal macroalgal community dynamics and alert reef managers to permanent changes of RAM in these unique reef habitats.

## ACKNOWLEDGEMENTS

Table 1: RAM habitat comparisons: r-values of two-way nested ANOSIM (5,000 permutations).

| Sample Statistic (Global R) | Sample Statistic (Global R) | Significance level of sample statistic | Number of permuted statistics > or = to Global R |
|---|---|---|---|
| Tests for differences between sites (averaged across all habitats) | 0.372 | 0.% | 0 |
| Tests for differences between habitats (using sites as samples) | -0.346 | 100.% | 5000 |
| Sample statistics of pairwise tests: | | | |
| Fore-reef to backreef | -0.164 | | |
| Fore-reef to lagoonal reef | -0.463 | | |
| Back-reef to lagoonal reef | -0.233 | | |

Table 2: RAM island comparisons: r-values of two-way nested ANOSIM. FFS = French Frigate Shoals, PHR = Pearl and Hermes Atoll (5,000 permutations).

| | Sample Statistic (Global R) | Significance level of sample statistic | Number of permuted statistics > or = to Global R |
|---|---|---|---|
| Tests for differences between sites (averaged across all islands) | 0.321 | 0 % | 0 |
| Tests for differences between islands (using sites as samples) | -0.162 | 100 % | 5000 |

Sample statistics of pairwise tests:

| | Kure | Midway | PHR | Lisianski | Laysan | Maro | Gardner | FFS | Necker |
|---|---|---|---|---|---|---|---|---|---|
| Necker | -0.152 | -0.323 | -0.089 | -0.545 | -0.600 | -0.631 | 0.333 | -0.621 | |
| FFS | -0.020 | 0.122 | -0.205 | -0.115 | -0.370 | 0.020 | 0.132 | | |
| Gardner | -0.435 | -0.414 | -0.474 | -0.428 | -0.364 | -0.348 | | | |
| Maro | -0.227 | 0.091 | -0.179 | -0.510 | -0.457 | | | | |
| Laysan | -0.370 | 0.068 | -0.282 | -0.222 | | | | | |
| Lisianski | -0.232 | 0.171 | -0.185 | | | | | | |
| PHR | -0.408 | -0.104 | | | | | | | |
| Midway | -0.003 | | | | | | | | |

Table 3:  RAM year comparisons: results of two-way crossed ANOSIMs (5,000 permutations).  Pairwise tests between sites not shown.  FFS = French Frigate Shoals, PHR = Pearl and Hermes Atoll.  One site for Laysan Island was included in the NWHI test between 2003-2004 but is not listed independently.

| Island | # sites | Tests for differences in RAM among sites between 2002, 2003, 2004. | | | # sites | Tests for differences in RAM among sites between 2003 and 2004. | | |
|---|---|---|---|---|---|---|---|---|
| | | Sample statistic (Global R) | Significance level of sample statistic | Number of permuted statistics > or = to Global R | | Sample statistic (Global R) | Significance level of sample statistic | Number of permuted statistics > or = to Global R |
| NWHI | 17 | 0.277 | 0.% | 0 | 55 | 0.229 | 0.% | 0 |
| FFS | 3 | 0.253 | 0.% | 0 | 11 | 0.217 | 0.% | 0 |
| Gardner | - | - | - | - | 2 | 0.097 | 1.3% | 63 |
| Maro | - | - | - | - | 7 | 0.162 | 0.% | 0 |
| Lisianksi | 2 | 0.281 | 0.% | 0 | 8 | 0.206 | 0.% | 0 |
| PHR | 4 | 0.169 | 0.% | 0 | 12 | 0.149 | 0.% | 0 |
| Midway | 4 | 0.337 | 0.% | 0 | 5 | 0.313 | 0.% | 0 |
| Kure | 4 | 0.340 | 0.% | 0 | 9 | 0.437 | 0.% | 0 |



**Figure 1.**  Map of the Hawaiian Archipelago.  The 10-NWHI span from Nihoa Island to Kure Atoll.
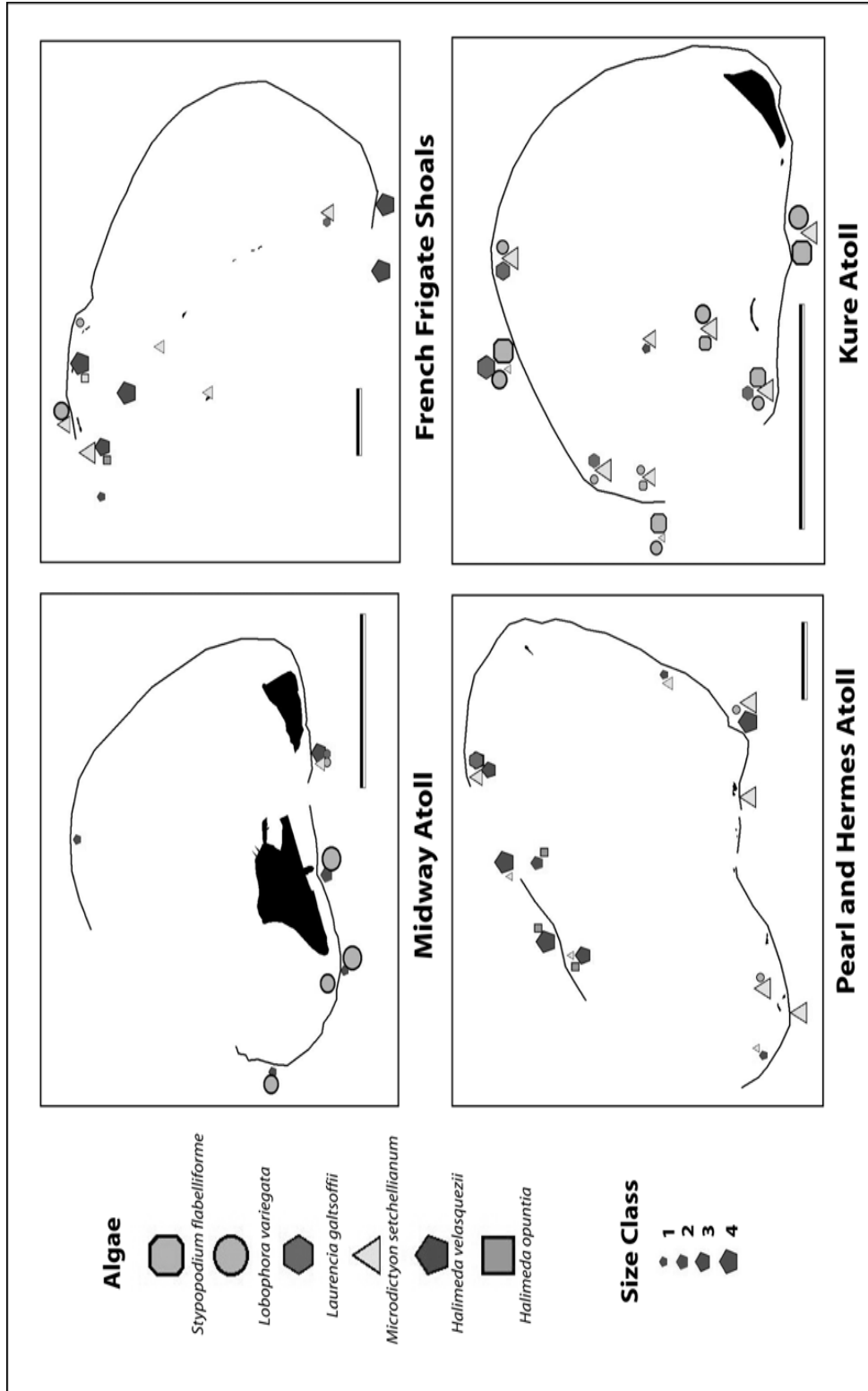
**Figure 2.** Outline drawings of the four atoll systems located in the Northwestern Hawaiian Islands overlaid with algal distributional maps. Solid black lines indicate position of reef crest. Scale bars = 5 km. Size classes refer to the percentage of quadrats in which an alga occurred at a given site: 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%.

544
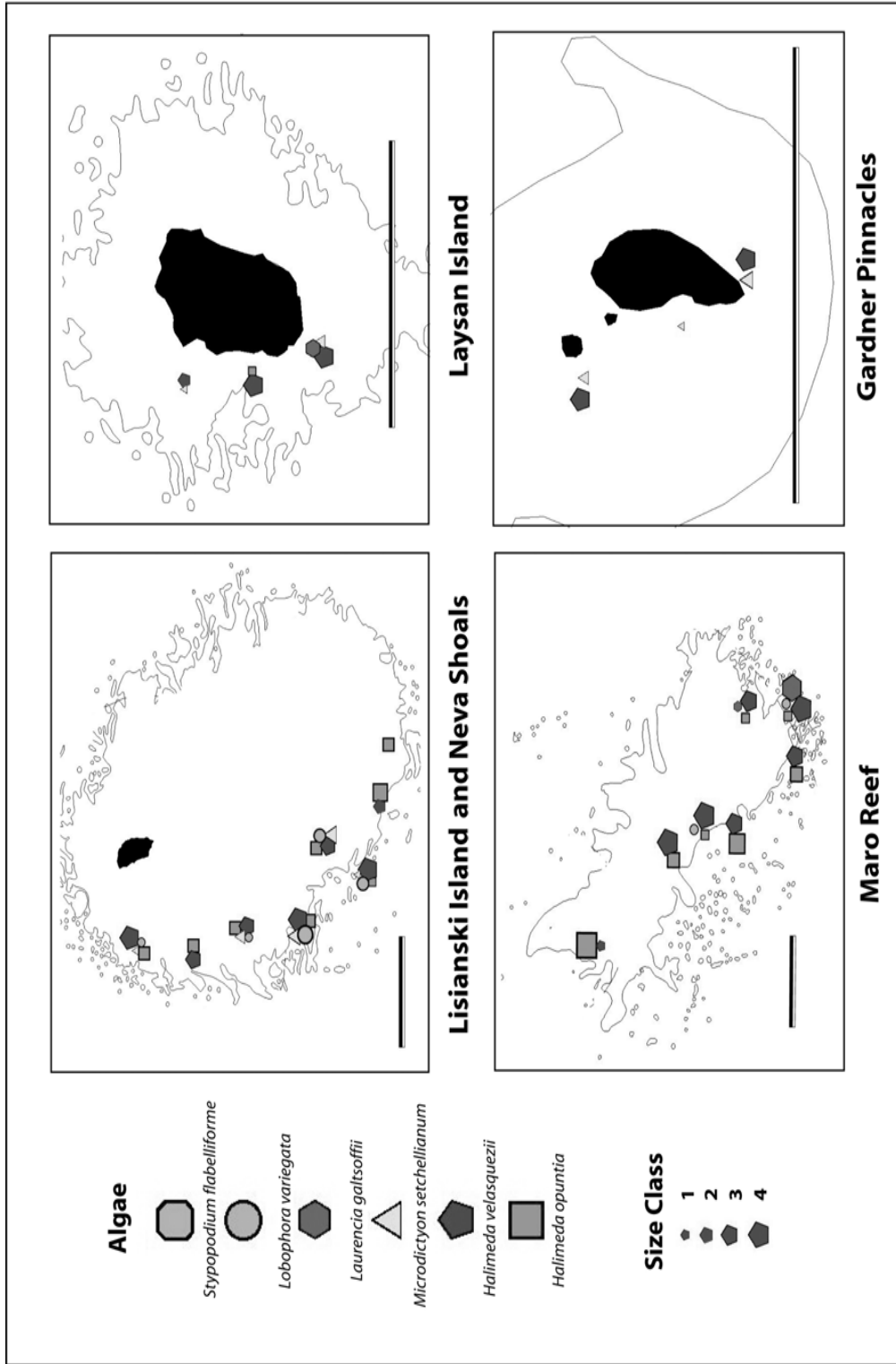


**Figure 3.** Outline drawings of four island reefs in the Northwestern Hawaiian Islands overlaid with algal distributional maps. Thin black lines indicate a 10-fathom isobath. Scale bar for Lisianki, Laysan, Maro = 5 km. Scale bar for Gardner = 1 km. Size classes refer to the percentage of quadrats in which an alga occurred at a give site: 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%.
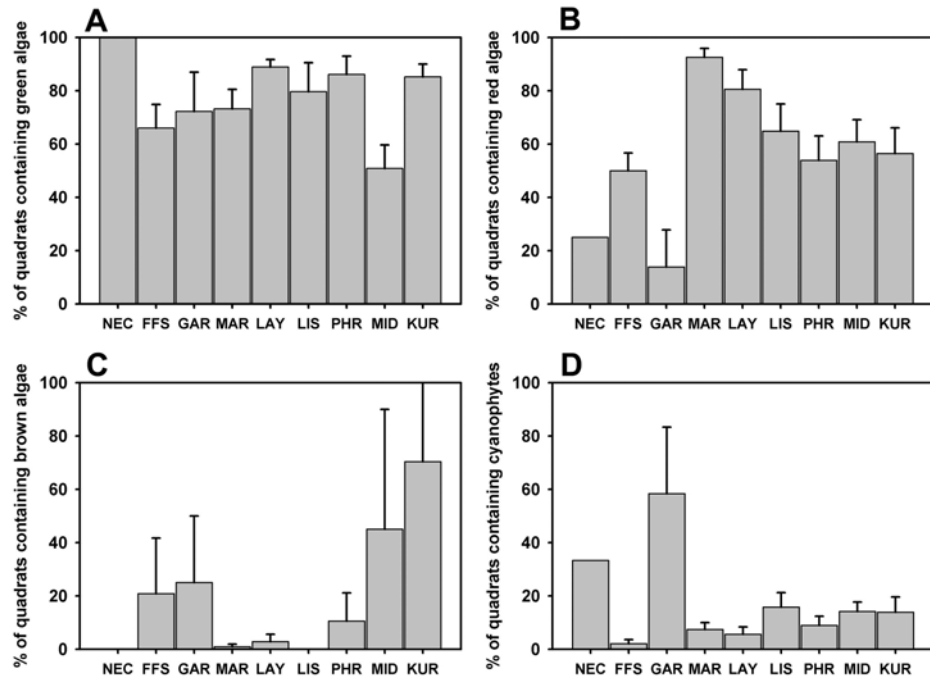
**Figure 4.** Prevalence of major algal lineages in the Northwestern Hawaiian Islands. Bars = standard deviation. A. Green algae; B. Red algae; C. Brown algae; D. Cyanophytes.
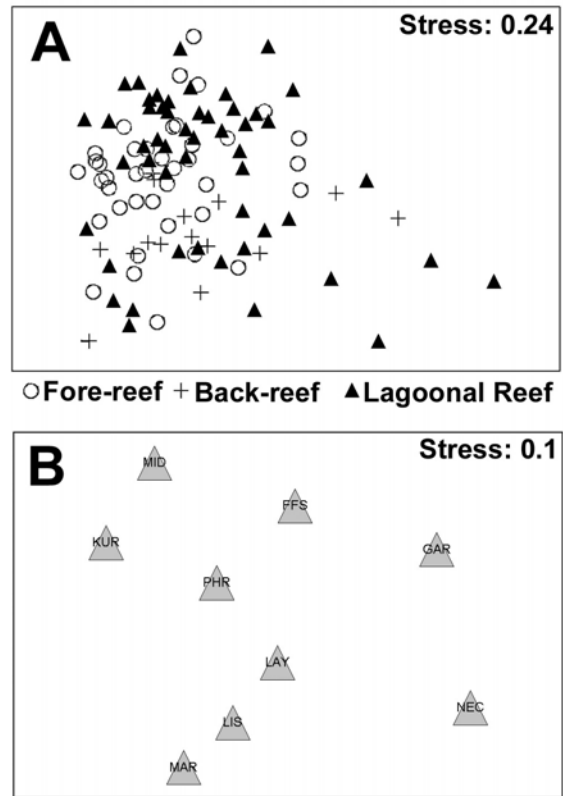
**Figure 5.** MDS plots. A. Relationships of 107 sites sampled throughout the NWHI based on relative abundance of macroalgae (RAM). Symbols indicate habitat type in which each site was located. B. Relationships among the NWHI based on RAM.

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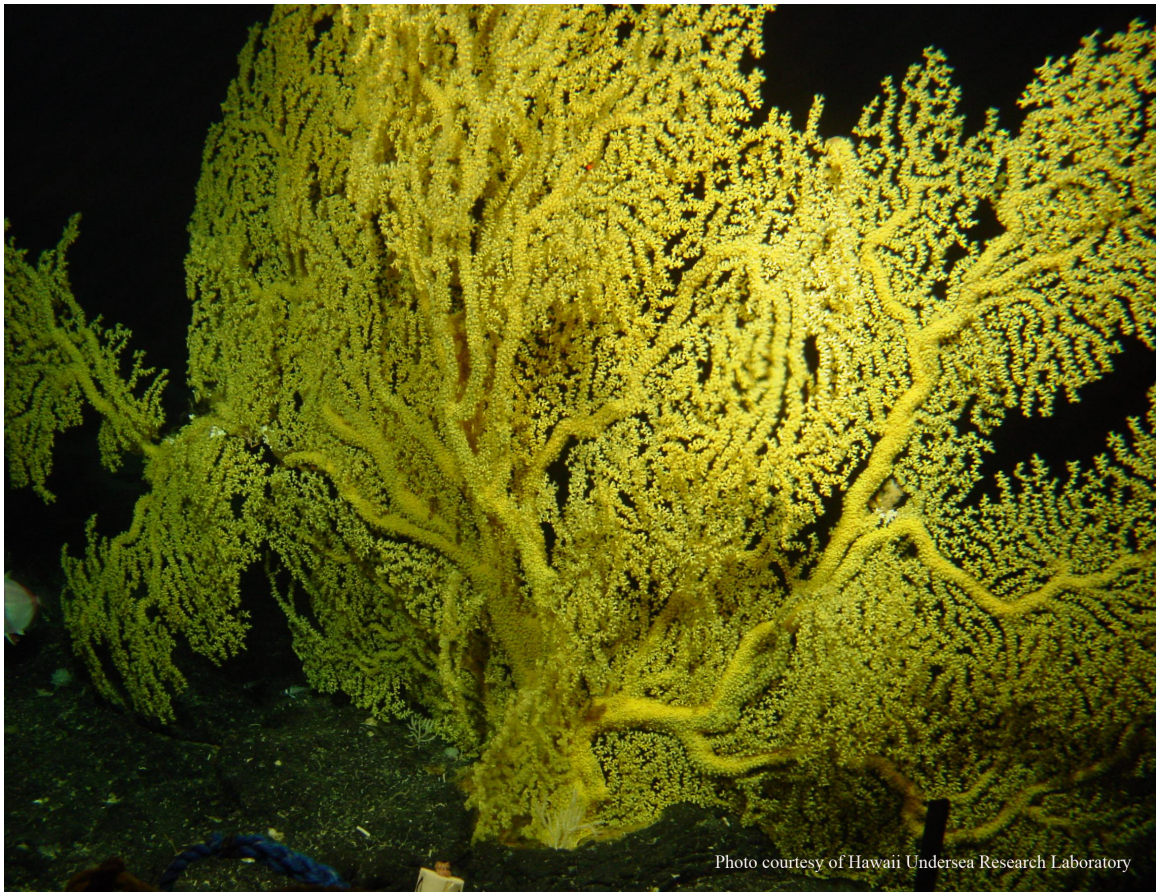        Honolulu, Hawaii, 40 pp.

## CLOSING

Since the end of the tripartite research initiative, there has been an increase in the scientific infrastructure of the Northwestern Hawaiian Islands (NWHI). This includes routine research cruises, establishment of field stations, and annual support of remote field camps. Exploration and baseline assessments continue to be a large part of the research, but more effort has been committed to establishing and maintaining physical and biological time series. Many of these time series were instigated to monitor specific fishery and protected species but have since become invaluable data sets to address emerging ecosystem science objectives. Time-series data paired with current mapping efforts provide an unprecedented database to use with rapidly advancing analytical software. In particular, the synoptic nature of satellite remote sensing has revealed the structure and changing nature of the north Pacific water mass in and around the NWHI. Understanding the implications of oceanographic changes to the NWHI ecosystem is a primary challenge for future scientific research. Scientists should frame their research questions within an archipelagic context using the NWHI in comparative designs to help manage and restore natural resources in the Main Hawaiian Islands. More insight can be achieved if this type of research is coordinated across agencies where projects are directed and prioritized by emerging ecosystem principles. A commitment to this multiagency approach and having periodic symposia to review and reflect on research findings would assist in the implementation of ecosystem-based management. The remote location, spatial structure, and documented history of the Hawaiian Archipelago make it an important case study to advance ecosystem science – an international priority.


Gerard DiNardo and Frank Parrish
Chairs, NWHI Third Scientific Symposium

550

**Northwestern Hawaiian Islands Third Scientific Symposium**
November 2 - 4, 2004
Hawai`i Convention Center, Honolulu, Hawai`i

# APPENDIX



Photo courtesy of Hawaii Undersea Research Laboratory

**Northwestern Hawaiian Islands**

**Third Scientific Symposium**

**November 2 - 4, 2004**

Hawai`i Convention Center, Honolulu, Hawai`i

*Exhibition and Reception*
Wednesday, November 3, 2004
6:00 pm - 8:30 pm
Hawai'i Convention Center, Palolo Room 306
FREE Admission, Light Refreshments, FREE Parking
www.hawaiianatolls.org/sym3

Photo by: James Watt
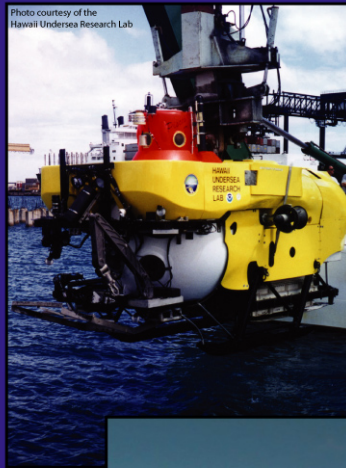
Photo courtesy of the
Hawaii Undersea Research Lab

Photo by: James Watt

Photo by: James Watt

*...30 years of research and exploration*

3D map courtesy of the Hawaii Undersea Research Lab

## Program Schedule

| **Day One** | **Tuesday, November 2, 2004** | **7 a.m. – 7:30 p.m.** |

**Registration (throughout Symposium)**
7 a.m. – 4:30 p.m.
Room #304

**Exhibits and Posters**
Room #306

**Continental Breakfast**
7 a.m. – 8:30 a.m.
Room #306

**Welcome Remarks,** *Gerard DiNardo*
    **Hawaiian Blessing**
8:30 a.m.

**Keynote Address,** *Richard Shomura*

**Plenary Session I** (moderated by *Gerard DiNardo*)
An historical overview of the Northwestern Hawaiian Islands' ecosystem
with the perspective of science & research, resource utilization, and
conservation & management.
9 a.m. – 11:30 a.m.
Room #310

    The History of Marine Research in the Hawaiian Archipelago;
Lessons From the Past and Hopes for the Future, *Richard Grigg*
9 a.m.

**Morning Break and Coffee**
9:45 a.m. – 10 a.m.

    Contemporary Research in the Northwestern Hawaiian
Islands: Where We Are Now, Where We Are Heading,
*Frank Parrish and Gerard DiNardo*
10 a.m.

    The Northwestern Hawaiian Islands Ecosystem – "Aspects of the
Ocean Dynamics of the NWHI Derived from Satellite Remotely-Sensed
Oceanographic Data," *Jeffrey Polovina, Lucas Moxey, Russell Moffitt*
10:45 a.m.

**Lunch on Own**
11:30 a.m. – 1 p.m.

**Plenary Session I** (cont.)
1 p.m. – 2:45 p.m.
Room #310

    History of Management in the NWHI, *Robert Shallenberger*
1 p.m.

    Resource Utilization in the NWHI: A Look Into the Past,
Present and Future, *Jarad Makaiau*
1:45 p.m.

**Afternoon Break and Refreshments**
2:30 p.m. – 2:45 p.m.

**Concurrent Session 1**
2:45 p.m. – 4:30 p.m.
Room #310

    **A. Environmental Trends** (moderated by *Frank Parrish*)

- Diurnal Trends in the Mid-Water Biomass Community of the
NWHI Observed Acoustically, *Marc O. Lammers, Russell E
Brainard, Whitlow W.L. Au*
2:45 p.m.

- Interannual Variability in Larval Transport and Oceanography
in the NWHI Using Satellite Remotely Sensed Data and Computer
3:10 p.m.

Simulation, *Donald R. Kobayashi and Jeffrey J. Polovina*

- Ten years of Shipboard ADCP Measurements Along **3:35 p.m.**
  the NWHI, *June Firing, Russell Brainard, Eric Firing*

- Spatial and temporal variability of key oceanographic **4 p.m.**
  processes influencing coral reef ecosystems of the NWHI,
  *Russell Brainard, Ronald Hoeke, Russell A. Moffitt, et al.*

B. **Seabirds** (moderated by *Beth Flint*) **Room #308**

- Distribution and Abundance of Seabirds in Waters of the **2:45 p.m.**
  Hawaiian Islands Archipelago, *Lisa Ballance, Robert L Pitman,*
  *Jessica Redfern*

- Populations and Conservation Status of Seabirds in the NWHI, **3:10 p.m.**
  *Maura Naughton and Elizabeth Flint*

- Demographic Parameter Estimates of North Pacific Albatross and **3:35 p.m.**
  Implications for Future Data Collection, *William Kendall,*
  *Paul F. Doherty, Jr., Scott Sillett, et al.*

- Demography and Reproductive Ecology of Great Frigate Birds, **4 p.m.**
  *Donald Dearborn and Angela Anders*

You are cordially invited to the
## Welcome Reception and Poster Session
- immediately following today's program -
### 4:30 p.m. 'til 7:30 p.m.
### Palolo Room #306
Hosted Bar and Heavy Pupu
Meet the Poster Presenters
& enjoy the sounds of slack-key guitarist,
Sean Naauao.

Televised National Election Results in Room #309

| Day Two | Wednesday, November 3, 2004 | 7 a.m. – 8:30 p.m. |

**Registration**  
7 a.m. – 4:30 p.m.  
Room #304

**Exhibits and Posters**  
Room #306

**Continental Breakfast**  
7 a.m. – 8:30 a.m.  
Room #306

**Concurrent Session 2**  
8:30 a.m. – 10:10 a.m.

    **A. Fisheries – Lobster** (moderated by *Don Kobayashi*)  
    Room #310

- Recent Life–History Research on Lobsters in the NWHI, *Edward DeMartini*  
  8:30 a.m.

- Preliminary Estimates of Hawaiian Spiny Lobster (Panulirus marginatus) Growth and Movements at Necker Island, NWHI, *Joseph O'Malley and Gerard DiNardo*  
  8:55 a.m.

- Spatial and Temporal Patterns in Lobster Trap Bycatch, *Jami Johnson, Gerard DiNardo, Robert Moffitt, et al.*  
  9:20 a.m.

- Causes for the Switch in Lobster Species Dominance in the NWHI, *Gerard DiNardo and Don Kobayashi*  
  9:45 a.m.

    **B. Sea Turtles, and Other Endangered *or* Threatened Flora and Fauna** (moderated by *Jason Baker*)  
    Room #308

- Recovery Trend Over 31 Years at the Hawaiian Green Turtle Rookery of French Frigate Shoals, *George Balazs and Milani Chaloupka*  
  8:30 a.m.

- Laysan Finch Population Viability Analysis: Data Needs and Management Options, *Andrew McClung*  
  8:55 a.m.

- Population Estimates and Breeding Success of the Laysan Island's Endangered Duck, *Michelle H. Reynolds and Elizabeth Flint*  
  9:20 a.m.

**Morning Break and Coffee**  
10:10 a.m. – 10:25 a.m.

**Concurrent Session 3**  
10:25 a.m. –12:05 p.m.

    **A. Fisheries – Fin Fish** (moderated by *Walter Ikehara*)  
    Room #310

- Ecological Effects of Fishing on Coral Reef Fish Assemblages in the Hawaiian Archipelago, *Alan Friedlander and Edward E. De Martini*  
  10:25 a.m.

- An Assessment of the Condition of Deepwater Snappers and Groupers in the NWHI Under Various Exploitation Rates, *Bert Kikkawa, Walter A. Machado, David Kaltoff*  
  10:50 a.m.

- The Impacts of Bottom-fishing on Raita and West St. Rogatien   **11:15 a.m.**
  Banks, *Christopher Kelley and Robert Moffitt*

- Ecological Effects from Fishing: Lessons from the North   **11:40 a.m.**
  *Timothy Ragen*

**B. Cetaceans/Hawaiian Monk Seals** (moderated by *Irene Kinan*)   **Room #308**

- Population Structure and Connectivity of Spinner Dolphins in   **10:25 a.m.**
  the NWHI, *Leszek Karczmarski, Susan H. Rickards,*
  *Bernd Würsig, Cynthia Vanderlip, et al.*

- Population Assessment of the Hawaiian Spinner Dolphin   **10:50 a.m.**
  (Stenella longirostris) Through Genetic Analysis,
  *Kim Andrews, Whitlow W.K. Au, Leszek Karczmarski, et al.*

- Increasing Taxonomic Resolution in Dietary Analysis of the   **11:15 a.m.**
  Hawaiian Monk Seal, *Ken Longenecker, Robert A. Dollar,*
  *Maire Cahoon*

**Lunch On Own**   **12:05 p.m. – 1:30 p.m.**

**Concurrent Session 4**   **1:30 p.m. – 3:10 p.m.**

**A. Oceanography/Mapping** (moderated by *Rick Grigg*)   **Room #310**

- Oceanographic Atlas of the Hawaiian Archipelago: A Tool for   **1:30 p.m.**
  Marine Resource Management, *Russell Moffitt, Russell E.*
  *Brainard, Alan E. Strong, et al.*

- Mapping NWHI with High-Resolution Satellite Imagery:   **1:55 p.m.**
  Techniques and Results, *Kris Holderied and Richard Stumpf*

- Bathymetric Atlas and Web Site for NWHI, *Joyce Miller,*   **2:20 p.m.**
  *Ronald Hoeke, Scott Ferguson, et al.*

- Mega to Macro-Scale Descriptions of Bottom-fish Habitats on   **2:45 p.m.**
  Raita Bank, West St. Rogatien Bank, Brooks Bank and Bank 66,
  *Christopher Kelley, Robert Moffitt, Walter Ikehara, et al.*

**B. Hawaiian Monk Seals** (moderated by *Gerard DiNardo*)   **Room #308**

- Hawaiian Monk Seal (Monachus schauinslandi): Status and   **1:30 p.m.**
  Conservation Issues, *George Antonelis, Jason D. Baker,*
  *Thea C. Johanos, et al.*

- Foraging Biogeography of the Hawaiian Monk Seal in the NWHI,   **1:55 p.m.**
  *Brent Stewart, George A. Antonelis, Jason D. Baker, et al.*

- Movement of Monk Seals Relative to Ecological Depth Zones   **2:20 p.m.**
  in the Lower NWHI, *Frank Parrish and Kyler Abernathy*

- Assessment of Immature Hawaiian Monk Seals Foraging Behavior,   **2:45 p.m.**
  Behavior, Habitat Use and Prey Type Using Crittercam,
  *Charles Littnan, Frank A. Parrish, Jason D. Baker, et al.*

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| **Afternoon Break and Refreshments** | **3:10 p.m. – 3:25 p.m.** |

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| **Concurrent Session 5** | **3:25 p.m. – 5:05 p.m.** |

**A. Socio-Economics /Ecosystem Science and Research Needs** (moderated by Jarad *Makaiau*)   **Room #310**

- Economic Research on the NWHI – An Historical Perspective, S*amuel G. Pooley and Min Ling Pan*   **3:25 p.m.**

- Estimating the "Overfishing" of Marine Debris by Pairing Debris Removal Efforts and Accumulation Rates, *Raymond Boland, Brian Zgliczynski, Jacob Asher, et al.*   **3:50 p.m.**

- Northwestern Hawaiian Islands Spatial Bibliographic GIS: A Science Planning Tool, *Christine Taylor and David Moe Nelson*   **4:15 p.m.**

- Northwestern Hawaiian Islands Science Needs Assessment, *Randall Kosaki, Charles Alexander, Stephen R. Gittings, et al.*   **4:40 p.m.**

**B. Living Marine Resources – Invertebrate** (moderated by *Robert Humphries*)   **Room #308**
- Distribution and Abundance of the Pearl Oyster, Pinctada margaritifera, *Elizabeth Keenan, Russell E. Brainard, Larry B. Basch*   **3:25 p.m.**

- Deepwater Marine Plants from the NWHI: New Perspectives on Biogeography, *Karla McDermid and Isabella A. Abbott*   **3:50 p.m.**

- Quantitative Algal Rapid Ecological Assessments in the NWHI, *Peter Vroom and Kimberly Page*   **4:15 p.m.**

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| **Public Exhibition and Reception** | **6 p.m. – 8:30 p.m.**<br>**Room #306**<br>**Room #310** |

## Public Exhibition and Reception

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| **Doors Open/Registration** | **5:45 p.m.** |
| **Welcome:** *Gerard DiNardo*, NOAA Fisheries, PIFSC | **6:10 p.m.** |
| **Video Montage and Presentations**<br>"In the Wake of Canoes" (video by NOAA NOS Coral Reef Ecosystem Reserve)<br>Bird Capture and Banding, *Andrew McClung*, University of Hawaii<br>Coral Reef Tow Board Sampling, *Joe Laughlin*, NOAA Fisheries, PIFSC<br>NWHI Lobster Tagging Program, *Gerard DiNardo*, NOAA Fisheries, PIFSC<br>Bottom-Fish Research, *Chris Kelley*, Hawaii Undersea Research Laboratory<br>Monk Seal Foraging, *Frank Parrish*, NOAA Fisheries, PIFSC | **6:15 p.m.** |
| **Reception and Exhibit Viewing** | **7:10 p.m.** |
| **Grand Prize Giveaway** (in the Exhibit Room) | **8 p.m.** |
| **Pau** | **8:30 p.m.** |

| Day Three | Thursday, November 4, 2004 | 7 a.m. – 5 p.m. |
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**Registration**  
7:30 a.m. – noon  
Room #304

**Exhibit and Posters**  
Room #306

**Continental Breakfast**  
7 a.m. – 8:30 a.m.  
Room #306

**Exhibits and Posters**  
Room #306

**Concurrent Session 6**  
8:30 a.m. – 10:10 a.m.

**A. Living Marine Resources – Vertebrate**  
(moderated by *Alan Friedlander*)  
Room #310

- Movement Patterns of Tiger and Galapagos Sharks Around French Frigate Shoals and Midway Atoll, *Christopher Lowe, Bradley M. Wetherbee, Carl G. Meyer, et al.*  
8:30 a.m.

- Shark and Jack Abundance, Biomass and Spatial Distribution: Towed Diver Surveys 2000 – 2003, *Stephani Holzwarth, Robert E. Schroeder, Edward E. De Martini, et al.*  
8:55 a.m.

- Patterns and Processes in Shallow-Water Reef Fishes of the NWHI, *Edward DeMartini*  
9:20 a.m.

- Monk Seals, Precious Corals and Subphotic Fish Assemblages, *Frank Parrish*  
9:45 a.m.

**B. Living Marine Resources** (moderated by *Rusty Brainard*)  
Room #308

- Preliminary Results from NWHI Seamount Surveys of Deep-Sea Fauna in Relation to Geological Setting, *John Smith, Amy Baco-Taylor, Christopher Kelley, et al.*  
8:30 a.m.

- Ecological Characteristics of Coral Patch Reefs at Midway Atoll, NWHI, *Robert E. Schroeder and James D. Parrish*  
8:55 a.m.

- Mass Coral Bleaching on High-Latitude Reefs in the Hawaiian Archipelago*, Jean Kenyon, Greta Aeby, Russell Brainard, et al.*  
9:20 a.m.

- The Role of Oceanographic Conditions & Reef Morphology in the 2002 Coral Bleaching Event in the NWHI, *Ronald Hoeke, Russell Brainard, Russell Moffitt, et al.*  
9:45 a.m.

**Morning Break and Coffee**  
10:10 a.m. – 10:35 a.m.

**Plenary Session II** (moderated by *Gerard DiNardo*)  
Future research needs and priorities in the Hawaiian Archipelago particularly with regard to ecosystem science and management.  
10:35 a.m. - noon  
Room #310

Toward Ecosystem-Based Management: What Can the NWHI Contribute?*, David Fluharty*  
10:35 a.m.

Conducting Multidisciplinary Research in a Multi-agency              **11:30 a.m.**
Management Setting: A Possible Framework for Success,
*Gerard DiNardo*

**Hosted, Prepared Lunches To-Go**                                   **noon – 1 p.m.**
                                                                     **Room #306**

**Expert Panel Discussion and Recommendations,** *Sam Pooley, Facilitator*    **1 p.m. – 5 p.m.**

Panelists:
Dr. Shelia Conant, Dept. of Zoology, University of Hawai`i, Manoa
Dr. Bruce Wilcox, Division of Ecology and Health, John A. Burns
 School of Medicine
Dr. James Parrish, Hawai`i Cooperative Fishery Research Unit
Dr. Jeffrey Polovina, NMFS Pacific Islands Fisheries Science Center
Dr. David Fluharty, School of Marine Affairs, University of Washington

Discussion:

   1. Comments and/or questions regarding Dr. Fluharty's talk on
      ecosystem science and management.

   2. How well does the research that has been conducted in the NWHI fit
      into the general elements of ecosystem science and management?

   3. Where are the gaps and opportunities for insightful research?

   4. What are the merits of closing and protecting the NWHI versus
      conducting research specifically to advance ecosystem science
      including fishery science?

   5. Comments on the proposed research framework and the value of having a
      future workshop to address actual components and implementation.

**Afternoon Break and Refreshments**                                 **3 p.m. – 3:15 p.m.**

**Panel and Open-Floor Discussion** (cont.)

**Wrap up & Closing Remarks,** *Gerard DiNardo*

**Conclusion of Symposium**                                          **5 p.m.**

# Submitted Posters

Coral recruitment and encapsulation on derelict fishing gear in the Northwestern Hawaiian Islands.  Jacob M. Asher and Molly Timmers

Acanthaster planci distribution and predation at Pearl and Hermes Atoll.  Elizabeth E. Keenan, Russell E. Brainard, and Larry V. Basch

Surface velocity and profiling drifters track potential larval pathways in Northwestern Hawaiian Islands.  June Firing, Ronald Hoeke, and Russell Brainard

Coral recruits to settlement plates at six Northwestern Hawaiian Islands.  Matt Dunlap and Jean Kenyon

Ecosystem science to support ecosystem-based management of the Northwestern Hawaiian Islands.  Russell Brainard, Greta Aeby, Joseph Chojnacki, Edward DeMartini, Matthew Dunlap, Scott Ferguson, June Firing, Alan Friedlander, Scott Godwin, Jamison Gove, Ronald Hoeke, Stephani Holzwarth, Randall Kosaki, Elizabeth Keenan, Jean Kenyon, Marc Lammers, James Maragos, Joyce Miller, Kim Page, John Rooney, Molly Timmers, Peter Vroom, Casey Wilkinson, Kevin Wong, and Brian Zgliczynski

Variability and change: Long-term oceanographic monitoring in the Northwestern Hawaiian Islands.  Russell Brainard, Ronald Hoeke, June Firing, Kevin B. Wong, and Dave Foley

Geographical distributions of *Acanthaster planci* from towed-diver surveys in the Northwestern Hawaiian Islands.  Molly A. Timmers, Stephani R. Holzwarth, and Russell E. Brainard

Distribution, dispersal and genetic population structure of vermetids (Vermetidae: Gastropoda) in Hawaii.  Anuschka Faucci and Michael G. Hadfield

Health status of the reefs of the Northwestern Hawaiian Islands.  Greta S. Aeby

Remote video cameras to observe marine turtles and their habitats:  A powerful new research, monitoring, and educational tool for the Northwestern Hawaiian Islands.  George H. Balazs, Marc Rice, and Daniel Zatz

Construction of benthic substrate prediction maps using topology, rugosity, and acoustic signatures.  Joe Chojnacki, John Rooney, Joyce Miller, and Russell E. Brainard

A classification scheme for benthic habitat mapping in the Northwestern Hawaiian Islands.  John Rooney, Joyce Miller, Frank Parrish, and Michael Parke

Geologic features on the Northwestern Hawaiian Island chain revealed by swath mapping.  John R. Smith, Benjamin Evans, Joyce Miller, and Jeremy Weirich

A quantitative assessment of the benthic marine macroalgae and coral of Neva Shoal near Lisianski Island.  K. A. Peyton and J. Kanekoa Kukea-Shultz

Responses to cetacean strandings and a new method for testing whale hearing.  Paul Nachtigall, Robert Braun, and Marlee Breese

Inferences of lagoonal and near-shore circulation at Pearl and Hermes and Kure Atolls.  Ronald Hoeke, Jamie Gove, Kyle Hogrefe, Russell Brainard, and June Firing

Monitoring corals and macro-invertebrates at permanent sites in the Northwestern Hawaiian Islands.  James Maragos and Allison Veit

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