FORAGING LANDSCAPE OF THE HAWAIIAN MONK SEAL

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By
Frank A. Parrish

Dissertation Committee:

Lyndon Wester, Chairperson
Charles Birkeland
Sheila Conant
Matthew McGranaghan
Ross Sutherland

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DEDICATION

This was an adventurous and risky topic to undertake for a dissertation. Aside from the usual stress that comes with sea time, data punching, analysis, and writers block there was uncertainty right up to the end about whether the necessary submersible time would be obtained to complete the project. Through it all, my parents and wife were helpful and supportive. Deb was even understanding about my leaving for sea before I could escort her home from the hospital after she had delivered our son Scott.

I enjoyed this research. Much of it was classic exploration which exposed me to some wondrous submarine landscapes. These included coral beds, immense geologic sculptures, and some bizarre animals. All the color, scale and history of the subphotic realm is are a spectacular backdrop to the challenges that monk seals face in their daily lives. It was a privilege to have a glimpse of it.

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ABSTRACT

Habitat and fish assemblages of the Northwestern Hawaiian Islands were compared with movement patterns of the endangered Hawaiian monk seal. The seals' foraging pattern could not be attributed to the area, distance or effort associated with feeding in reef, bank, slope or subphotic habitats. Seals did not target areas with the largest fish body size, fish number, or fish biomass. Comparing the fish assemblages with the fish guilds seals' are known to eat (derived from scat studies) indicated the fish composition of the bank and slope habitats were the most similar to the seals' diet.

Submersible surveys of areas with and without deepwater corals, were conducted to see if greater fish density, size or biomass were found near deepwater corals. Areas with tall morpho-types of deepwater corals (e.g. *Gerardia* sp.) often supported greater fish densities than adjacent areas without deepwater corals. The guild "benthic hoverer" was the most commonly seen fish using the coral branches as shelter. However, an analysis of fish and coral data accounting for habitat effects indicated fish and deepwater corals co-occur in areas of high relief, each likely exploiting improved flow conditions, with little inter-dependance.

Fish data were compared with indices of regional primary productivity and insular predation pressure (including monk seals) from the euphotic zone. Fish density and biomass weakly agreed with a 3-region model based on satellite sea-surface temperature measurements. However, this relationship was excluded as not significant from a multiple regression model that considered insular predation pressure, in particular monk seals. The size of the nearest colony and its distance from the station best explained the variance in

fish biomass at the subphotic stations surveyed. This suggests that seal populations and perhaps other species from shallow insular ecosystems are significant subphotic predators and influence the structure of subphotic fish communities.

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CHAPTER 1. INTRODUCTION

Where and what monk seals eat is a mystery that scientists and resource managers of the Northwestern Hawaiian Islands (NWHI) have attempted to address using a wide variety of methods. The endangered seals (*Monachus schauinslandi*) (Fig 1.1) differ from much of the marine community in that their foraging trips can involve movements between summits of the Hawaiian Ridge. This ridge is a series of volcanic pinnacles that rise from the abyssal floor of the Pacific plate to form the islands, reefs, banks and seamounts that comprise the Hawaiian Archipelago. Recent movement data collected on foraging seals indicates they routinely travel from peak to peak, feeding on the fish communities of the ridge's summits and deep slopes. Some of the seals' movements extend down to subphotic depths exposing the seals to a broad range of habitats. The scale of the monk seals' movements gives them a familiarity with the archipelago's submarine landscape that few bottom feeding marine animals have. The unexpectedly wide-range seal movements have challenged some long standing assumption about seals' habitat use and highlighted the need for information about prey patterns in the seals' forage grounds.

One of the highest priorities for those interested in monk seal conservation is to understand obvious and persistent geographic differences in survivorship between the six primary seal colonies of the archipelago (Fig 1.2). Recent satellite oceanography has identified regional differences in oceanic productivity that may influence the seals' foraging success. However, these oceanographic patterns have yet to be linked to

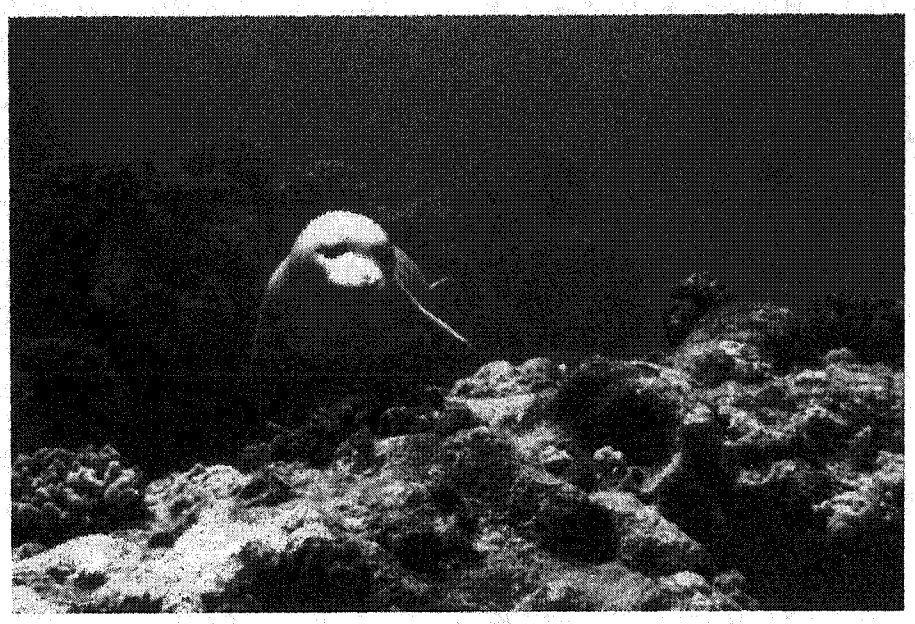


Figure 1.1. An endangered Hawaiian monk seal at French Frigate Shoals. Photo by Raymond Boland.

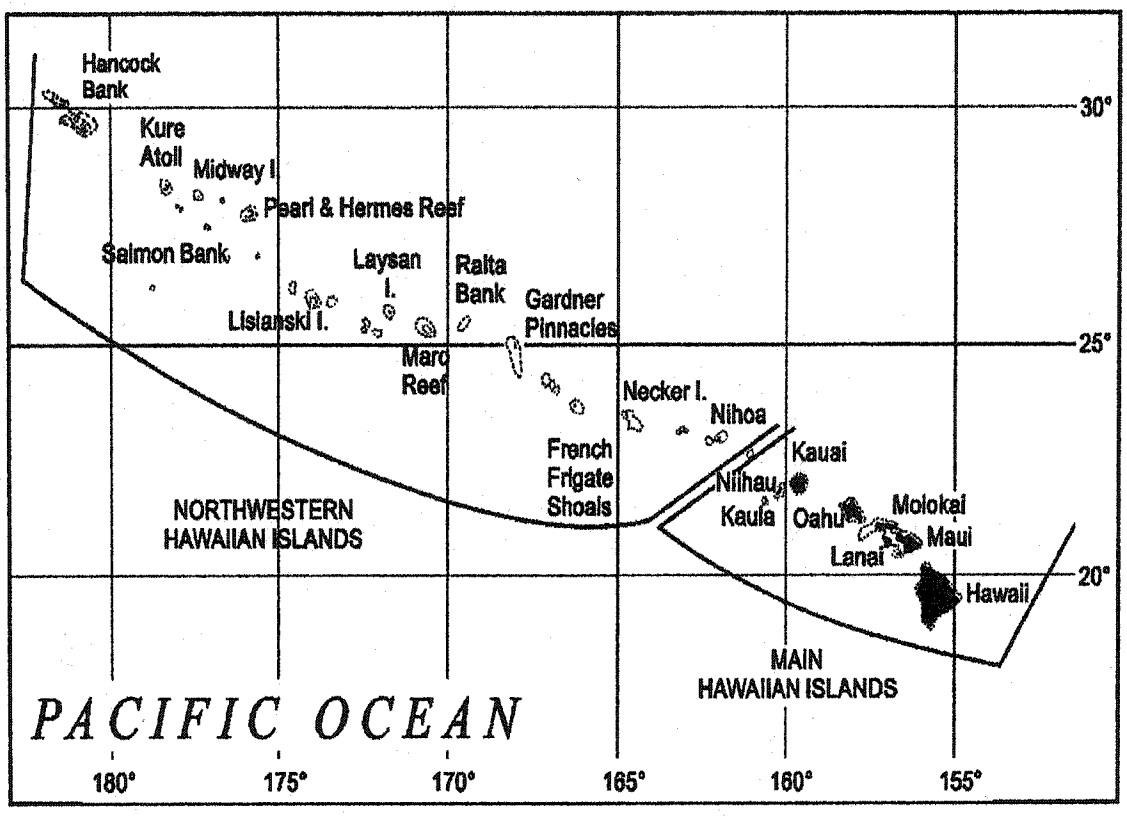


Figure 1.2. Map of the Hawaiian Archipelago with the major peaks of the ridge labeled including the six primary monk seal colonies of Kure, Midway, Pearl and Hermes, Lisianski, Laysan and French Frigate Shoals.

changes in the seal's prey base. Because the endangered status of monk seal's has made it the focus of much study for the last two decades, there is now enough data form a preliminary description of the seals' submarine landscape. This work will use this unpublished data, published literature, and faunal surveys to examine patterns across the depths that seals forage (vertical patterns) and will test for latitudinal differences in habitat and oceanic productivity (horizontal patterns) that could explain the varied survivorship among seal colonies. This opening chapter reviews literature relevant to the study of Hawaiian monk seal foraging patterns, addressing both vertical and horizontal patterns. The second chapter is dedicated to the vertical analysis and two chapters to the horizontal analysis. Each will detail hypotheses, methods, findings and discuss the research conducted. The final chapter is a geographic synthesis of the findings from the earlier chapters.

VERTICAL GEOGRAPHIC PATTERNS

Secondary data sources

Monk seals have been resident in the Hawaiian Archipelago for millions of years (Ragen and Lavigne 1999) and cluster around six atoll reef systems that have sand islets on which the seals deliver and nurse their pups. Total population is estimated between 1200 and 1400 individuals. Populations of the six different seal colonies range between 71 and 342 individuals (Johanos and Baker 2002). Because of the limited haulout areas and documented declines in their populations' the monk seal was listed as an endangered species in 1976. The seal populations are monitored on an annual basis by staff of the

National Marine Fisheries Service (NMFS), which conduct tagging studies and track the births and survivorship of each year's cohort (Gilmartin et al. 1993, Craig et al. 1994, Craig et al. 1995, Gilmartin and Eberhardt 1995, Craig et al. 1996, Craig et al. 1997, Craig et al. 1999). Annual beach counts of tagged seals at all the colonies indicates there is little movement of seals between colonies suggesting that seals primarily feed in nearby waters. However, little work has addressed the habitats and associated prey communities used by these seals.

Of the six seal colonies, French Frigate Shoals (FFS) is the largest, and concern about poor seal survivorship (an annual reduction by 5-6%) at this colony has made it a focus of study. Three types of studies are needed to describe the seals' foraging landscape; these involve diet information, movement data, and surveys of habitat and the communities within them. The data types will be discussed briefly below, and specific data sets to be used in this analysis will be identified.

Seal diet

The diet of the monk seal is poorly known, and the best data come from studies examining prey fragments found in seal scats left on the beach (Kenyon and Rice 1959, Kenyon 1981, Delong et. al. 1984). Goodman-Lowe (1998) did the most complete study using this technique. Her study spanned 3 years and included five of the six seal colonies in the NWHI. FFS was the best sampled of the colonies, with diet determined from 361 scats. The dominant prey items across all the colonies reported by Goodman-Lowe were families of benthic and epibenthic reef

fish and invertebrates. A primary source of bias in the use of scat data are the rates of passage through the seals' digestive system. Prey eaten at distant locations, such as neighboring banks, are likely to pass through the monk seal's digestive system, in as little as 9 h (Goodman-Lowe et al. 1997), well before the seal returns to the beach where it could leave a scat to be collected by researchers. Because of this, the diet information from the scat data are expected to best represent prey taken in the nearby shallow coral reefs. Regardless, the findings of this study are based on extensive sampling and provide the most comprehensive diet model for the monk seal.

Movement Data

Seals show a high degree of fidelity to their own colony but are capable of inter-island travel (Fairaizi 1984). Re-sights of tagged animals from annual census of seals at each of the six colonies indicate that less than 10% of the Hawaiian population travels between colonies (Johanos and Baker 2000). However, studies employing telemetry equipment mounted on seals show that movements and dive patterns range far from the host atoll during foraging trips. The seals' activities are clustered along the peaks of the atolls and banks of the Hawaiian ridge and suggest that the animals do not range out in the open ocean (Schlexer 1984, Delong et al. 1984, Stewart 1998). One of the most extensive studies was conducted at FFS by Abernathy (1999) using satellite linked time depth recorders. FFS seals were documented to have behavior similar to those in the previous studies using the

submerged summits and slopes of banks that neighbor FFS. These seals ranged more than 160 km from their atoll on these foraging trips. A small percentage of FFS seals concentrated their diving below the photic layer (>300 m). Tags reported the activities of the 24 instrumented seals for an average duration of six months, revealing that many seals returned to the same grounds. Other telemetry data collected farther north at Pearl and Hermes Atoll (Stewart 1998) contrasted with the FFS data by showing nearly all tagged seals feed closer to the atoll and at shallower depths. The differing foraging patterns between the two seal colonies could be related to differences in prey availability driven by regional productivity and the seals' foraging success.

Surveys of the prey community

Surveys documenting fish number, fish size and overall fish biomass density by habitat type have been conducted by the National Marine Fisheries Service, Pacific Island Fisheries Science Center in an attempt to update parameters in revision of a trophic model of the coral reef ecosystem called ECOPATH (Polovina 1984). These surveys use divers, remote operated vehicles, trawls, and submersibles with established survey methods to collect information on the fish community. All of these surveys measure the area they survey to normalize comparisons between sites. Much of this work has been focused on areas where seals are known to concentrate their foraging activity. Whenever possible, information from studies using seal mounted video cameras has been relied upon to identify habitats that are important

forage grounds (Parrish et al. 2000, 2002, In review).

Seals and their foraging habitat

All available data (reviewed above) indicates that seals feed on fish that are bottom associated. This is supported by prey items found in the scats, activity patterns from seal telemetry focused on the Hawaiian ridge (not in the open ocean), and recent work using video cameras attached to seals that show all seals feeding on the bottom. For this reason, the treatment of the seal's foraging landscape will be limited to the ecosystems on the summits of the Hawaiian Ridge. As stated earlier, unlike most insular marine taxa, monk seals can choose to move between reef ecosystems of the summit peaks or dive to feed in deeper communities. The seal's prey types may change with the faunal composition of deeper fish communities. The physiography of the summits will, to a large degree, determine the composition of the fish community and may dictate its value as a prey source for monk seals.

The Hawaiian volcanic ridge has been modified by a long history of sea level change, with the summits corresponding well with general notions about the glacio-eustatic cycles (Grigg and Epp 1989), although a specific chronology for the summits, terraces and sea level notches has not been developed. Based on their morphology and faunal communities, the summits of peaks in the FFS region can be divided into four depth related zones (Fig. 1.3). The first obvious zone is the shallow "reef" of FFS (<20 m) that hosts the sand islets where the monk seal subpopulations rest and rear their

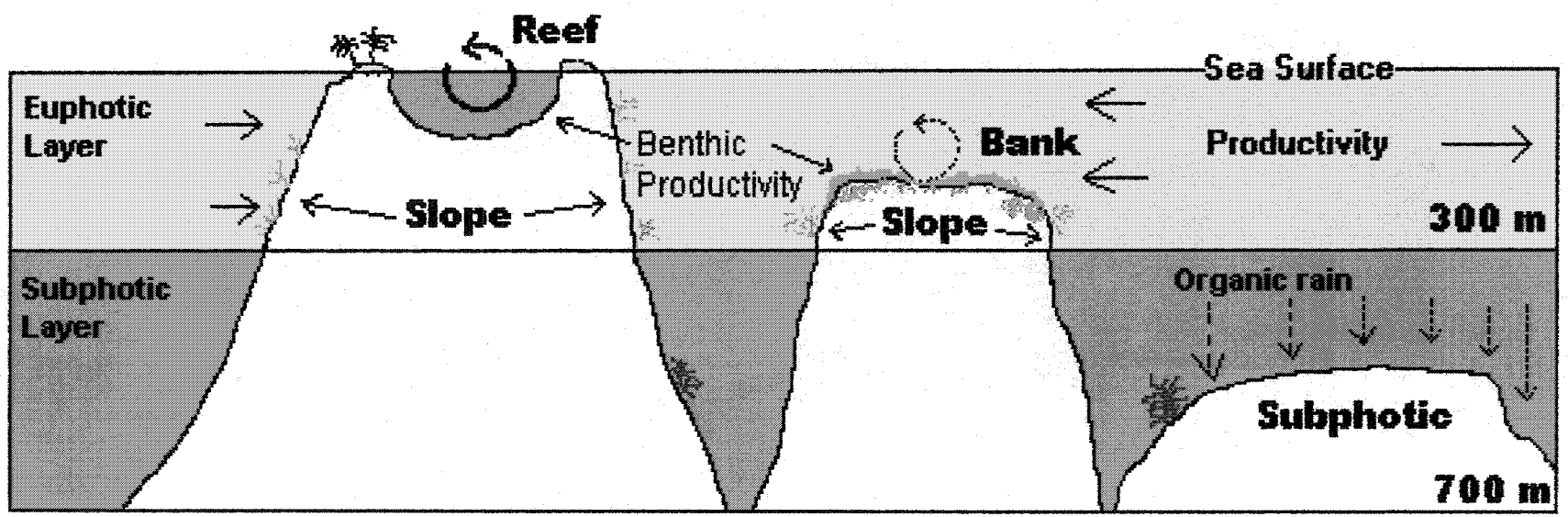


Figure 1.3. A conceptual, drawing of the four habitat zones: reef, slope, bank and subphotic. Productivity in the euphotic layer includes surface oceanic primary productivity, benthic primary productivity and on-site recycling. The subphotic layer is entirely dependent on the organic rain from the above euphotic layer.

young. Seals can haul out at the NW and SE extremes of their foraging range (Abernathy 1999) on the emergent unprotected rock pinnacles of Gardner and Necker Banks, but the protected water of the shallow reef at FFS atoll provides the seals' primary residence. The next most prominent zone consists of the submerged "banks" at 30-50 m that occur SE and NW of FFS. The extensive and uniformly level summits of these banks indicate a prolonged low stand of sea level. A number of studies on sea level chronology have been conducted in the main Hawaiian Islands addressing marine terraces (Jones 1993, Fletcher and Sherman 1995) and subsidence rates (Campbell 1986, Grigg 1997). Prolonged low stands of sea level, which could correspond with bank summit depths, have been proposed to date from as recently as 8 or 9000 yrs ago (Fletcher and Sherman 1995). These bank tops support minimal coral coverage and are primarily covered with sand and algae. At the edge of the reef or bank, the "slope" zone begins. At the base of the steepest slope segments, often around 60 m depth, talus accumulates, with smaller sizes of rubble sorting below. At 80-100 m are found extensive sand pools on a terrace, and then the slope continues steeply down to 300 m. Deepwater black corals (*Cirripathes* sp.) are often 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 will be called "subphotic." Bottom types include carbonate, basalt, manganese crust and sand with occasional patches of deepwater corals in areas of high current flow.

Research questions

Patterns of seal activity (Abernathy and Siniff 1998) were compared with the available area of each zone and its distance from the seals' haulout at FFS. National Ocean Survey bathymetry was used to delineate the four zones and determine the available forage areas and their distances from the seals' haulout. In addition to area and distance, an index of seal foraging cost was computed by multiplying the depth of the contour at a site by the distance from the seals' haulout at FFS atoll. Data from prior studies of communities in each of these zones were used to assess differences in fish numerical density, size and biomass density. The fish from these surveys were divided into four functional groups according to their position in the water column (e.g. on the bottom, midwater) and usual activity pattern (e.g. hovering, perching) with the idea these attributes could influence the fish's exposure to predation by a monk seal. Applying the same functional grouping to the reef taxa found in monk seal scats (Goodman-Lowe 1998), permitted assessing the association between the seals' diet and the numerical density and biomass density of the fish community of the four zones. This investigation is detailed in the Chapter 2 of the dissertation.

HORIZONTAL GEOGRAPHIC PATTERNS

For years there have been differences in the overall survivorship of monk seals among the six seal colonies of the NWHI. This has prompted speculation that forage grounds vary significantly throughout the island chain. At FFS, which supports 30% of all NWHI seals, declines as much as 60% have been documented over the last 2 decades

(Forney et al., 1999; Johanos and Baker 2000). A decade of poor survivorship of young FFS seals now threatens the reproductive viability of the colony (Gilmartin et al. 1993, Craig et al., 1994, 1995, 1996a, 1996b, 1997). Epidemiological studies prompted by the seals' emaciated condition and numerous deaths have failed to attribute the poor survivorship to disease (Reif et al. In prep). Therefore, a recent reduction in prey availability remains the most likely explanation proposed for the poor condition of young seals at FFS. Differences in prey abundance could relate to the relative availability of premium foraging grounds, regional differences in oceanic productivity, or a conjunction of both factors. The two factors will be assessed separately and checked for interactions.

Premium forage grounds

Determining whether the seals are targeting premium forage habitat is difficult because they range over a wide area crossing many types of habitat. The most spatially concentrated effort seen in the FFS satellite telemetry data (Abernathy 1999) was a few seals directing their effort at sites in the subphotic zone. Since subphotic diving requires considerable energy expenditure by the seals, it seems likely that these sites are more productive than surrounding areas. Preliminary surveys conducted at these subphotic sites determined that seals were feeding around deepwater octocorals (Parrish et al. 2002). Deepwater corals form "trees" that, when mature, range in height from ~10 to 90 cm and tend to grow in patches referred to as "beds." This led to the hypothesis that seals may have more success in obtaining prey in deepwater 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 obtained by attaching video cameras to the backs of seals. Seals were documented repeatedly targeting specific habitat types to feed (Parrish et al. 2000), including deepwater black coral colonies (Parrish et al. 2002). This work will assess subphotic fish assemblages in relation to known deepwater coral beds. In many respects, the uniform temperature, flow conditions and largely mono typic habitat that predominates at these depths provides a more "controlled" condition for the evaluation than would have been possible at shallower depths. Review of telemetry data obtained at the north end of the archipelago (Stewart 1998) shows little subphotic diving. This suggests that (1) either premium forage habitat (such as deepwater corals) does not occur at northern sites or (2) FFS seals are extending their efforts deeper than seals at northern colonies to compensate for generally lower oceanic productivity in the region.

Research questions

A series of submersible dives was made to survey the fish and habitat at the two identified subphotic foraging sites in the FFS region, and the data collected were compared with data from other known precious coral locations in the southern portion of the archipelago. Surveys were made in and outside of the coral beds at each site to look for differences in fish numerical density, median size and biomass density which might support a premium forage habitat hypothesis. Additional subphotic surveys were conducted at central and northern sites of the archipelago to test the hypothesis that the north end of the chain is without precious coral beds. Such a finding might explain why

seals in the northern part of the archipelago do not dive as deep as seals around FFS. The results of this work are detailed in the third chapter of the dissertation.

Regional oceanic productivity

The history of poor seal survivorship at FFS prompted the hypotheses that oceanic productivity and availability of prey is lower in southern latitudes of the archipelago. Using satellite remote sensing data, temporal changes in primary productivity were identified, and periods of low oceanic productivity were tested for association with declines within regional faunal communities (Polovina et al. 1995, DeMartini et al. 1996, Antonelis et al. 2003). Schmelzer (2000) used geographically referenced remote sensing data to identify statistically stable regions of sea surface productivity (using temperature as a proxy) and correlated them with the survivorship of monk seal subpopulations throughout the archipelago. Schmelzer's biogeographic model of productivity defines three geographic regions; the northern region, with the highest productivity, stretches from Kure Atoll to just north of Lisianski Island; the central region, of moderate productivity, extends from Lisianski Island to north of Raita Bank; the southern region occurs south of Raita Bank (Fig. 1.2). Higher seal survivorship was associated with increased productivity at the northwest end of the chain and poor survivorship at the southeast end.

Linking oceanic productivity to the seals' forage base has been historically difficult because the dynamic variability of the coral reef ecosystem. Comparisons of prey availability from annual surveys of reef fish at FFS atoll and northern atolls have been difficult to reconcile (DeMartini et al. 2002). The linear distribution of the islands over

seven degrees of latitude has resulted in a series of shallow reef systems that are inherently complex. Habitat and fish communities vary with the reefs' physical structures, exposures to weather, temperature regimes, thermoclines, and their history of sea level change. These variables result in a variety of reef morphologies ranging from fringing reefs on a basalt pinnacle island to an atoll with an extensive lagoon. There is even considerable difference in the morphology of NWHI atolls, which is evident in the recently published NOAA atlas on the region (NOAA 2003). Recycling of nutrients in shallow systems, together with prolonged residence times of water in reef lagoons and the large photosynthetic component of coral reefs, are likely to buffer the effects of adjacent oceanographic waters (Hatcher 1997). Surveying fish assemblages in habitats less complex than reefs such as bank summits or deep slopes, reduce the number of variables, but these fish communities still benefit from significant benthic primary productivity in the form of extensive algal beds (Parrish and Polovina 1994, Parrish and Boland in press). In contrast, the subphotic zone, is considerably removed from surface conditions, experiences a stable temperature regime year round, and, being without light, has no in-situ source of primary productivity. The faunal assemblages at these depths are dependent on the rain of particulate organic material that drifts down from the photic layer (Graf 1989, Siegel and Deuer 1997). Consequently, faunal assemblages at subphotic depths may best reflect the regional biogeographic oceanic productivity identified by Schmelzer (2000). This study will limit impact of confounding variables by moving to the deep extreme of the seals' foraging grounds.

Research questions

A series of submersible dives was made to sample each of the archipelago's three regions of productivity (north, central, south) as described by Schmelzer (2000). Differences in habitat, fish numerical density, fish size and fish biomass density were evaluated, with the expectation that northern sites should support higher fish values. To look for differences in the organic rain between the three productivity regions, the organic fraction of sediment samples collected from each region was measured using a loss on ignition technique. This investigation is detailed in the fourth section of the dissertation.

CHAPTER 2. VERTICAL ANALYSIS

Understanding the seals' foraging landscape requires knowledge of their movements, diet, and the status of their prey base. Historically, a lack of these data at any one location has prevented an integrated analysis. However, a decade of poor survivorship of the seals at FFS Atoll (FFS) has focused much of the recent monk seal foraging research in this one place. This dissertation will draw on data from three studies at FFS to characterize the foraging landscape of the seal colony. This analysis will begin with a spatial evaluation of seal movements in relation to the physiography of the region using four defined habitat zones. Then it will compare the potential 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. Using these data, the following hypotheses will be tested.

2.1) Seals feed more in the nearest habitats and less in distant ones.

2.2) Seal feeding is governed by the structure (body size, numerical density or biomass density) of the fish community available.

2.3) Different patterns in seal feeding found between habitats are not related to morphological or behavioral differences in the prey types.

METHODS

Hypothesis 2.1 - Physiography of the region

An extensive foraging study by Abernathy (1999) in the early 1990's fitted satellite tags to 24 adult seals and documented their movements to neighboring banks more than 200 km distant. The dive profiles from the tags indicated that monk seals were visiting a wide range of ecological subsystems available in the region. 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 it could be compared.

Plotted activity patterns for 24 FFS monk seals (males and females) from the Abernathy and Siniff 1998 satellite tag study, were used to represent the seals movements in the FFS region. For this dissertation, Abernathy's plots were entered into a raster based geographic information system(GIS) (IDRISI) for manipulation and analysis. Each of the plots represented the entire duration the individual seals were fitted with satellite tags (median 87 days). The individual satellite plots are included in Appendix 1. Seal movements were monitored between April and July in 1992–94, and 1996-1997. The GIS base map used was ~ 600 by 600 km area representing a section of the archipelago from Necker Bank to Gardner Bank, the extent of travel documented for the FFS seals. The resolution of the coverage was 0.13 km^2 per GIS raster cell. Abernathy and Siniff (1998) reported that the seal's dive profiles reflected the stepped regional morphology of the Hawaiian ridge in the FFS region. For this reason the stepped physiography of the NWHI summits in the FFS region were used to designate four zones, reef (0-30 m), bank

(31-50 m), slope (51-300 m) and subphotic (301-500) as the primary test categories. Isobaths from National Ocean Survey charts were used to delineate the four habitat zones throughout the foraging range of FFS seals and were entered into the GIS and used as the base map to assess the seal data (Fig 2.1).

Satellite tags can only provide positions of seals if they are on the surface during the daily pass of the orbital ARGOS satellites. A wet switch on the tag prevents signaling while the seal is hauled out on land. The reliability of the position can vary depending on the angle of the satellite. The positional error of satellite tags reported by Abernathy averaged 16 km ± 13 km (sd). To refine confidence in seal positions, Abernathy evaluated these data using a 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 seals, actual swimming velocity. These poor positions were excluded from further analysis. Finally, even with "good positions," it should be remembered these are surface positions and represent seals surfacing from dives, which can be as long as 17 min (Abernathy and Sniff 1999, Parrish et al. 2002). For each of the 24 seal plots, 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 areas within the perimeter of these clusters were

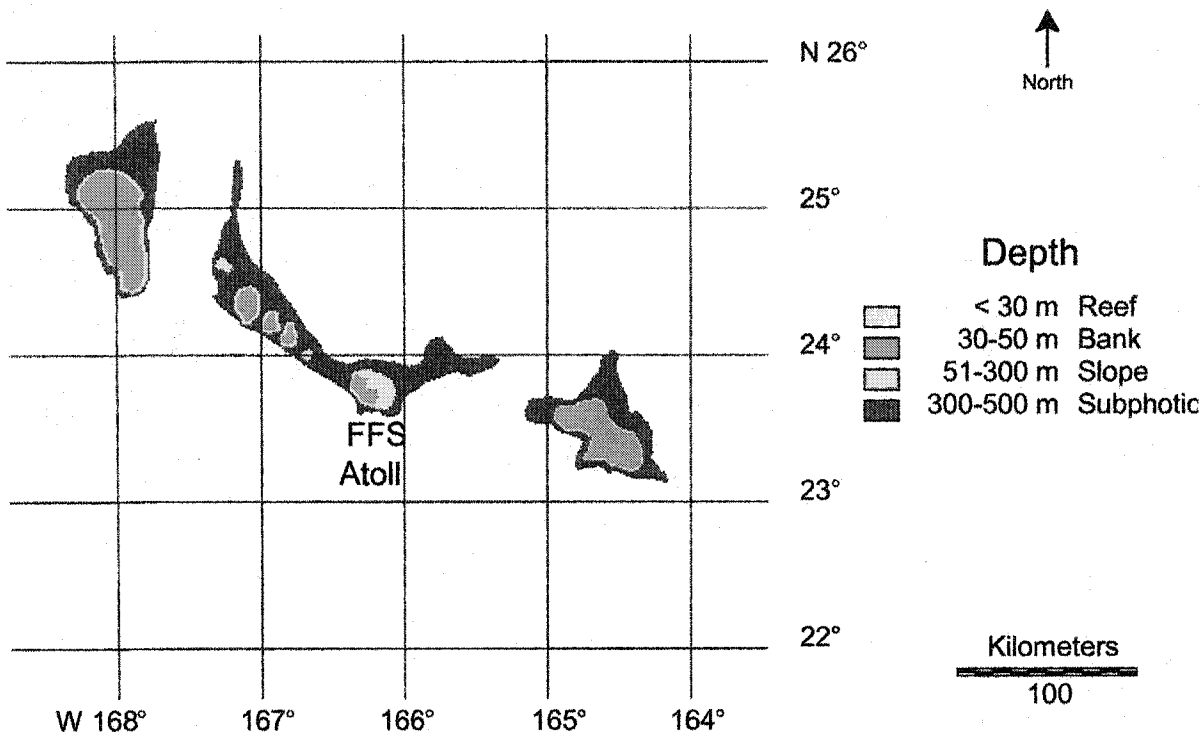


Figure 2.1. Base GIS coverage of the FFS region with each of the four habitat zones represented.

entered in the GIS as separate coverages. When overlaid, these 24 coverages represented the cumulative area, or "footprint" of the seals' foraging.

Three comparisons were made using the GIS data. First, the fraction of available planar area of the four zones was compared with the planar area of the seals' cumulative footprint for each zone. Second, a GIS surface was generated with distance values radiating from the seal haulouts at FFS (the six sand islets in the atoll). Distance values were then extracted from 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. The third comparison multiplied the distance surface (km) by the depths (m) of the habitat zones to generate a "cost" surface. Larger units were used for distance than depth because all seals appeared capable of traveling great distances but only a few exhibited deep diving behavior. Consequently diving deep is thought to affect cost more than traveling distance. This cost surface provides a relative numeric scale of the investment to travel and dive to the bottom in the four habitat zones throughout the FFS region. Again the seals' footprint was overlaid to extract the cost incurred by the seals (from here on called effort) while visiting their foraging grounds. The cost of visiting the four habitat zones was then compared to the effort the seal actually expended.

Hypothesis 2.2 - Fish community structure

Fish communities of the four zones were represented using data collected by the author while an employee of the National Marine Fisheries Service, Honolulu Laboratory. All scuba diving was conducted under the auspices of the NOAA Diving program, which

accepted all liability. The primary reason for the surveys was to establish parameters for a NMFS regional ecosystem model, but their stratification by the four zones, and the attributes they measured, make them equally suitable for this study. Logistic constraints led to using different survey methods with each zone. Divers conducted shallower surveys' and submersibles were used for deeper work. However, all variables assessed are defined in a similar manner. The taxa, numerical density and body sizes of a fish assemblage were recorded for a given area. Thus they were standardized for area-based comparisons. The author was the observer in all these surveys, in order to minimize the observational bias between sites. Thirty-five stations were established in each of the zones and were stratified as much as possible over the range of habitats encountered. For the extensive sand reservoirs on the deep slopes, quantitative trawls were used in place of visual counts. Divers observed the trawl gear in operation at shallower depths and determined its effective fishing swath to derive area based estimates. Table 2.1 details the method, area surveyed and citations for full descriptions of the survey methodologies used in each of the four habitat zones.

Table 2.1. Method, area, number of stations and other details for surveys made in each habitat zone.

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)

Stations were distributed across the reef using published (NOAA 2003) benthic maps (Fig. 2.2) derived from 4 m resolution Ikonisis imagery to represent all the primary habitat types. For deeper zones no such data are available. Surveys on the bank summits were placed arbitrarily across three banks, the southernmost (Necker), central (Brooks) and northern (Gardner). Recent Landsat (blue channel) imagery suggests that banks are comprised of largely the same habitat type over extensive areas (NOAA 2003). The slope differs from the reef and bank in that its habitat is largely determined by gravity sorting of talus, rubble and sand along its gradient. Based on habitat data from previous cross contour surveys using remote operated vehicles (Kelley Unpub data), 35 stations were located to survey the slopes: talus/rubble belt (divers - 60 m depth), the sand reservoirs (trawls - 100 m depth), and exposed carbonate bottom (submersibles - 150-300 m depth). Submersibles were exclusively used to survey the subphotic depth range. Financial support for use of the *Pisces V*, *Pisces IV* , and *RCV-150* submersibles was provided by

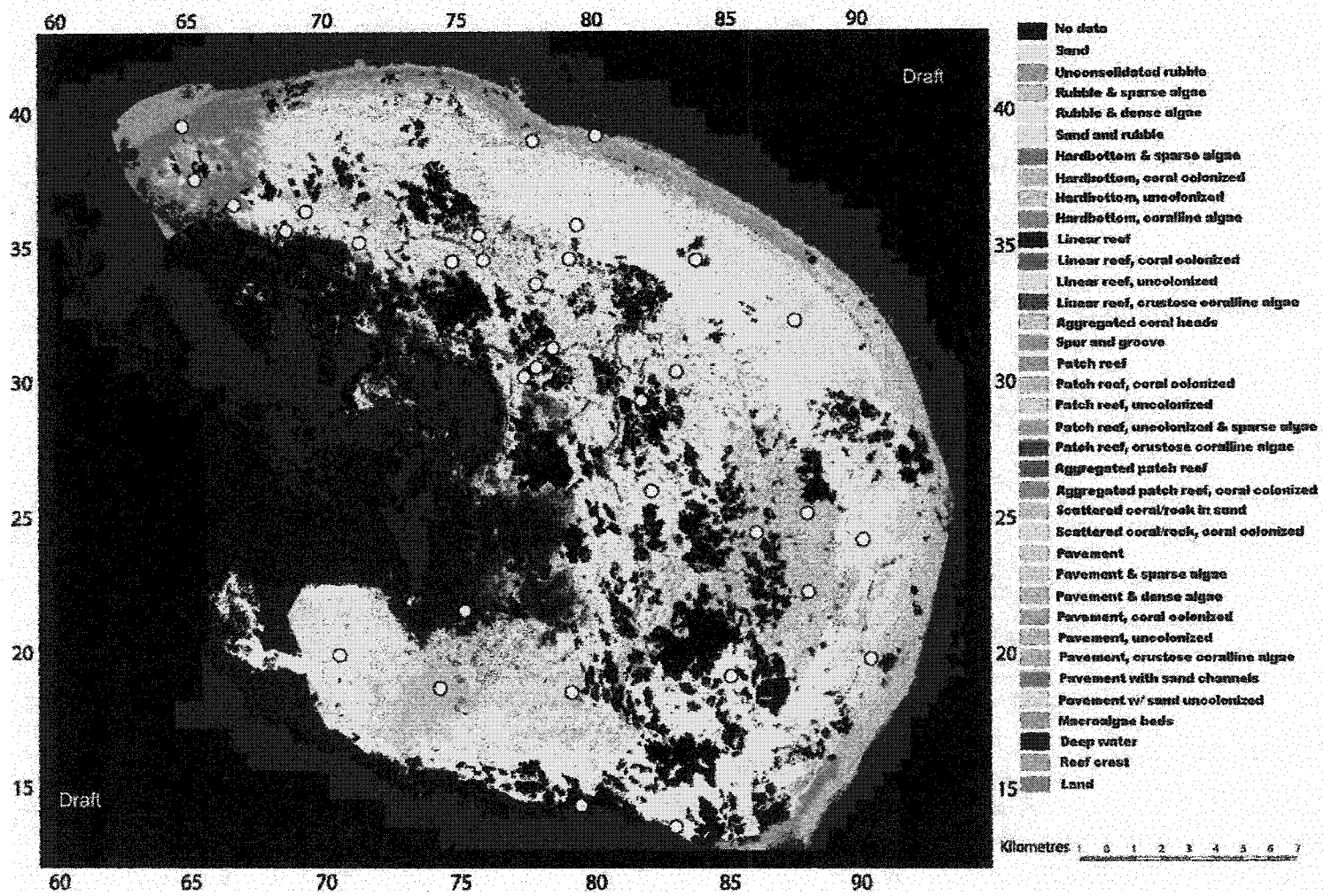


Figure 2.2 National Ocean Survey (NOS) unsupervised reef habitat classification map of FFS atoll with white dots to indicate the location of surveys. Axis coordinates are a subsection of the1000 m UTM grid zone 3 (DatumWGS 84) .

the Hawaii Undersea Research Laboratory (HURL) of NOAA's Undersea Research Program. Figure 2.3 shows the distribution of survey stations in the FFS region.

In all surveys, the fish counted were identified to genus, if not species, and their sizes were estimated to the nearest 5 cm standard length. The author and assisting staff were practiced at estimating fish lengths from prior projects (Schroeder 1987, Moffitt et al. 1989, DeMartini et al. 1996, DeMartini et al. 2003) and had conducted some preliminary calibration training prior to collecting these data. Length estimates made with the submersibles were verified with a laser scale projected on the bottom next to the fish being measured. Length estimates for reef, bank and slope taxa were then used with species-specific length-weight coefficients (Friedlander and Parrish 1998) to obtain an estimate of biomass density. Large apex predators, including jacks, sharks, and snappers were excluded from all the counts because they were too large to be considered seal prey. Trawl specimens from sand reservoirs were weighed to the nearest gram. No length-weight coefficients are available for subphotic species, so size specific weights were obtained from historical catch data from Honolulu Laboratory fish trapping and trawling. In the few instances where no fish were available for weight reference, proxies of similar body shape were employed to provide weight values. The estimates of prey size, numerical density, and biomass density of the community were then compared across the four zones.

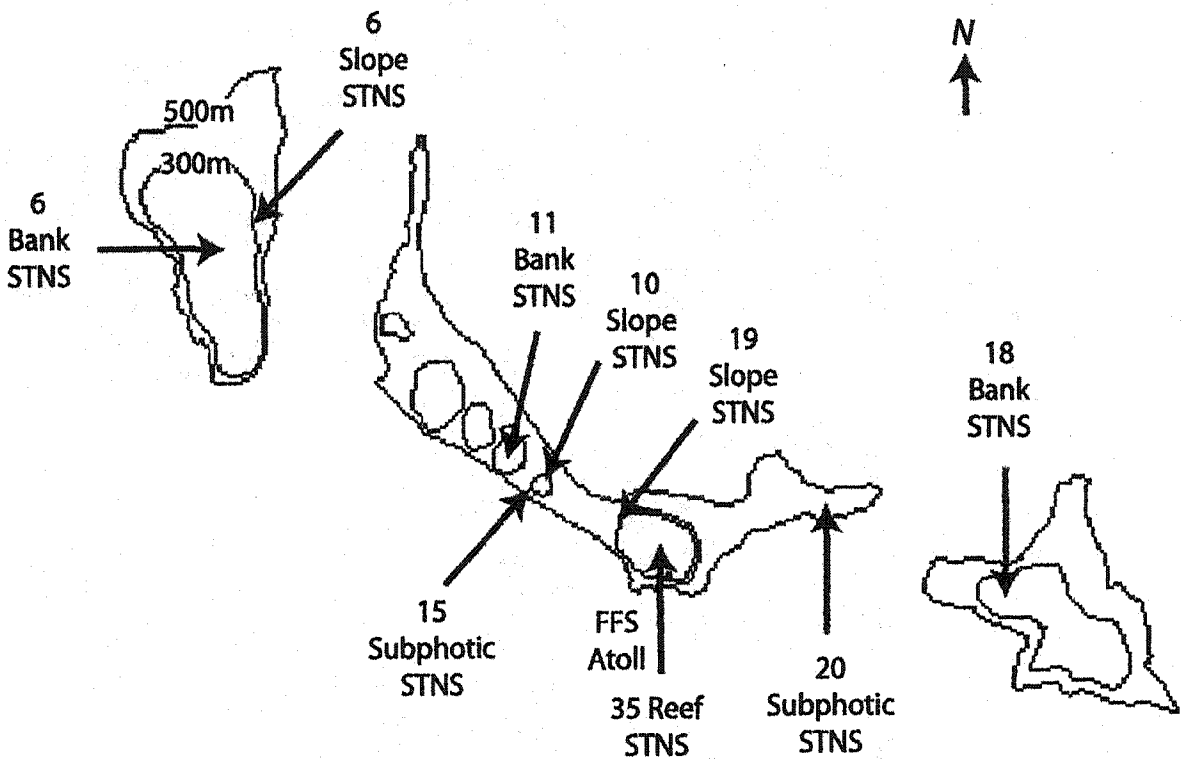
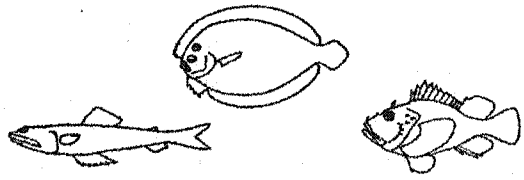
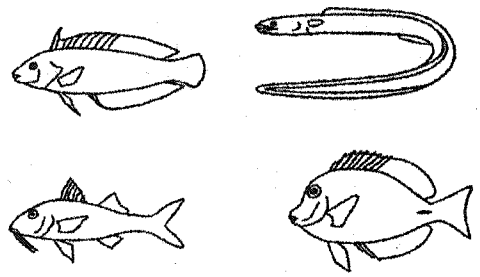
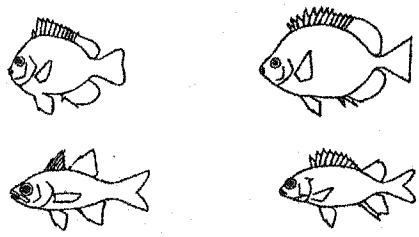
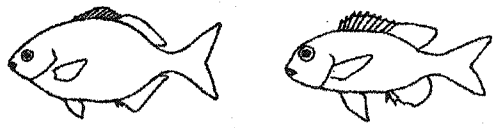


Figure 2.3. Contour plots of FFS and neighboring banks. The location of fish survey stations (STNS) in each of the four habitat zones are listed.

Hypothesis 2.3 - Prey preference of seals.

Finally, to assess the value of the fish communities to monk seals as prey, the diet data reported in Goodman-Lowe 1998 were classified into functional groups. The reported frequency of occurrence of taxa found in the scat data was used as a proxy for prey abundance and classified into functional groups reflecting the prey's general location in the water column (bottom and midwater) and feeding activity type (e.g. searcher, ambush, hovering). Four functional groups were developed, bottom ambush, bottom searcher, bottom hoverer, and midwater hoverer (Table 2.2). The fish survey data from each of the four habitat zones were classified using these functional groups, and their numerical density and biomass density were then compared with the frequency of occurrence of the functional groups in the seals diet (Goodman-Lowe 1998). This analysis assumes that a high fraction of a particular functional group found in the seals' diet means the seals will target that functional group of prey across all four zones. Furthermore, the zone with the fractional make up that best mirrors the relative fraction in the seals diet is the zone most used by the seals.

Table 2.2. Monk seal diet by functional groups derived from analysis of scats (Goodman-Lowe, 1998).

Functional Group	Taxa found in seal scat	Example taxa morphology
Bottom Ambush BA	*Synodontidae* *Cirrhitidae* *Bothidae* *Scorpaenidae* *Octopodidae*	
Bottom Searcher BS	*Labridae* *Scaridae* *Acanthuridae* *Muraenidae* *Congridae* *Kuhlidae* *Ophichthidae* *Mullidae* *Lutjanidae*	
Bottom Hoverer BH	*Pomacentridae* *Tetraodontidae* *Pomacanthidae* *Chaetodontidae* *Holocentridae* *Pricanthidae* *Apogonidae*	
Midwater Hoverer MH	*Kyphosidae* *Monacanthidae* *Balistidae*	

Analysis

Owing to the categorical and non-normal nature of the data used to test these three hypotheses, all statistical comparisons were nonparametric (Siegel and Castellan 1988). Analyses were run using SPSS software version 11.5. Testing the seal movement data in relation to the availability of the four zones, relied on simple chi-squared comparisons using the seal data as expected values. The prey community of each zone was sampled with 35 stations to provide this study with a power of 0.80 to detect large effects at the 0.01 level (Cohen 1988). Despite efforts to balance and stratify sampling, the length, numerical density, and biomass data for fish significantly differed from a normal distribution. Consequently the communities of the four zones were first evaluated together using a Kruskal-Wallis (K-W) analysis of variance (ANOVA) and then with *a posteriori* Tukey comparisons. The comparisons of functional group differences in seal prey were addressed with chi-square using the seals' diet data as the expected values. Finally, the proportion of functional differences 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.

RESULTS

Seals' use of foraging grounds

The potential area, median distance and cost of foraging in each of the four habitat zones of the FFS region were queried from the GIS surfaces and the values are presented in Table 2.3.

Table 2.3. Calculated values from GIS coverages that were used as the expected values in the chi-square analysis.

Zone	Available area (km^2)	Distance to grounds median km	Percent cost, median Distance*depth
Reef	371	4.6	0
Bank	5,806	171.3	0.09
Slope	1,831	136.8	0.107
Subphotic	12,384	132.7	0.63

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. 2.4). Overlap of seal movements was highest closer to the seals' haulouts in the shallows of the island (Fig. 2.5). 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 (χ^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 (Fig. 2.6).

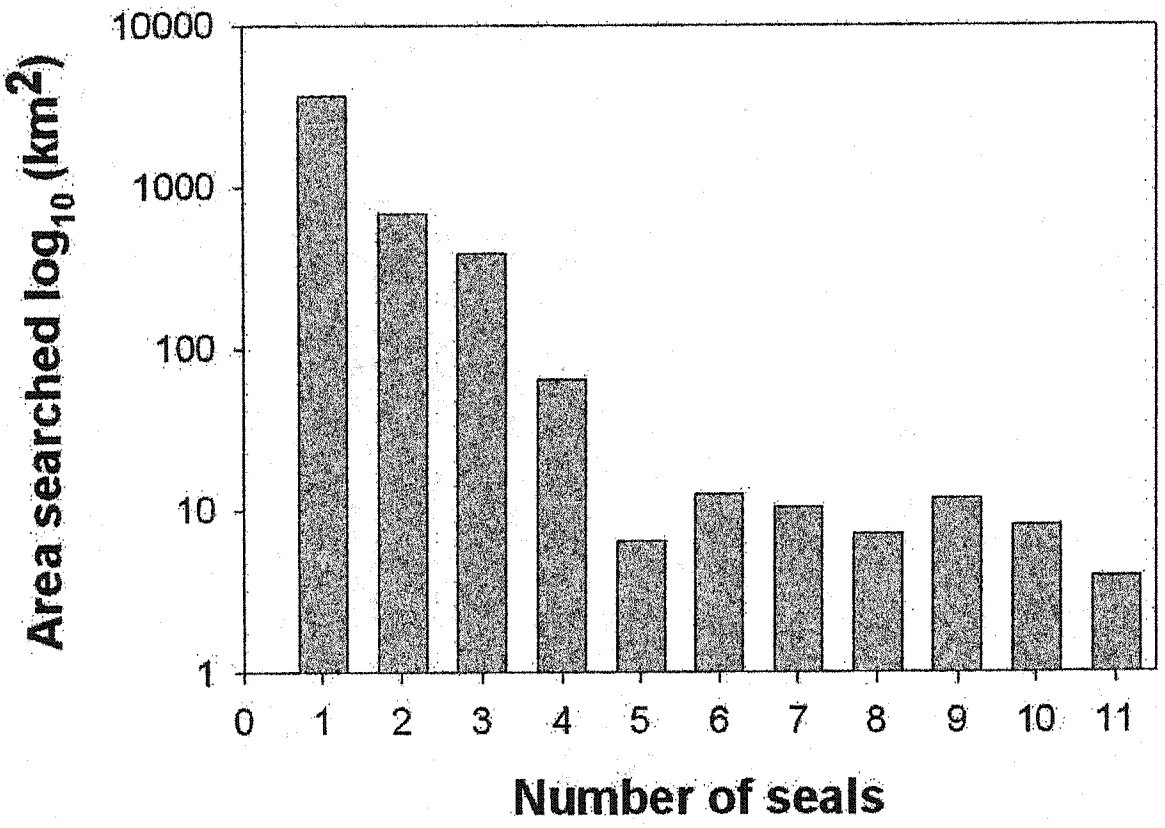


Figure 2.4. Area of forage grounds searched by number of seals. Little overlap is evident between the forage area of individual seals.

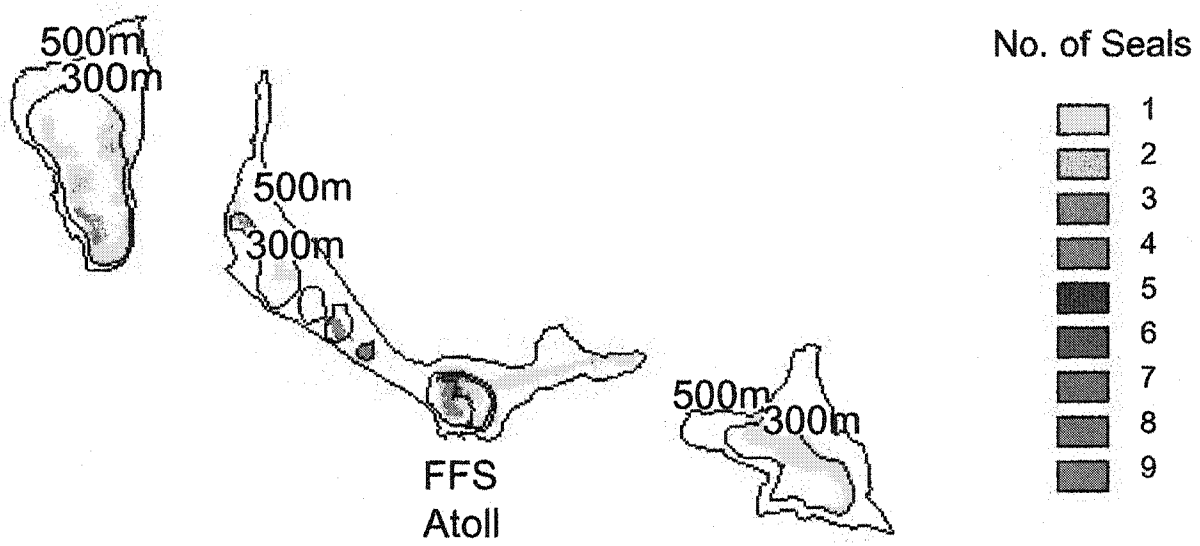


Figure 2.5. GIS coverage showing the "footprint" of seal movement within the FFS region. The depths of isobaths are in meters.

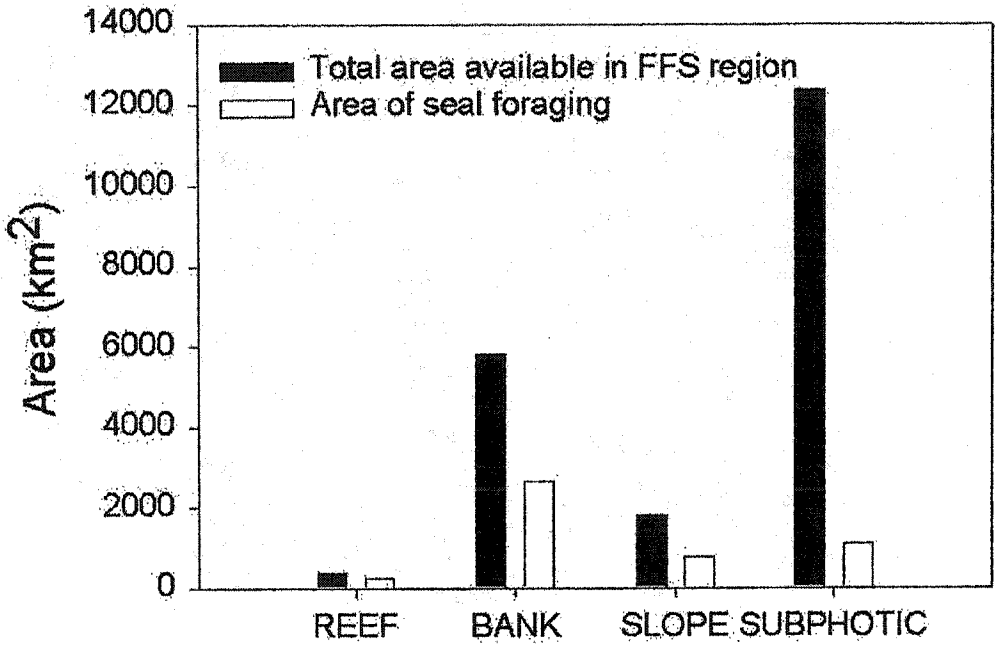


Figure 2.6. The area available versus the area seals visited for the four zones of the FFS region. Roughly half of the grounds are used for each of the zones except the subphotic slopes which comprises the majority of the area and receives the least visitation.

Comparing the median distance of the four zones from grounds with the average distance traveled by the seals did not significantly differ (χ^2 =3.19, df=3, P= 0.4), indicating seals generally spread their effort over the extent of grounds (Fig. 2.7). Surprisingly, the median foraging effort expended by seals did not significantly differ (χ^2 =4.57, df=2, P=0.1). Cost of using the reef at the atoll was indistinguishable from zero and excluded from the analysis. The seals' effort differed most from the cost surface for subphotic visits (Fig 2.7). GIS surfaces for the cost and the seals, foraging effort appear in Figure 2.8.

Fish community structure

Fish size, numerical density and biomass data all were found to differ significantly from a normal distribution (Kolmogorov-Smirnov, Z=2.4 - 4.3, df=139, P<0.01). Significant difference in fish size, numerical density and biomass density were detected when comparisons were made between the four habitat zones (K-W χ^2 = 26.6 - 77.5, df =3, P<0.01). Results from the *a posteriori* comparisons using the Tukey tests are detailed in Table 2.4. As expected, the highest numerical density was in the reef zone, and the lowest occurred at subphotic depths (Fig 2.9). However median fish size exhibited a contrasting pattern with the largest fish at subphotic depths and the smallest in the reef (Fig. 2.9). Finally, reef biomass density was significantly greater than bank and slope biomass density which were significantly greater than the subphotic zones (Fig. 2.9).

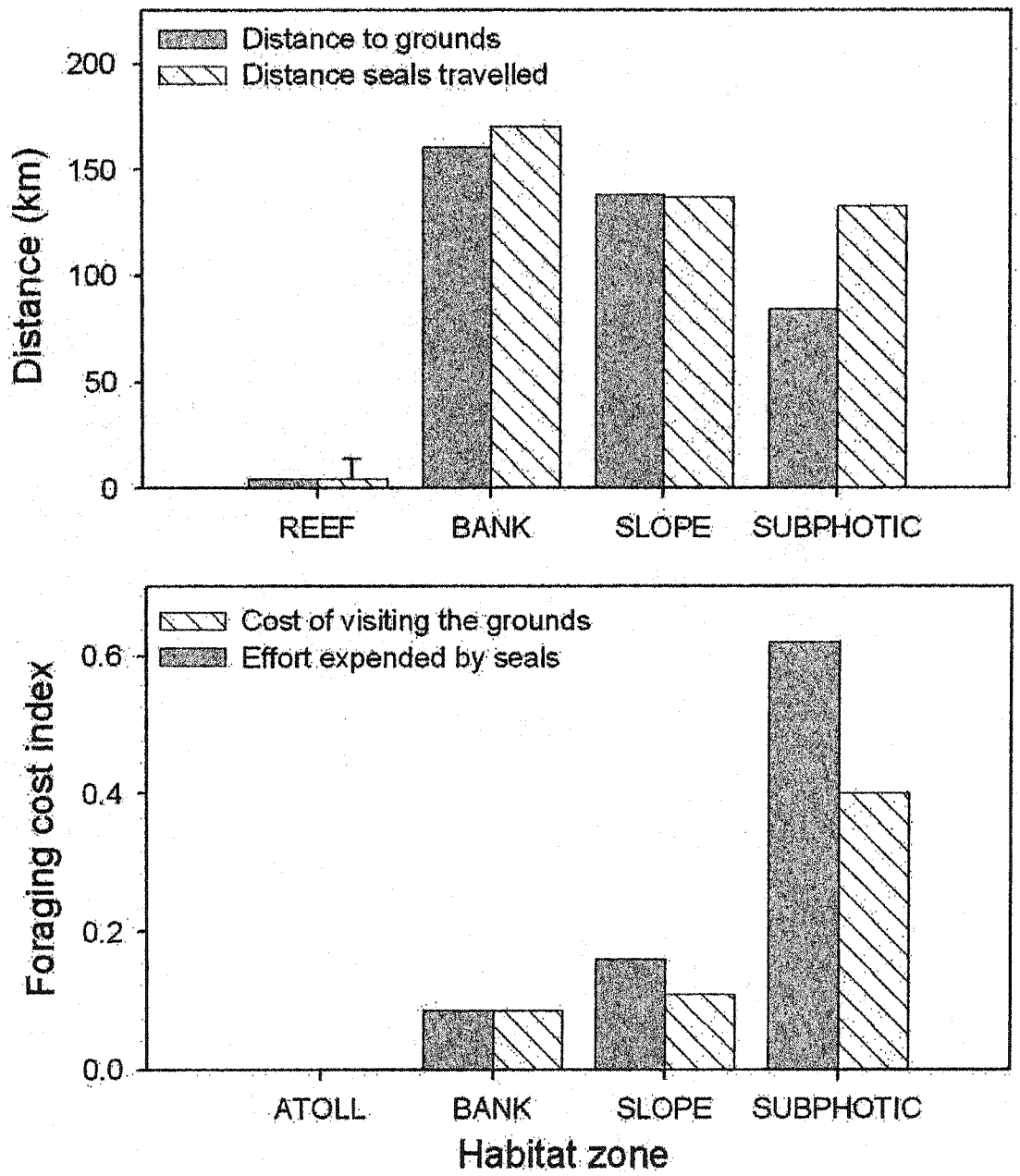


Figure 2.7. GIS derived median distance (top) and cost (bottom) to visit the forage grounds of the four zones around FFS. The distance the seals traveled and their effort (cost incurred by the seals) are shown for comparison.

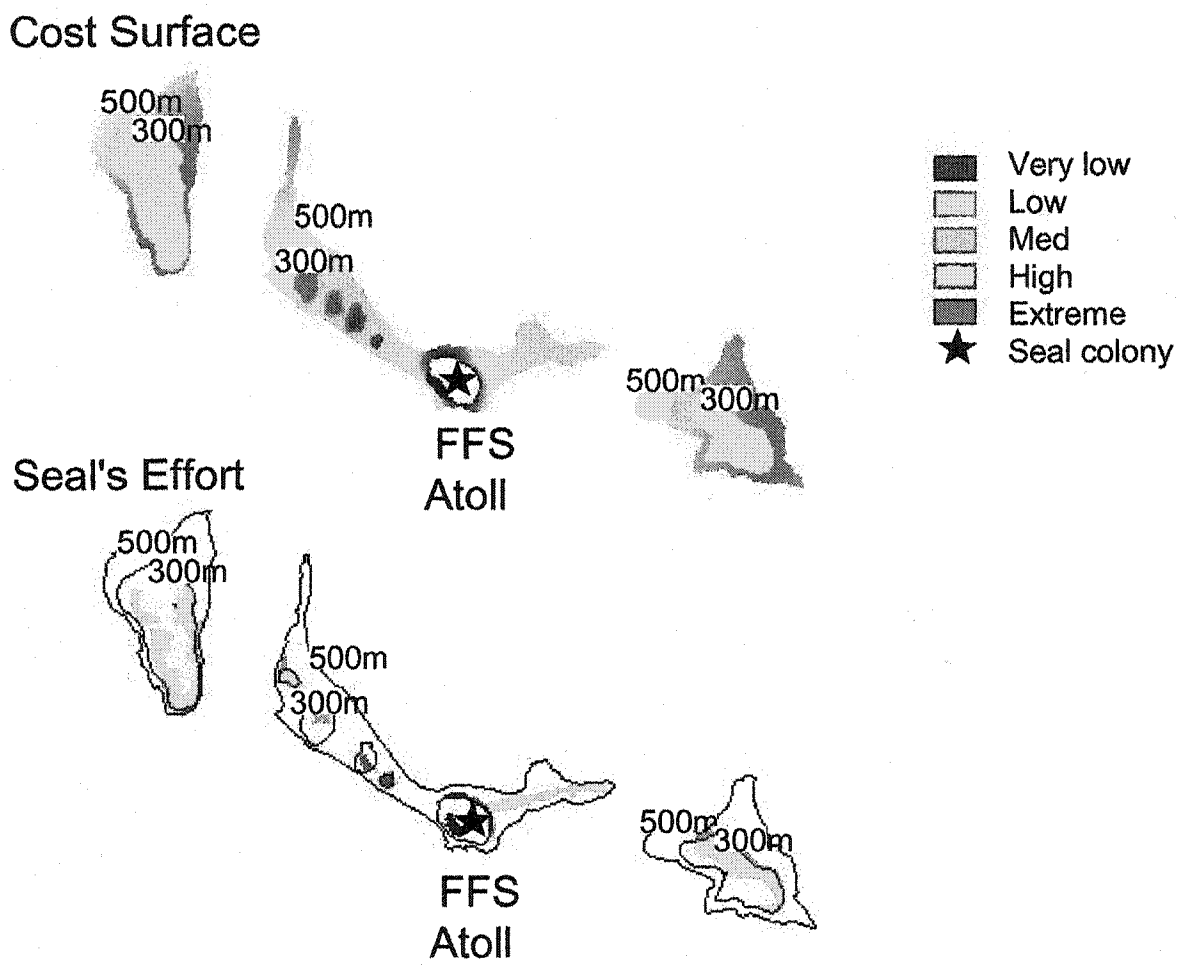


Figure 2.8. GIS coverage of the cost of visiting the forage grounds throughout the FFS region (top) with a second coverage showing the movements or "effort" of the monk seals (bottom). The color scale indicates the degree of cost and/or effort.

Table 2.4. Results from K-W analysis of variance of numerical density, body size, and biomass density by habitat zone 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 ≤ bk ≤ sp
Biomass g/m^2	16.0	5.46	0.69	0.35	<0.01	sp < sl, bk ≤ rf

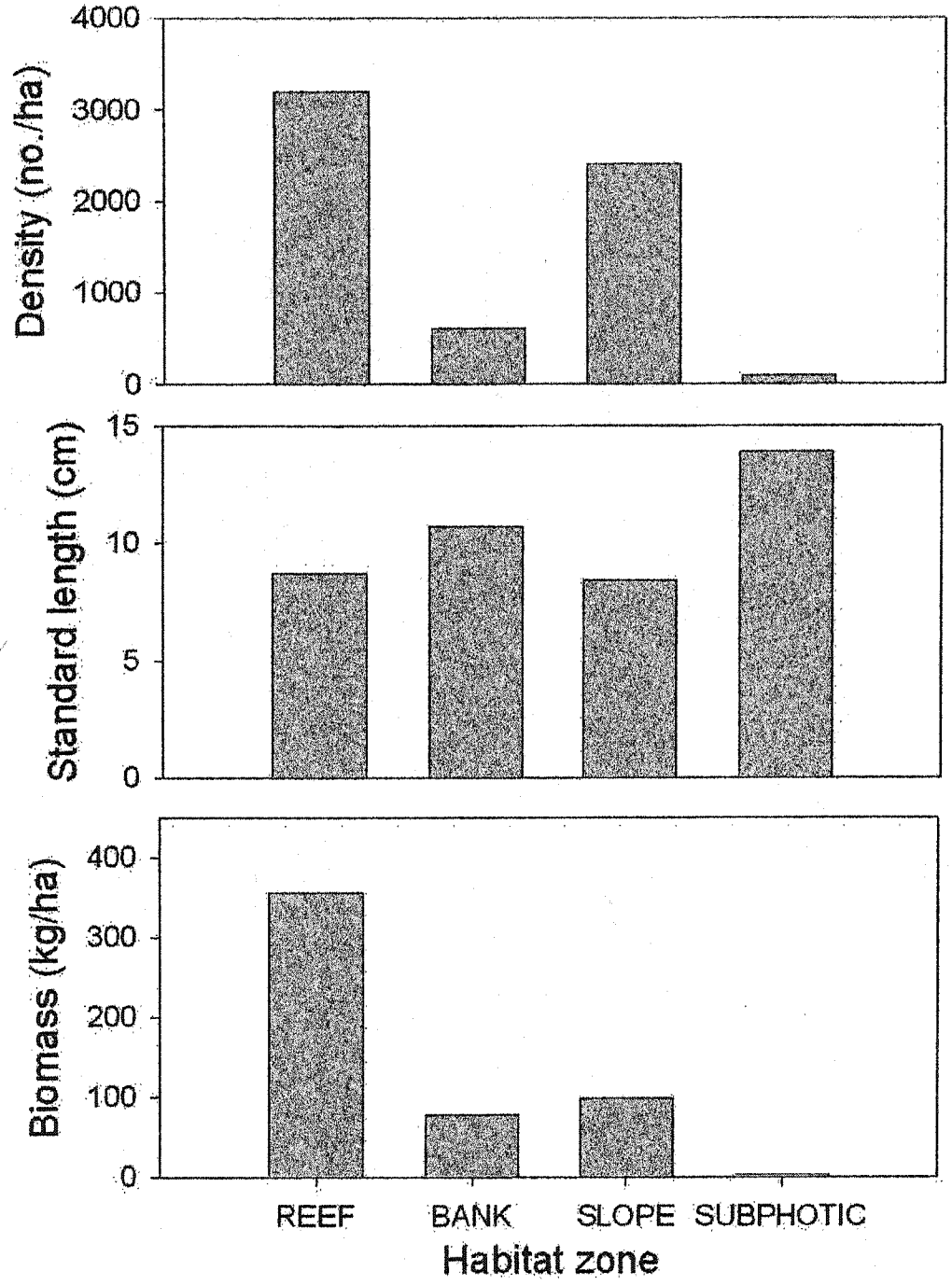


Figure 2.9. Numerical density, standard body length, and biomass density of fish for the four habitat zones in the FFS region.

Prey functional groups

Dividing the prey items reported in the Goodman-Lowe (1998) analysis of scat into the four functional groups by their frequency of occurrence, provides a fractional diet of 23% bottom ambush predators (BA), 49% bottom searchers (BS), 26% bottom hoverers (BH), and 2% midwater hoverers (MH). This diet composition was used as the expected values for all comparisons with the composition of the four habitat zones. Of the four functional groups, only the midwater hoverer category had a notably low number of families in each of the habitat zones (Table 2.5). 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 added four deeper ones. The largest difference in family composition was evident in the subphotic zone where only four families mostly bottom ambushers persisted from the shallow atoll depths. The percent composition of the seals' diet and the four functional groups were plotted by habitat zone for numerical density and biomass density (Figs. 2.10). Chi-square tests indicated that the observed composition of the functional groups for each zone significantly differed from the composition expected based on the seals' diet (density χ^2 =37.5-77.6 $P<0.001$; biomass χ^2 =20.1-73.8 $P<0.001$). Failing to identify a zone that was not significantly different from the seal diet, scores were generated for numerical density and biomass density using the functional group compositions in a dissimilarity index (Fig. 2.11). 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 2.5. Taxa by functional group and habitat zone. Bold font indicates encountering a new family in a deeper habitat zone.

Functional Group	Reef < 30 m	Bank 30-50 m	Slope 51-300 m	Subphotic 301-500 m
Bottom Ambush BA	*Synodontidae* *Cirrhitidae* *Bothidae* *Scorpaenidae* *Octopodidae*	same	same	***Chlorophthalmidae*** ***Percophidae*** ***Chaunacidea*** ***Lophiidae*** *Bothidae* *Scorpaenidae* *Octopodidae*
Bottom Searcher BS	*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 Hoverer 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 Hoverer MH	*Kyphosidae* *Monacanthidae* *Balistidae*	same	*Balistidae*	***Grammicolepididae*** ***Myctophidae*** ***Zeidae***

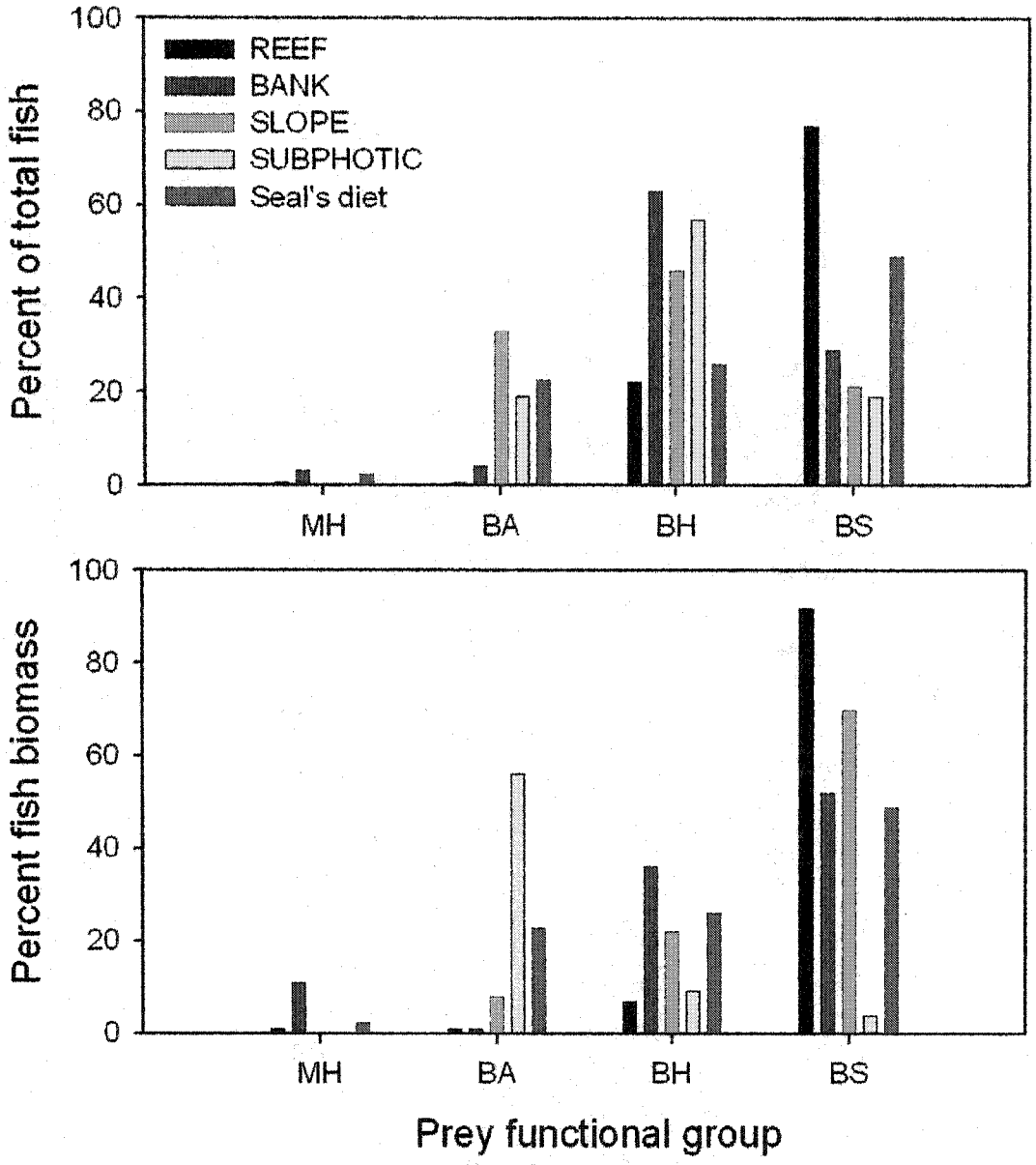


Figure 2.10. Percent fish density (top) and biomass density (bottom) broken down by prey functional group and habitat zone. The seal diet as derived from frequency of occurrence scat data was included for reference. MH = midwater hoverers, BA=benthic ambush predators, BH=benthic hoverers, and BS=benthic searchers.

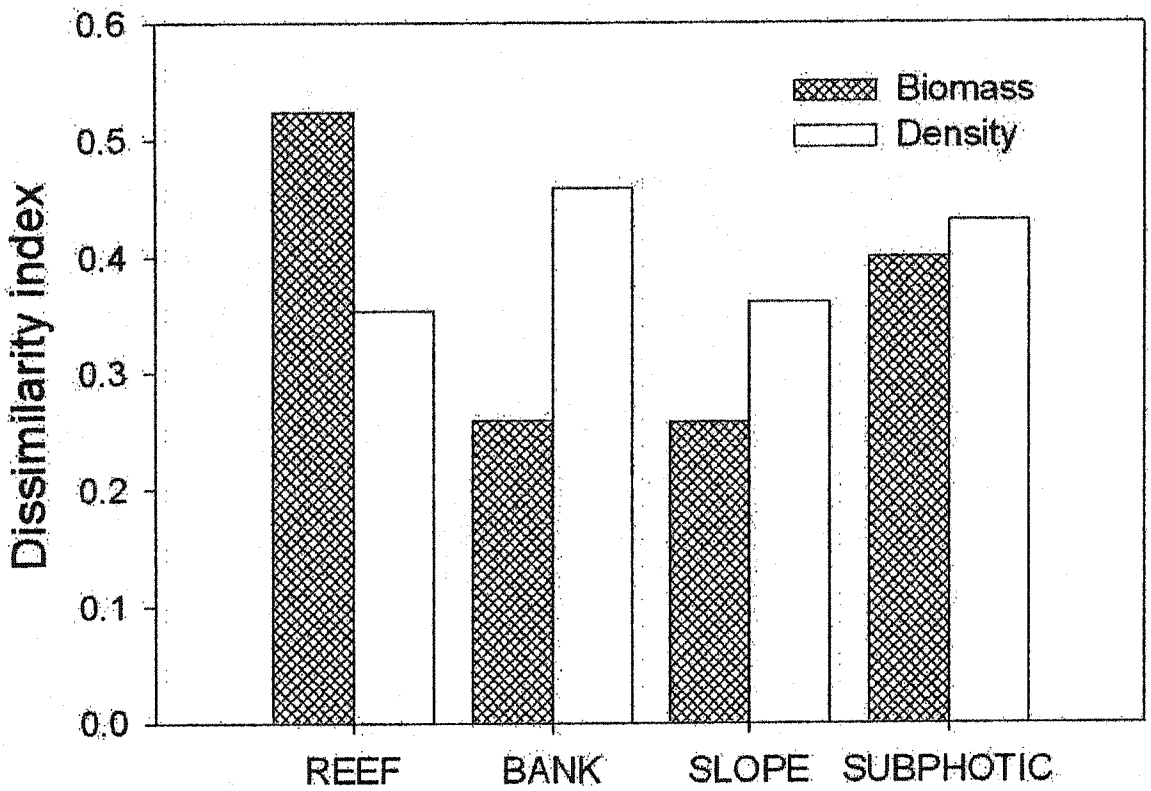


Figure 2.11. Results of a dissimilarity analysis assessing fish numerical density and biomass density for each of the four habitat zones. Biomass density of bank and slope zone differed least from the seal diet (derived from scats).

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. Abernathy's (1999) telemetry study of ~5% of the FFS subpopulation serves as the proxy for this. Differences in foraging patterns between individuals are clearly evident, and these differences are addressed at length by Abernathy (1999). However, it is important to keep this variety of patterns in mind while considering the primary results of the GIS analysis below. Since all seals start their foraging trips from the reef, there is an inherent tendency for a higher foraging overlap closer to the reef. This is particularly evident for areas at the reef as represented in Fig. 2.5. Even so, the fact that 25% of the reef was never visited suggests that seals are not entirely focusing their efforts on the reefs at the atoll. Away from the atoll, the area of overlap that exceeds 2 individuals was less than 10% of the total seal foraging footprint.

The significant difference in the cumulative area seals used, versus the available area in the four habitat zones, indicates that seals did not divide their effort equally among the four zones. The lack of significant difference between the distance traveled or the foraging cost (distance multiplied by depth) among habitat types indicates that the seals' pattern of habitat use is not simply governed by the relative effort associated with reaching these areas. These findings support the notion that the habitat types targeted are spread over the range of banks and occur at a variety of depths. Had distance or foraging cost

experienced by seals differed significantly among habitats, the positions of the seals would probably have been increasingly clustered closer to the atoll (minimizing travel effort) or strongly within the shallow habitat zones (minimizing foraging cost). Despite the spread of the seal effort across different zones and the lack of significant differences in cost investment, there appears to be an increased cost of foraging for seals that chose to move beyond the slope down to subphotic depths (Fig. 2.7).

The footprint of the 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. A focus on the slope 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 (Fig. 2.5).

Other instrument studies of monk seals have similarly 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 video cameras fitted to the backs of seals documents seals targeting a variety of slope habitats to feed (Parrish et al. 2000, 2002, in review).

Fish community structure

Counts of the fish in each of the zones are likely to be subject to some survey specific bias. These surveys were stratified as much as possible by the range of available habitat. This included types of bottom that are often ignored such as sand, rubble fields, pavement, etc. The most common bias inherent in visual surveys is the under representation of cryptic species. It is likely that this bias is relatively constant throughout the different survey types except for the trawls of the sand fields conducted in the slope zone. Sand fields which cover the 100 m depth contour on most of the banks, make up a large part of the slope habitat area. Unfortunately it is too deep for divers and too shallow to warrant the investment of a submersible to survey. Surveying with a bottom trawl is less than ideal to compare with visual fish survey data, but the alternative was to exclude the fish community from the most dominant habitat type in the slope zone. 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. 2003, Friedlander and DeMartini 2002). The numerical density was much lower on the bank summits. 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 Colin1986; 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 on these results, monk seals would 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; Parrish et al. in review) also indicate minimal 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 1999). 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 fed was on the slopes. Since the surveillance time of the seal-mounted videos is limited to a few days, the findings of longer duration 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 may have shortcomings, but at present there is nothing better to use in its place (Cottrell 1993). 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 could ultimately bias the representation of fragments that pass through the digestive tract.

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 ambush predator 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 suggests that 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's diet. The scores for fish densities showed no trend, whereas the comparison with fish biomass density suggested that the communities of the bank and slope were most consistent with the seal diet. The seals' diet data are derived from the undigested fragments of the prey left in the scat, and their prevalence is a function of the prey number and body size. Measures of fish biomass density, which includes the number

and size of fish, are likely to exhibit more agreement than numerical density alone. A counterintuitive finding was that the seals' diet was the least similar with the reef community, which, because of its proximity to haul out and pupping areas, was expected to be the most similar to seals.

CONCLUSION

The GIS comparisons failed to attribute the seal's foraging movements to the amount of available area, distance, or cost associated with feeding in the four habitat zones used in this analysis. This suggests that the seals were exploiting a resource throughout the region and not focusing on areas close to the atoll or exclusively in shallow habitat. Similarly, the structures of the fish communities in these four habitat zones were inconsistent with the seals' use of the four zones. If seals were seeking the habitat zone with the greatest numerical density, size and biomass density of fish, they would stay in the shallows of the atoll; instead the seals fed well away from the atoll. Comparing the composition of fish types in the seals' diet (based on scat data) to that of the fish surveys in the four habitat zones indicated the seals' diet was closest to the fish composition of the bank and slope.

CHAPTER 3. PREMIUM FORAGE HABITAT

Monk seals' are clearly able to find and return to the same areas repeatedly to feed. This behavior has been shown for their foraging activities on bank summits and the deep slope (Parrish et al. 2000, 2002, in review). The minority of seals that venture into the subphotic realm may be employing the same strategy. If the 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 choose 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 deepwater corals are one of the few exceptions that diversify the substrate. It is unknown whether fish and macroinvertebrates are associated with the coral "trees", using them for shelter or facultatively. Subphotic diving by FFS seals at two deepwater coral beds (Parrish et al. 2002) prompted a hypothesis that deepwater corals create exceptional forage habitat and somehow improve the seals' access to prey. This chapter will explore potential links between deepwater corals and the fish assemblages that could be prey for monk seals.

Many of Hawaii's deepwater corals are as yet undescribed, and the best known are the few that are commercially harvested. Two genera, *Corallium* (pink coral) and *Gerardia* (gold coral), are the main commercial species and are good representatives of the two primary forms of trees found in deepwater corals (Fig. 3.1).

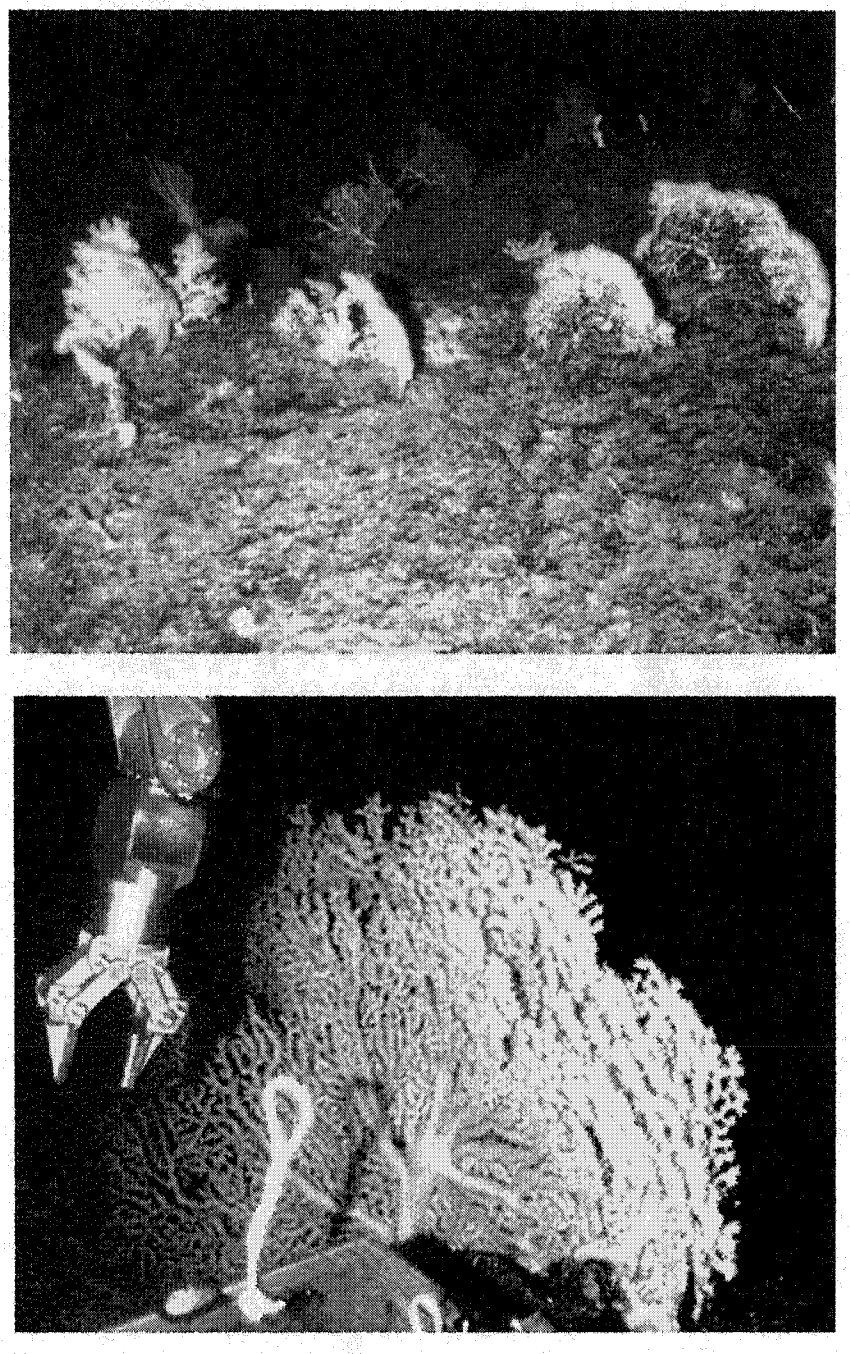


Figure 3.1. Example morphology of the two genera of deepwater corals assessed in this work. *Corallium regale* and *C. secundum* form colonies less the 30 cm in height (top), and *Gerardia* sp. forms colonies as much as 150 cm in height (bottom).

Corallium is a crustose octocoral in the Alcyonacea which occurs in pink (*C. secundum*) and red *(C. regale)* 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 well over 100 cm high. Both genera are known to colonize locations of high flow (Grigg 1993) and were found at the two subphotic sites visited by FFS seals. This analysis will focus on these two genera and address the following three hypotheses.

3.1) Areas with deepwater coral are premium forage habitat and support greater numerical densities, sizes, and biomass density of fish (seal prey) than adjacent areas without precious corals.

3.2) The lack of subphotic foraging by seals at the north end of the archipelago can be explained by an absence of deepwater corals (premium subphotic forage habitat) in northern waters.

3.3) There are fish taxa that routinely use deepwater corals as shelter, and these taxa fall into the fish functional groups targeted by seals as described in Chapter two.

METHODS

Submersible survey methodology

All the subphotic data were collected in a series of submersible dives focused on surveying depths between 300 and 500 m. This was the subphotic depth range visited by monk seals, and it is also the known depth range for pink and gold corals. In total, 54 dives (28 sub and 26 ROV) were made using the *Pisces V, Pisces IV* and *RCV-150* submersibles. Dive sites, hereinafter referred to as stations, include representation from both the main Hawaiian Islands (MHI) and the NWHI (Fig 3.2). The stations in the MHI and the lower portion of the NWHI were directed at known beds of deepwater coral, and stations at the remote north end of the chain were exploratory. Whenever possible, prior to each dive the bathymetry of the station was mapped using the HURL vessel's multibeam acoustic mapper (SEABEAM) (Fig 3.3). With such a map of the dive site, the *Pisces* could investigate areas with features that characterize high flow environments where deepwater corals might occur. Some of the most remote exploratory stations were not mapped because there was inadequate ship time.

Ideally, submersible surveys at each station were planned to consist of four transects (350 m, 400 m, 450 m, 500 m) run parallel to the contour. However, the physiography of the slope varied considerably and often dictated restructuring of transects within the 350 to 500 m depth range. The author was the chief scientist for all of the dives. The submersibles were three person vehicles with the pilot situated in the center and observers on either side (Fig 3.4). Each person can see an illuminated bottom area of ~55 m^2 through view ports directed diagonally forward and down.

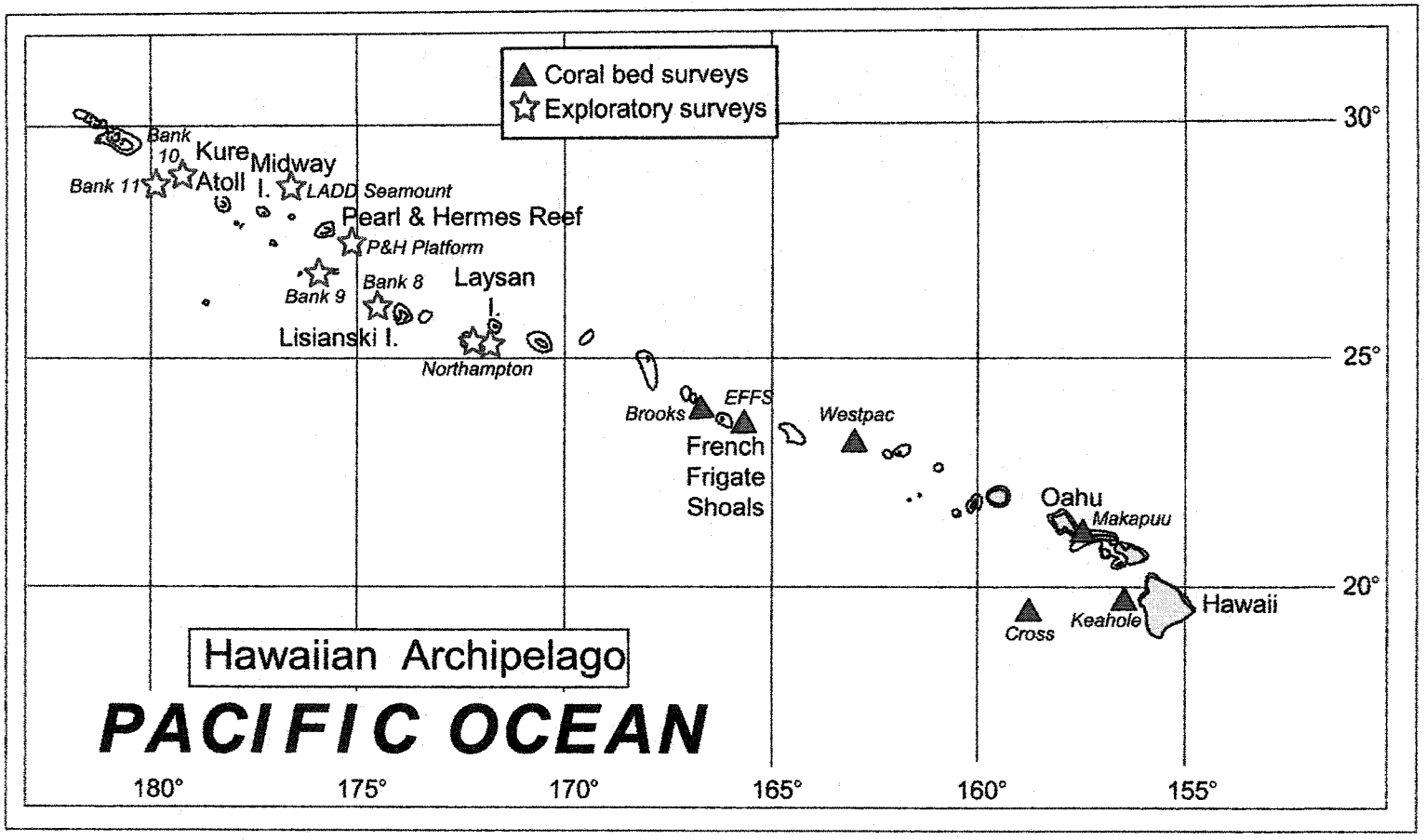


Figure 3.2. Map of the Hawaiian Archipelago with locations of dive stations indicated by triangles and stars. Triangles are stations known to have deepwater coral beds and were used for the premium habitat analysis. Stars indicate exploratory dives to look for new sites with corals and collect data for regional productivity comparisons discussed in Chapter four.

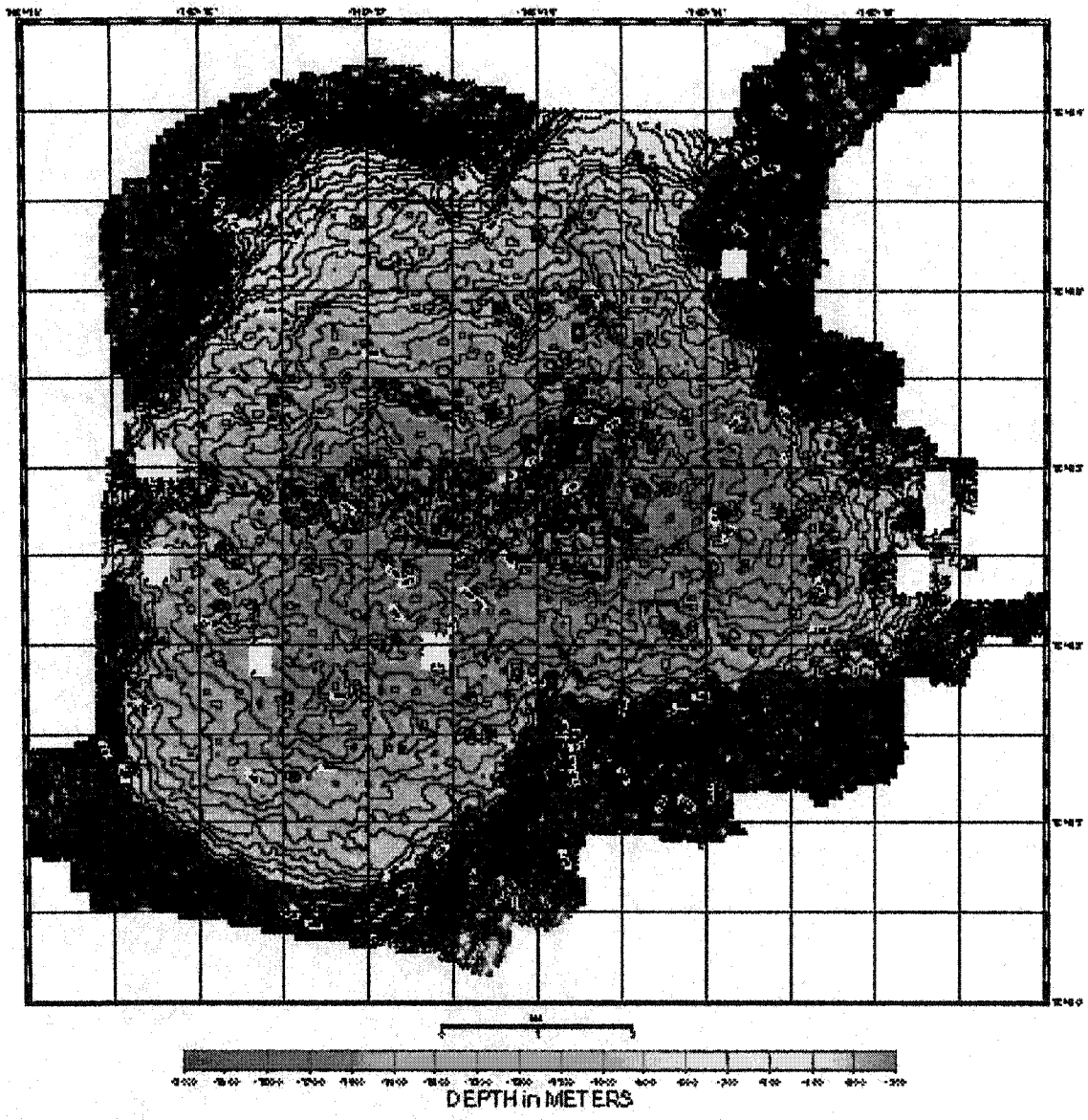


Figure 3.3. Bathymetric map of the summit of Cross Seamount as an example of the data obtained by SEABEAM survey prior to deploying the submersible.

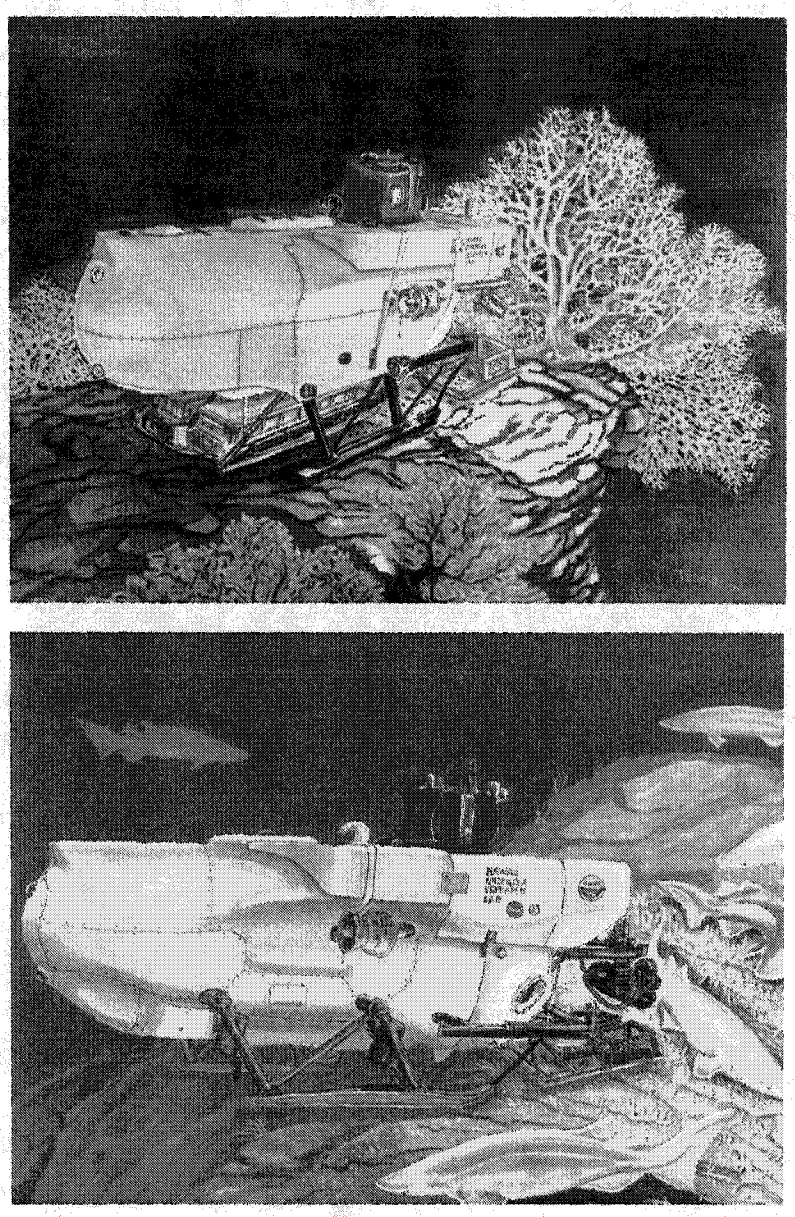


Figure 3.4. Artist rendition of the submersible *Pisces V* in gold coral bed of FFS and the *Pisces IV* on the summit of Cross Seamount. Images used with permission of Terry Kerby, artist and chief pilot of the *Pisces* submersibles.

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 are operated continuously, and the edited video feed from the cameras was recorded on a video log 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 .

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 at 5 min intervals (equivalent to a cumulative area of 3600 m^2) to obtain numerical density and size structure information. A brief break (~30 sec) was taken between each count. 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 5 min period is also roughly equivalent to the bottom time documented for monk seals at subphotic depths (Parrish Unpublished data). A laser reference scale was projected on the bottom within the view of the video cameras used on each of the submersible 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 into three primary 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.

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 of fish and coral data. Some assessment of year effects was attempted using a fixed transect across a range of substrates and relief types. The fixed transect was established at FFS and was surveyed in 1998, 2000, and 2001. Archival temperature recorders were deployed for two years on the summit of the FFS platform (NWHI) and Cross Seamount (MHI) coral beds to document regional differences in temperature and seasonal dynamics.

Hypothesis 3.1 - Deepwater corals enhance fish abundance

The hypothesis that corals support more fish (numerical density, body length and biomass density) than adjacent areas without coral, the stations at Brooks Bank, East FFS, WestPac Bank, Makapuu Pt., Keahole Pt., and Cross Seamount were used in the analysis. Known to have beds of precious corals these stations were close enough to port to be surveyed multiple times, which increased the sample size and power of the analysis. Any effects detected in the comparison were checked using follow-up comparisons. This analysis was then repeated using the taxa of the fish data reclassified into seal prey functional categories used in the earlier chapter. General descriptions of the stations are detailed in Table 3.1 and their locations marked with triangle symbols in Figure 3.2.

Table 3.1. The number of dives, general morphology, information source and references for the six stations selected for deepwater coral habitat.

Station	# dives	Morphology	Information source	Reference
S.E. Brooks Bank	2	Slope of bank	Seal telemetry data	Parrish (2002)
French Frigate Shoals	4	Platform summit	Seal telemetry data	Parrish (2002)
WestPac Bank	2	Slope of bank	Exploratory surveys	Grigg (1993)
Makapuu Point, Oahu	2	Slope of island	Commercial harvest	Grigg (1993)
Keahole Point, Hawaii	2	Slope of island	Commercial harvest	Grigg (1993)
Cross Seamount	4	Seamount summit	Exploratory surveys	Kerby pers com

Hypothesis 3.2 - Deepwater corals in the northern archipelago

In 2002 and 2003 exploratory submersible surveys were extended to the northernmost part of the archipelago, providing dives at eight stations. These exploratory stations are represented in Figure 3.2 with star shaped symbols. Only the depths and distances from seal colonies were known for these stations when they were selected. Whenever possible the station was the summit of a seamount or platform that would meet many of the objectives of the oceanic productivity comparison presented in the next chapter. Only at the stations at the two Northampton summits and Bank 8 was the bathymetric data adequate to refine the placement of the dives in areas most likely to support precious corals. All other sites relied solely on the crude pre-WWII chart data. I selected dive sites by identifying the areas with the tightest isobaths that would be the most likely to constrain flow. At the beginning of each dive the submersible would descend well beyond precious coral depths (~700 m) and then do a cross contour survey as

it ascended. This improved the chances of finding corals. If corals were found, the surveys were conducted parallel to the contours as in the southern stations. If no corals were found, the surveys were conducted at the preplanned depths of 350, 400, 450 and 500 m (slope physiography permitting). If corals were encountered, the coral taxa, numerical density and size structure were recorded to compare with coral beds farther south in the archipelago. Physical variables including substrate, relief, depth and temperature were documented and considered across all subphotic surveys archipelago-wide.

Hypothesis 3.3 - Deepwater corals as shelter for seal prey

The degree to which fish used corals as shelter was assessed by pooling pseudo replicates from all stations archipelago-wide (premium habitat analysis and the exploratory dives) in which precious corals were present. The fish taxa seen using the corals as shelter were detailed, and the effects of coral type and tree height on fish sheltering was then assessed. Depth and station effects were also evaluated. Finally, the taxa of fish found sheltering in corals were reclassified into the functional groups used in Chapter 2 and were compared with the primary groups targeted by the monk seals.

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 and K-W tests respectively. Effect of year on the subphotic fish data was tested using a K-W test on the fixed transect data from FFS. 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 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 employed to describe the linear association between two variables while controlling for the effects of a third.

The numerical density and size structure of coral trees in beds of the southern portion of the archipelago were plotted and compared with the coral beds of the northern archipelago using Mann-Whitney tests. 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 prey functional group (as defined in Chapter 2) that comprise the fish assemblage 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

General description of subphotic habitat

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 3.2. Some stations were on summits, such as Cross Seamount, whereas the 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 (Fig. 3.5).

Table 3.2. Number of pseudo replicates, mean depth, prevalent substrate type, relief type and coral type for each of the known coral beds. 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

* Includes pseudo replicates of 4 years of inter-annual fixed transects.
** Pink-R indicates *Corallium regale*.

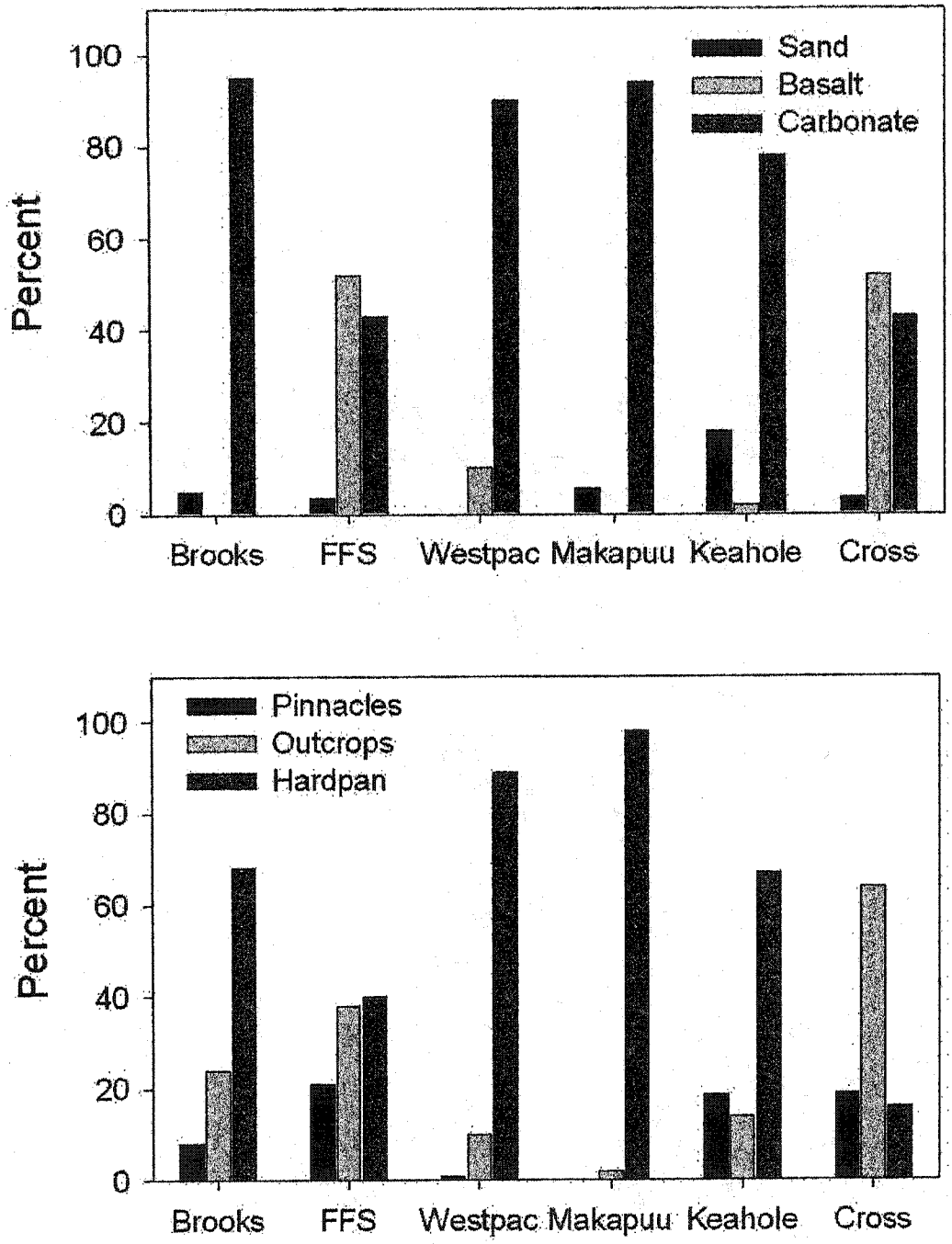


Figure 3.5. Percent of total survey data by substrate type (top) and relief type (bottom) for each of the stations.

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 3.2). Corals at all stations grew in discrete patches, referred to as "beds." 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)(Fig. 3.6). When a submersible transect first encountered a coral bed, the initial sightings of individual corals would quickly increase 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, $P<0.05$). Finally, the archival temperature recorders deployed for the years 2001 and 2002 at FFS and Cross Seamount detected temperatures that ranged from 7 to 13°C with mean annual temperatures at Cross Seamount on average 2°C cooler (Fig 3.7).

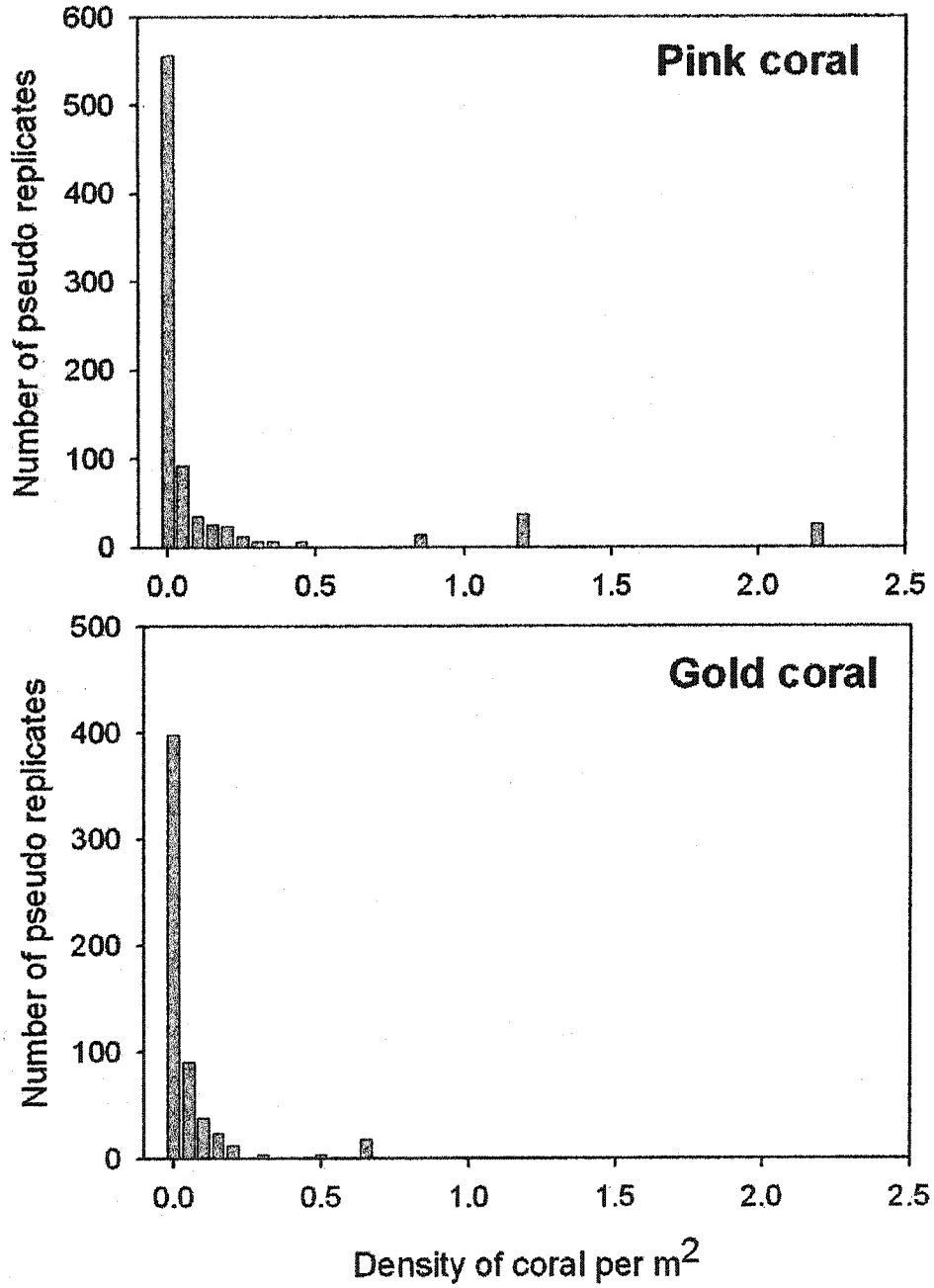


Figure 3.6. Number of pseudo replicates by density of coral with pink coral on the top and gold coral on the bottom.

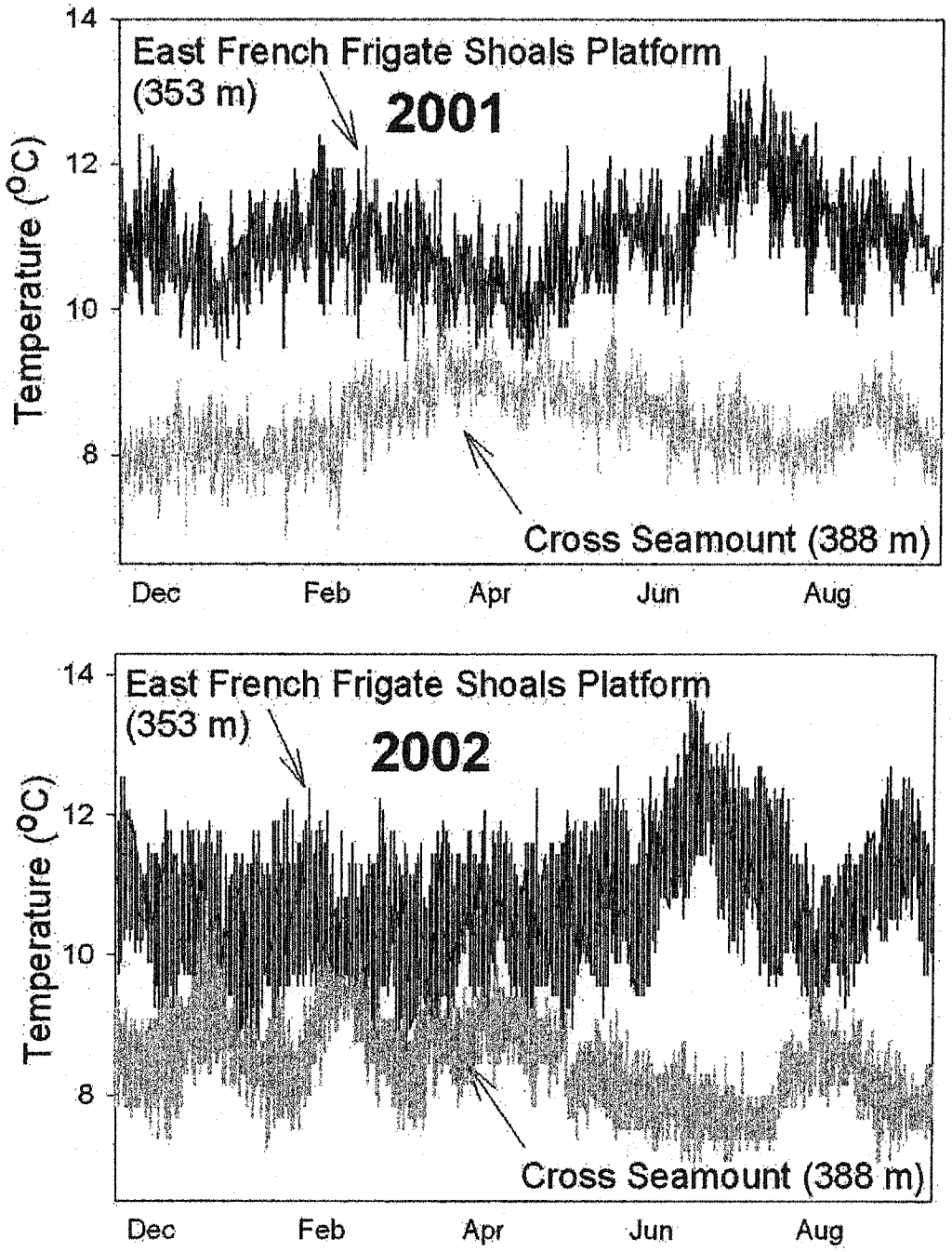


Figure 3.7. Plot of temperature profiles for 2001 and 2002 from recorders left at FFS and Cross Seamount. The 2001 recorders sampled 4 times a day and the 2002 recorders sampled 24 times a day.

Fish diversity, density, size and biomass around coral beds

The surveys for premium forage habitat counted and estimated the size of 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 appreciably change 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 taxa number of fish sampled and are listed in Table 3.3 (Fig. 3.8). 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. Segments used in the analysis were any that fell within the depth range at which gold and pink coral were found.

Documenting temporal change was beyond the scope of this work. An impractically large number of dives would be needed to assess temporal variability across the archipelago. Only at FFS was a repeat transect conducted (N=3 yrs), and it ran from the gold coral bed on the summit of the extension, across the terrace, and down the southern wall of the east FFS platform. This track covers segments of

Table 3.3. 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 functional group (BA=benthic ambush, BS=benthic searcher, BH=benthic hoverer, MH=midwater hoverer).

Rank	Taxa	Mean No.	Functional group
1	*Symphysanodon maunaloae*	56.1	BH
2	*Polymixia* spp.	5.6	BS
3	Congridae	2.9	BS
4	Scorpaenidae	2.0	BA
5	*Beryx* spp.	3.6	BS
6	Myctophidae	21.6	MH
7	*Hollardia goslinei*	1.8	BH
8	Epigonidae	12.2	BH
9	Moridae	1.5	BS
10	*Chloropthalmus proridens*	2.6	BA
11	*Antigonia* sp.	3.0	BH
12	*Chrionema chryseres*	2.5	BA
13	*Owstonia* sp.	2.2	BS
14	*Grammicolepis brachiusculus*	1.7	MH
15	*Grammatonotus* spp.	13.4	BH
16	Macrouridae	1.9	BS
17	*Ijimaia plicatellus*	2.2	BS
18	*Chaunax* spp.	1.2	BA
19	*Satyrichthys* spp.	1.9	BS
20	Synaphobranchidae	1.7	BS

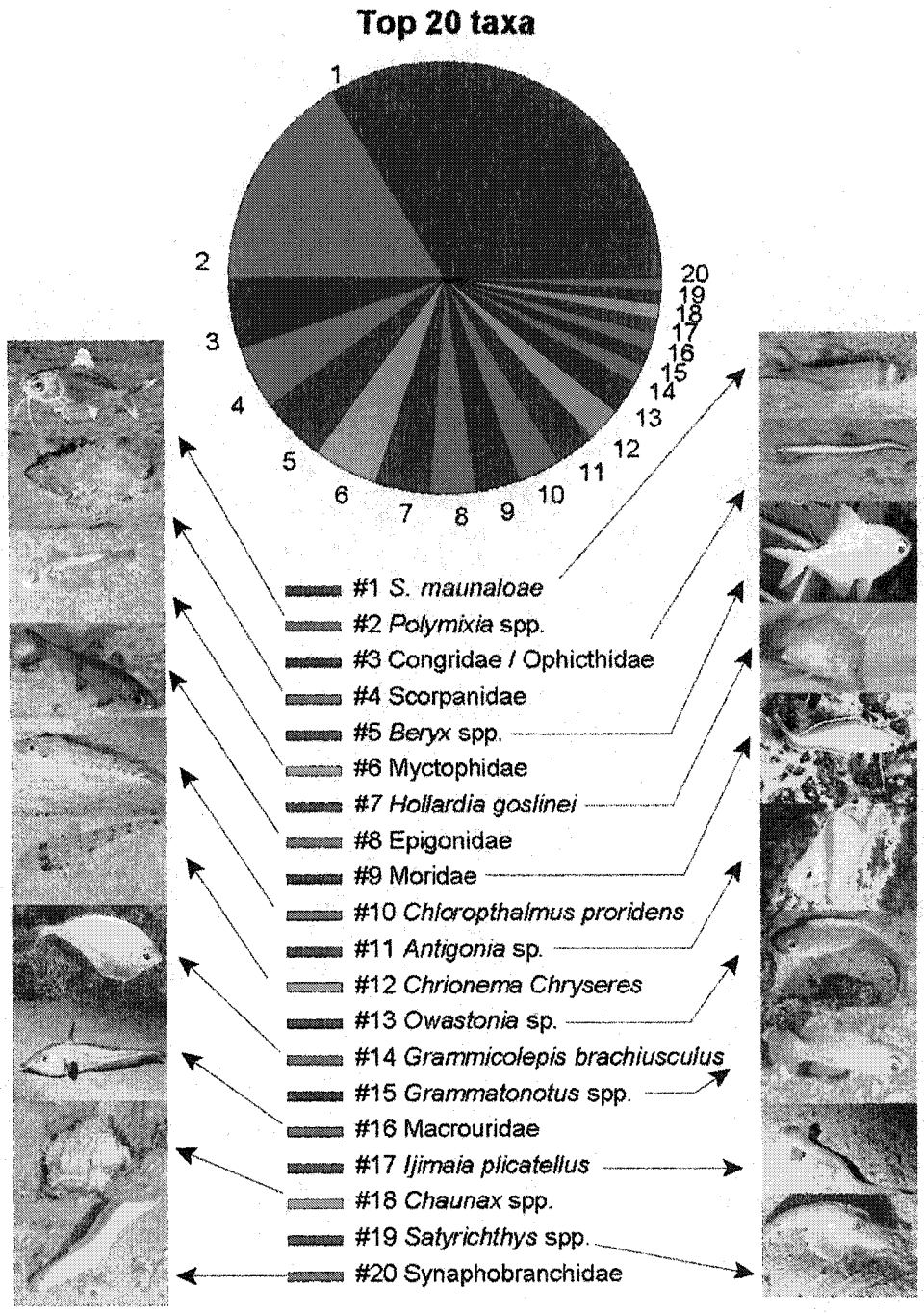


Figure 3.8 Overall numerical density of the top 20 taxa with their pictures. Only *Polymixia* sp., and Congridae/Ophicthidae have been reported from scat data.

bottom that are basalt, carbonate and manganese. Comparing data for 3 years (39 pseudo replicates) showed no significant difference in fish numerical density (K-W χ^2=0.668, df=2, P=0.72), body length (K-W, χ^2=0.274, df=2, P=0.872), or biomass density (K-W, χ^2=3.68, df=2, P=0.159).

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 *S. 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, χ^2=25.5 df=2 P<0.01) and fish size (KW, χ^2=9.1 df=2 P=0.01). Follow-up comparisons indicated that all differences were associated with pinnacle relief that significantly more fish were found around pinnacles (Tukey, Q= 5.0 & 3.5, P<0.05), and that 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 exclusively address 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, followup Spearman 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).

Functional groups comparison

The effect of corals on the numerical density of the seal prey functional groups was tested by comparing areas with and without corals. Areas with gold coral were found to have significantly more benthic hoverers (MW, Z= -4.03, P<0.001)(Fig. 3.9). However, again this finding lost significance when the FFS site was excluded (MW, Z= -1.4, P=0.14). The body lengths of functional groups 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 benthic ambush functional group (MW, Z= -2.8, P<0.01). Again this difference disappeared if the FFS station was dropped (MW, Z= -1.3, 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 functional categories differed significantly between sites with and without pink coral (MW, Z= -0.44 to -1.85, P=0.064 to 0.66). Figure 3.9 presents the means and standard deviation of the four functional groups in areas with and without coral.

Deepwater corals in the northern archipelago

The eight exploratory surveys established at the north end of the archipelago are represented in Figure 3.2. The slope between 350 and 500 m depth was considerably steeper at the northern end of the chain than at southern sites. Often the transect data were collected on steep faces of cliffs that dominated these depths. Regardless, dive sites were selected with a mixture of steep and sloped bottom to ensure a sample of

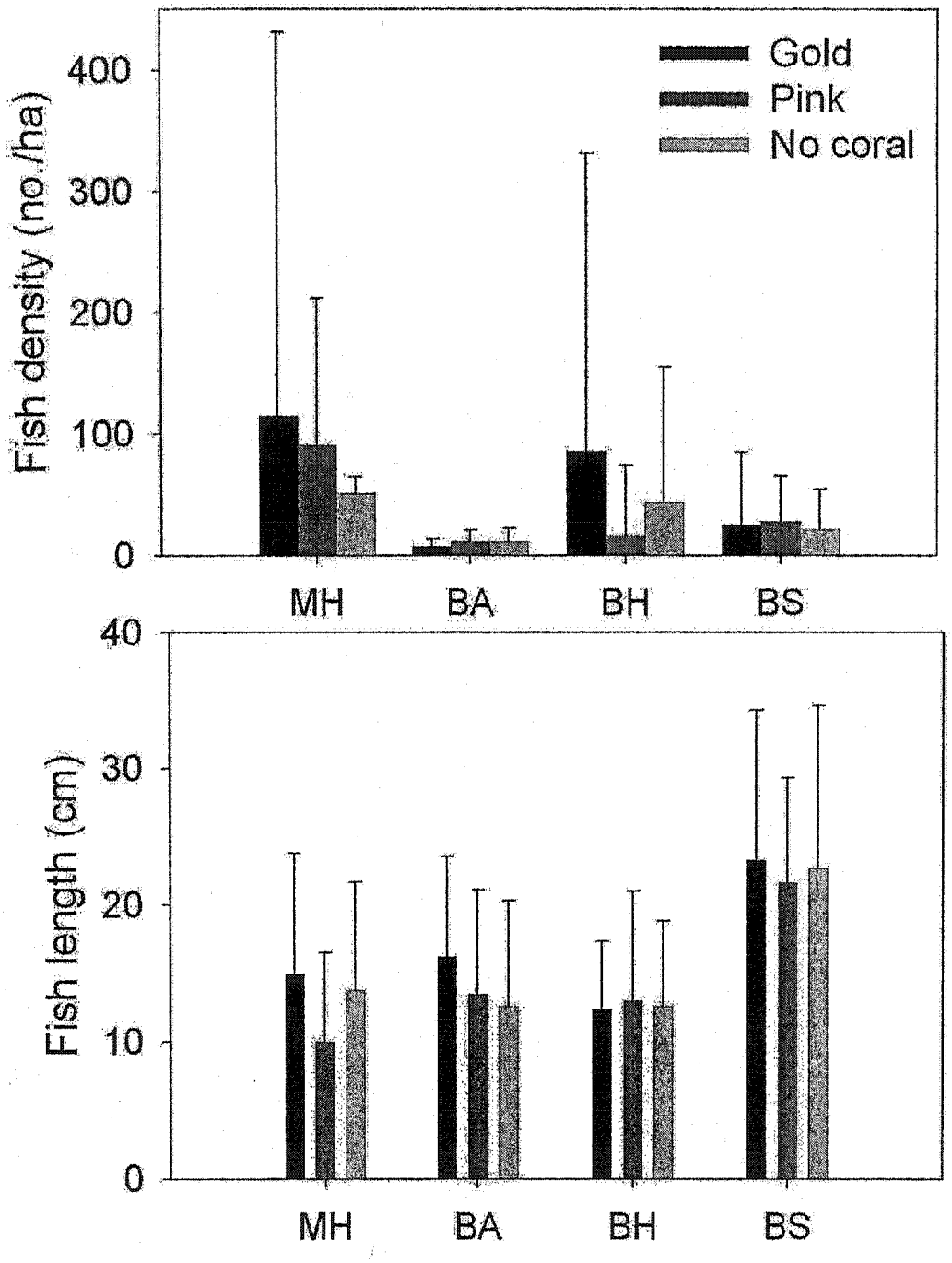


Figure 3.9. Mean numerical density (top) and body length (bottom) of fish data divided in to seal prey functional groups with values reported for sites with gold, pink and no coral (MH=midwater hoverer, BA=benthic ambush, BH=benthic hoverer, BS=benthic searcher). Error bars indicate standard deviation.

substrate and relief types roughly comparable to sites surveyed in the southern half of the archipelago. Since each site was only visited once, it was not possible to obtain a year-long temperature record for the northern region to compare with southern values. However, measurements from temperature profiles taken during each of the dives (Table 3.4) provide some limited comparison between stations. An interesting result from these data, together with values from the archival recorders at FFS and Cross Seamount, indicate colder waters at shallower depths at the southern extreme of the archipelago.

An estimated 25 linear kilometers (N=304 pseudo replicates) were surveyed on the exploratory dives at the 8 stations. This is a tiny fraction of the available habitat at these seamounts. Gold coral was found at East Northampton, West Northampton, Bank 8, Ladd Seamount and Nero Seamount. Gold coral at Ladd was limited to a single colony and Nero had a patch of only six corals. The density (MW, Z= -1.3, P=0.193) and median height (MW Z=-0.74, P=0.45) of gold coral at Northamptons and Bank 8 did not differ from corals in the southern part of the archipelago (Brooks, FFS, Cross, Keahole). Individual colonies of pink coral were seen at the exploratory stations but no "beds" comparable to those at Makapuu or WestPac Bank were identified. However, despite these observations, more recent survey work by others (October 2003 surveys by Baco-Taylor) has identified at least four new coral beds at the north end of the chain with gold, pink and red coral present.

Table 3.4. Temperature by depth for four stations throughout the Hawaiian Archipelago. FFS stands for French Frigate Shoals.

Temperature (°C)	Seamount 10	Bank 8	FFS	Keahole 2001
10	450	350	424	
9	530	400	465	310
8	575	500	510	415
7	600	540	574	440
6	650	591	630	500
5	690	650	700	595

Deepwater corals as shelter for monk seal prey

Using data from all stations surveyed archipelago-wide (N=1452 pseudo replicates), only 93 pseudo replicates documented fish using coral trees as shelter. These 286 fish represented 13 taxa are listed in Table 3.5. All these taxa were commonly seen using abiotic sources of benthic relief, so none are thought to be exclusively dependent on coral colonies. Almost all the taxa in the seal prey functional groups were benthic hoverers (>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 count of some of the same colonies on successive survey years. The median heights of colonies for survey segments with precious coral ranged from 5 to 180 cm for gold coral and 5 to 60 cm for pink coral (Fig 3.10). Most of the fish (73%) were seen with gold coral colonies.

Table 3.5. 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, and 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

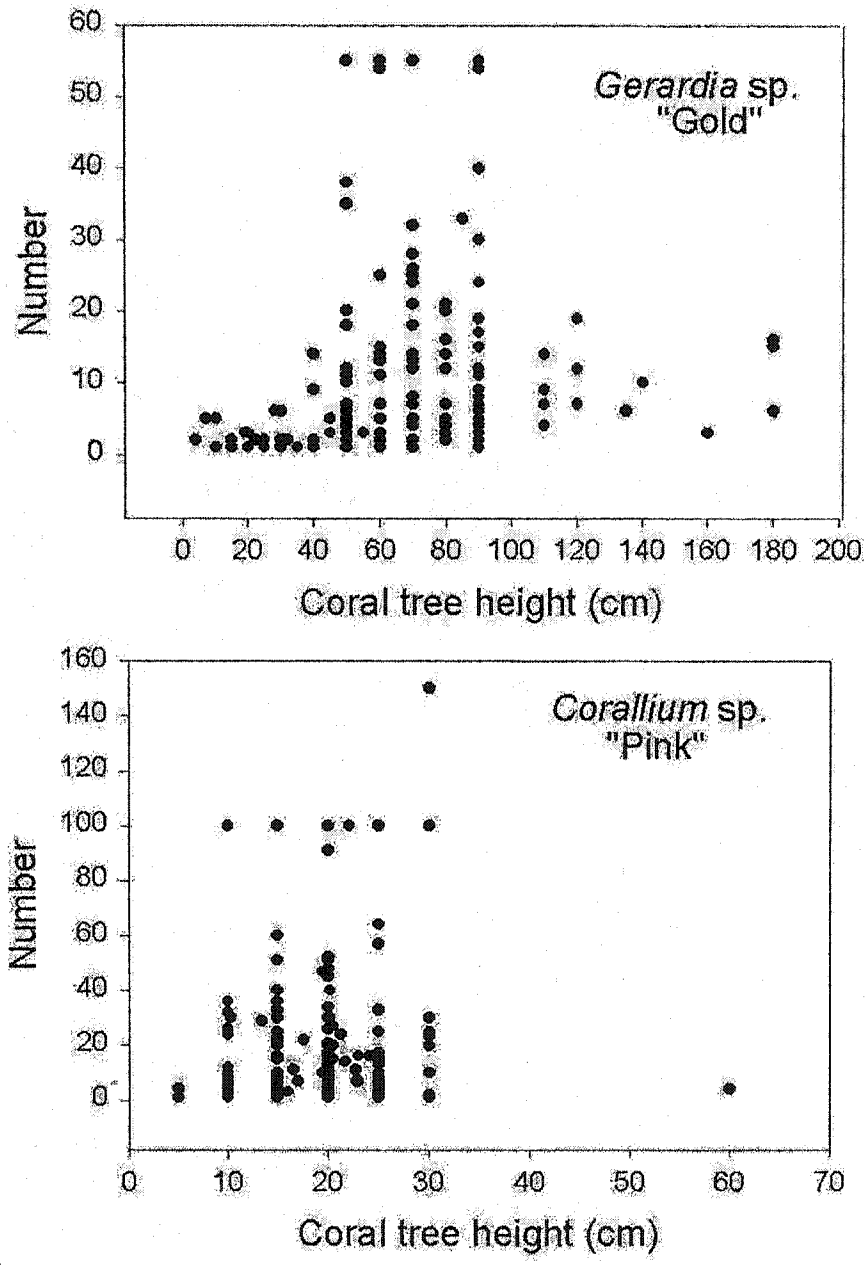


Figure 3.10. Median height of gold (top) and pink (bottom) coral trees found on surveys.

DISCUSSION

Subphotic realm

Substrate and relief

Little is known about deepwater corals. The two species examined here are species that are commercially sought as raw material for the jewelry trade. The patches they form provide unique habitat at subphotic depths where sources of high relief are often scarce. If these coral patches enhance the fish community relative to adjacent areas, then it is possible that seals are visiting them to exploit the concentrated prey and improve their foraging success. There were obvious differences between the substrate, relief type and corals at each of the stations (Table 3.2). 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 *C. regale* variety of pink coral. Although these habitat associations were for the most part consistent, coral success is also clearly related 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 (Grigg 1993). 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' success. 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 and lower speed flow than the more intense and perhaps multi-directional flow in which gold corals thrive. However, all this is speculation. Future work is planned to determine the water flow characteristics with which the two corals associate with.

Temperature

Based on the measurements from FFS and Cross Seamount temperature is relatively consistent at subphotic depths (300-500 m), varying no more than 3° C throughout the year. Similar data collected at a depth of 40 m in the FFS area indicates that temperatures at shallower depths fluctuate more than 5° C annually (Parrish and Boland, in press). The cooler temperatures documented at Cross Seamount could be attributed to the fact that it is more than 30 m deeper than the FFS site but, based on individual measurements taken from the submersible at all dive sites, the temperature never varied more than 3°C with a 30-m depth change (Table 3.4). These observations

suggest that the difference in temperature is a regional or latitudinal phenomenon. Temperature values from September dives at the northern summits of Seamount 10 and Bank 8 are closer to FFS than Keahole values. This similarity in temperature, together with the persistent year-round temperature difference between FFS and Cross Seamount, suggest regional, if not latitudinal, temperature differences. The variation in the temperature profile at Cross Seamount appears, annual whereas that at the FFS station looks monthly or tidal. It is unknown whether the difference in the pattern of the profiles at FFS and Cross Seamount relates to differences in regional oceanography (Seki et al. 2002) or is an effect of different summit morphology. Cross Seamount is a discrete peak rising from the sea floor, whereas the FFS station is an elongate platform extending out from the FFS Atoll complex.

Fish assemblage

Many of the logistic difficulties encountered when surveying fish at shallower depths were less troublesome in subphotic surveys. The general lack of bottom complexity (e.g. no coral matrix or algal meadows for concealment) and the absence of light meant that most fish were out in the open and easy to see with the submersible lights (especially since many of the fish are red). 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). Fish have been documented to move from surroundings to a single area around a source of shelter. 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 *S. 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.

Only in the past few years has work begun to assess the annual change in the abundance of Hawaiian subphotic fish populations, and these studies have focused on the commercially valuable deepwater snappers (Chris Kelley unpub. data). However, since all the fish surveyed are benthic/demersal associated, it is unlikely there will be any large

annual changes in their numbers, because the communities are confined to their respective slopes by the deep water that isolates the peaks of the Hawaiian ridge. Without any data on recruitment of deepwater fish communities, annual variability is assumed to be minimal. The only data available for the NWHI region are the three fixed transects at FFS, which showed no change between years.

Effect of coral on the aggregation of 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 why. 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, the data indicate greater fish numerical density 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 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 particulate, (detritus, zooplankton, etc.). 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.

Evaluation of fish data using seal prey functional groups showed significantly more benthic hoverers around gold coral. No other functional groups were associated with gold or pink coral. Benthic hoverers 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. Greater numbers of this functional group at the same sites as gold coral support the interpretation that greater numbers of fish co-occur with gold corals at sites with premium conditions (high relief and flow) but are not dependent on the corals.

Few studies have been done on fish associations with deepwater corals. In the Atlantic, Husebo et al. (2002) compared fish catches from conventional gear (longlines and gillnets) deployed at areas with coral beds (*Lophelia pertusa*) and at areas without coral. They reported significantly more *Sebastes marinus* (a benthic hoverer), and at least similar numbers of two other species. Larger body sizes were found in the corals beds but this difference was not statistically significant. They examined the fish stomach contents looking for prey that would be specific to the rock habitat of the coral bed and found none. Consequently they attributed the increase in *Sebastes marinus* to its use of

the corals' physical relief as shelter. Their results are consistent with the increased number of benthic hoverers observed in Hawaiian coral beds. Because the Husebo et al. (2002) study relied on fishing gear set in areas previously surveyed by an ROV, they were only able to account for habitat effects in a general sense. As with most deepwater fauna (Genin et al. 1992) *Lophelia pertusa* grows on rock outcrops and pinnacles and not in the mud flats that the authors report as the habitat surrounding the bed. Fish in the *Lophelia* bed, may be doing the same as Hawaii species, making use of the shelter of the rocky outcrops as much, if not more, than the corals. However, the contribution of *Lophelia* to the deepwater ecology differs from the pink and gold coral examined in this work. Unlike the Hawaii corals, *Lophelia* is a reef building coral forming high relief mounds of rubble that provide a matrix of interstitial spaces that is actively used by fish and invertebrates (Genin et al. 1992). Pink and gold coral only provide the relief by virtue of the height of their colony, and that relief is gone when they die.

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 re-surveying the fish community for a period of two 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 two 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 (in review) 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 deepwater corals interchangeably with abiotic relief sources with no significant difference.

In this analysis, two stations had fish abundances that were notably different from the other stations. FFS (gold coral bed) and WestPac (pink coral bed) supported much more fish than any of the other stations surveyed. The relevance of this will be considered in the regional analysis (Chapter 4).

Deepwater coral availability at the north end of the archipelago.

It is reasonable to assume that precious corals grow at the northern end of the chain. As discussed earlier, habitat, relief, and temperature are generally homogenous at subphotic depths (Genin et al., 1992). Species of *Gerardia* (Druffel et al. 1995) and *Corallium* (Abbiati et al. 1992) have been documented outside of the tropic water mass, suggesting that these organisms have wide temperature tolerance. Also, there were reports of illegal coral dredging on NWHI seamounts by Asian fleets in 1985 (Grigg 1993), which leads us to believe that coral beds were present at the north end of the archipelago.

Initial work using satellite telemetry (Stewart 1998) to study the movement of seals at the northernmost colonies revealed little or no diving to subphotic depths. This finding spurred the hypothesis that the lack of diving by seals in the north indicated fewer

coral beds in the region. However, at the time of this writing, more recent and comprehensive telemetry studies (Stewart 2004) have been conducted and have determined that subphotic diving is indeed a component of the seals' forging at northern colonies. Coral beds were identified in the exploratory surveys at the north end of the chain and their mean density and size were consistent with beds in the south. The most obvious differences among the beds was the steeper grade of the slope at northern stations. Finally, the recent documentation (Baco-Taylor pers comm. 2003) of four large coral beds at the northernmost extent of the archipelago indicates that habitat is suitable for these corals throughout the archipelago.

Deepwater corals as shelter for monk seal prey

Tall coral trees, most often gold coral, were used as shelter by some fish. Fish also used other genera of coral including *Callogorgia*, *Clyptiphora*, and *Leopathes*. Some of the same fish taxa seen sheltering in gold coral were seen using abiotic bottom topography for shelter. The original hypothesis that fish select gold coral trees as preferred shelter were inspired by anecdotal observations made in some submersible dives in the mid-eighties when large "balls" of eels were reported among the branches of gold coral trees. In the present study eels were seen infrequently in the trees, and rarely was there more than a single individual. Most often the fish was some type of benthic hoverer and the importance of this group as seal prey is largely unknown. At shallower depths, prey such as eels (benthic searchers), flounders, octopus (benthic ambush) are known to be targeted by seals (Goodman-Lowe 1998, Parrish et al. 2000) and it is

reasonable to expect that they would be taken at subphotic depths if encountered. The importance of benthic hoverers is less clear. At euphotic depth seals' have been documented to target benthic hoverers if they are away from shelter and exposed to capture. Benthic hoverers at subphotic depths should be relatively visible and slow enough for seals to catch with ease. Despite this, none of the species show up in the seal scat data (Goodman-Lowe 1998). This could be because they are not eaten, or because the subphotic sites are too far from the seals' haulout, and the prey passes through the seals, digestive system before it returns to the beach.

Intuitively it seems that more fish should be seen in the coral beds. However, this may be a preconceived notion derived from our familiarity with shallow fish assemblages and their strong association to reef structure. It is possible that some important ecological process was undetected by this study. For example, does the lack of eels mean there is no association with the corals, or could there have been a strong association, and could the foraging pressure of seals have reduced their populations to token numbers? This latter proposed scenario is not supported by surveys in the main Hawaiian Islands, where there are few foraging seals and still only small numbers of eels are seen. 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 would be undetected.

CONCLUSION

The range of substrate, relief and temperature was found to be relatively similar across all subphotic stations surveyed. Two stations, FFS and WestPac had fish populations well in excess of the other stations surveyed. The greater numerical density of the fish assemblage in the immediate area of gold coral beds could be attributed to high relief features that both gold coral and fish preferentially use. Heightened water flow, produced by these relief features, is thought to be an important variable in the colonization of coral and attraction of fish but this was not tested. Similarly, there was no detectable association of fish with pink coral. Exploratory surveys at the north end of the chain verified the presence of both coral types, which occurred in beds of comparable coral size and density. Benthic hoverers were the seal prey functional group that was most often found sheltering in the branches of coral trees (particularly gold coral). These taxa were also found sheltering in abiotic relief features of the bottom. So the corals serve as fish habitat, but no statistical association between the fish and corals could be found.

CHAPTER 4. REGIONAL PRODUCTIVITY

Hawaiian waters are relatively unproductive, but primary productivity increases at the north end of the island chain. Here the archipelago intersects with the southern subtropical front, which is the interface between the nutrient rich waters of the North Pacific and the impoverished water mass of central latitudes. Satellite remote sensing and ship-based oceanographic studies have documented the front extending across the North Pacific and seasonally oscillating north-south, encroaching to varying degrees on the archipelago (Polovina et al. 2001). Studies examining the survivorship of NWHI monk seals in relation to the front found that seals and their young were healthier at the more productive northern latitudes but faired poorly farther south. Based on the seal data and the remote-sensing data, Schmelzer (2000) proposed three productivity regions in the NWHI, with the highest productivity in the north and the lowest in the south. Studies of geographic patterns in lobster (Polovina et al. 1994), reef fish (DeMartini et al. 1996), and monk seals (Antonelis et al. 2003) have yet to effectively link the status of the seals and these potential seal prey with regional differences in oceanic productivity.

Attempts to survey prey abundance (e.g. counting reef fish) at FFS and Midway atolls have been inconclusive and possibly confounded by natural variability associated with the shallow marine systems. The on-site benthic primary productivity from corals and algae provides an important local contribution to supporting fish populations, which will make the effects of oceanic productivity hard to distinguish. The geomorphology of the different sites can change the degree to which oceanic productivity influences a fish community. For example, a fish community on a 40-m bank summit is completely

exposed to the open ocean, and thus is more apt to be influenced by oceanic productivity than a fish community in an atoll whose relatively stable lagoon waters are buffered from external ocean conditions. This work attempts to identify a link between fish populations and oceanic productivity by conducting comparative analysis of fish productivity at subphotic depths in the three regions defined by Schmelzer. Given that subphotic ecosystems are dependent on the organic rain from the photic zone above, it is expected that oceanic regions of high primary productivity will support more fish biomass density than low productivity oceanic regions. To evaluate Schmelzer's three biogeographic regions two hypotheses will be tested.

1) The organic fraction of sediment collected at subphotic depths is higher in areas of high oceanic productivity.

2) The subphotic (and presumably shallower ecological subsystems) at the north end of the archipelago support more prey (greater numerical density, body length, or biomass density) than the subphotic zone around FFS.

3) Fish of subphotic locations will be negatively correlated with the proximity and population sizes of euphotic predators.

METHODS

Submersible survey methodology

As described in Chapter 3, the subphotic data were collected in a series of submersible dives (Pisces V, *Pisces IV* and *RCV-150*) focused on surveying depths between 300 and 500 m. In total, 11 dive stations were distributed across the NWHI with representation in each of the three regions to be compared. The locations of the stations in relation to the three biogeographical regions (as defined by Schmelzer) to be examined are presented in Figure 4.1. The methodology of surveying from the submersible was detailed in Chapter 3 but is briefly reviewed here.

The author was the chief scientist for all these dives. Whenever possible, four transects, 350 m, 380 m, 410 m, 450 m were run parallel to the contour. However, the physiography of the slope varied considerably and often required modification of transects within this depth range. The submersibles (*Pisces V*, *Pisces IV*) were three - person submersibles with the pilot situated in the center an observer on either side. As the sub cruised a meter above the bottom each person can see a tract of bottom (est. area 55 m^2) through view ports directed diagonally forward and down. The cumulative view from the three view ports provides an effective illuminated survey area of 120 m^2. A video camera on each side of the submersible operates continuously and the edited video feed from the cameras is recorded on a video log throughout the dive. The robot sub *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. Its field of view was estimated at 45 m^2.

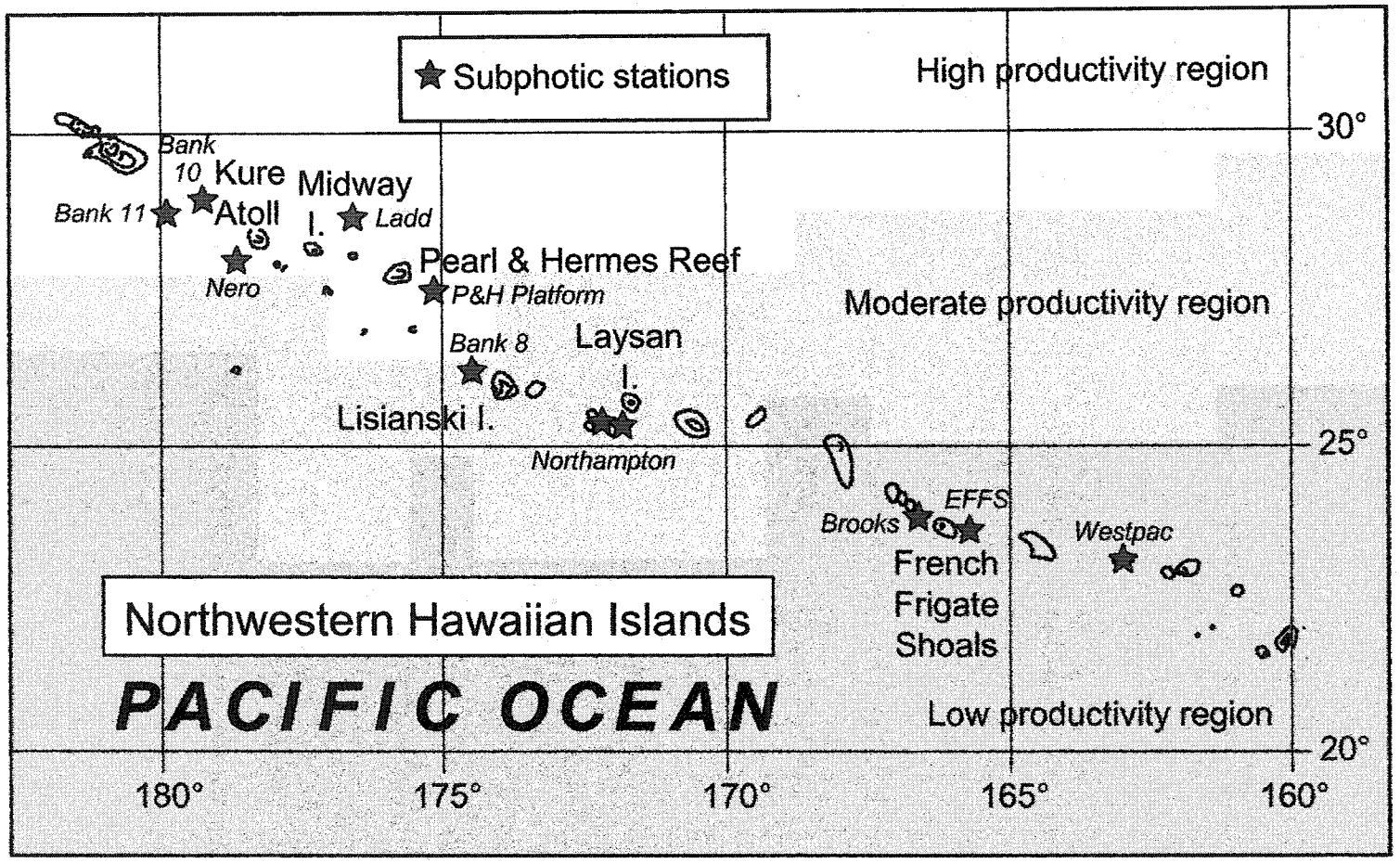


Figure 4.1. Locations of subphotic survey stations in the NWHI. The three productivity regions generated from satellite oceanography are denoted with different degrees of shading.

Taxa (fish and corals) were identified to genus or species, and counts and fish lengths/coral heights were recorded at 5 min intervals to obtain numerical density and size structure information. The 5 min survey segments hereinafter referred to as "pseudo replicates" represent a cumulative area of 3600 m^2 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 heights of corals. Substrate type and scale of benthic relief were recorded using the same categories specified in Chapter 3, to account for any effects of habitat in the comparison of the three regions.

Hypothesis 4.1 - Organic fraction in sediment

Sediment samples were collected at stations throughout the NWHI to measure the organic fraction at each station and see if its pattern is concordant with surface productivity patterns. Sediment was collected using self sealing bottles that were pushed into the sand using the submersible's manipulator. Pools of sand on seamount summits were the ideal sample for comparison because there is no alluvial transport of detritus to those areas from shallower photic depths. In cases where the summits of dive sites extended up into the photic layer, an attempt was made to collect samples in areas isolated from alluvial transport such as those found on a spur sticking out from the slope of the seamount. The logistics associated with submersible collections limited collections to two samples per station. Whenever possible sediment was collected between 350 and 500 m depths. The fraction of organic matter in all samples was estimated using the loss on ignition (LOI) technique (Johnson 1974, Rhoads 1974, Heiri

et al. 2001). Samples were dried at 105° C for 24 hours and then sieved to standardize particle size between 500 and 1000 microns. Five grams of the sifted material was placed in a crucible and allowed to stand in a desicator for 20 min. Sample mass was determined and then exposed to burn of 450° C for 16 h. The sample was then removed, allowed to sit in the desicator for 60 min, and re-massed. The organic data were then compared among Schmelzer's three productivity regions derived from satellite remote sensing. Comparisons were also made using measurements of primary productivity, based on density of chloropigment derived from a time series of water column casts that were collected from a ship running a north-south transect perpendicular to the subtropical front (Seki et al. 2002). The greatest density of chloropigment is stratified well below the surface in low latitudes, and thus is poorly represented by satellite imagery data. Using the ship transect data improves the resolution of the regional productivity estimate. Table 4.1 details the chlorophyll maximum density values used in these comparisons.

Hypothesis 4.2 - Fish community differences

Fish surveys were made at multiple stations in each of the three regions, with the expectation that regions of higher productivity would support more fish biomass density than the low productivity region surrounding FFS. Fish too large to be considered seal prey, including sharks, jacks, rays, and large bodied snappers, were excluded from the analysis. Except for eels, all fish longer than 40 cm (the maximum size of prey seen handled by adult male seals) were excluded. This comprised less than 1% of the fish surveyed. Fish data (body size, numerical density and biomass density) from sites

Table 4.1. Mean productivity values for ship-based oceanographic transect data (Apr-May 1997) reported by Seki et al. (2002). For each station, the latitude, density of primary productivity layer (chloropigment mg m^{-3}), layer thickness and depth are listed.

Region	Survey station	Latitude (Dec. degrees)	Chloropigment (mg/m^3)	Thickness of layer (m)	Depth of layer (m)
South	WestPac Bank	23.25	0.20	30-50	100
	East FFS	24.00	0.20	30-50	100
	Brooks	24.00	0.20	30-50	100
Central	E. Northampton	25.33	0.20	30-50	100
	W. Northampton	25.41	0.20	30-50	100
	Bank 8	26.16	0.30	30-50	100
North	Pearl & Hermes	27.50	0.40	50	75
	Nero	27.98	0.40	50	70
	Ladd	28.50	0.40	50	75
	Bank 11	28.88	0.40	50	70
	Bank 10	28.96	0.50	50	70

surveyed in the northern region (Bank 10, 11, Nero and Ladd), central region (east Northampton, west Northampton and Bank 8), and southern region (Brooks Bank, FFS, and WestPac Bank) were compared. Concerns about confounding effects from biogeographic differences between the communities of different stations prompted a series of size comparisons with taxa known to occur throughout the NWHI. Finally the fish were reclassified by habitat and motility guilds into the seal prey functional groups and compared between the three productivity regions. The four functional groups used were benthic ambush, benthic searcher, benthic hoverer and midwater hoverer.

Hypothesis 4.3 - Connectivity with predator populations

The numerical density, body size and biomass density of fish were considered in relation to the distance to populations of euphotic predators that might visit the subphotic stations to feed. Seal predation pressure was represented using the minimum distance to the closest seal colonies and the number of seals' at the colonies. Seals are not the only apex predators from the euphotic layer that feed on subphotic fish communities. Large jacks such as kahala (*Seriola dumerili*) were occasionally observed foraging at these depths. The amount of predation by these predators at a station is likely to vary with the distance of the station from a euphotic fish community and whether there is a continuum of bottom habitat, or "bridge" between shallow reefs and the subphotic station for predators to traverse. Stations that are topographically isolated from shallow euphotic communities will probably get less visitation by euphotic predators. Three measures of connectivity will be employed, and they are conceptually diagramed in Figure 4.2. For

the first measure, the linear distance (thin solid line) to the closest benthic habitat in euphotic depths was used. In this case, the three example stations in Figure 4.2 are all measured in relation to the same spot. Had the host pinnacle for station 2 and 3 extended into euphotic depths, their distances would have been much shorter. The second measure uses the summit depth of the pinnacle that hosts the subphotic station. Figure 4.2 indicates this point with dotted lines. In some cases, the host pinnacle extended into euphotic depths (station 1), and in other cases, the summit was subphotic (stations 2 & 3). The presumption is that station 1 gets greater visitation from euphotic predators than stations 2 and 3 because it is closer to the euphotic community and is connected by a habitat bridge. The third measure uses the distance to the nearest seal colony (thick solid line). In this case, the example station 1, 2, and 3 are all measured relative to the same point. The three measures and the seal populations of the subcolonies were then used together in an attempt to explain differences in subphotic fish assemblages. National Ocean Survey charts and SEABEAM maps were used to obtain linear distances and summit depths of stations. Table 4.2 lists the values used in the analysis.

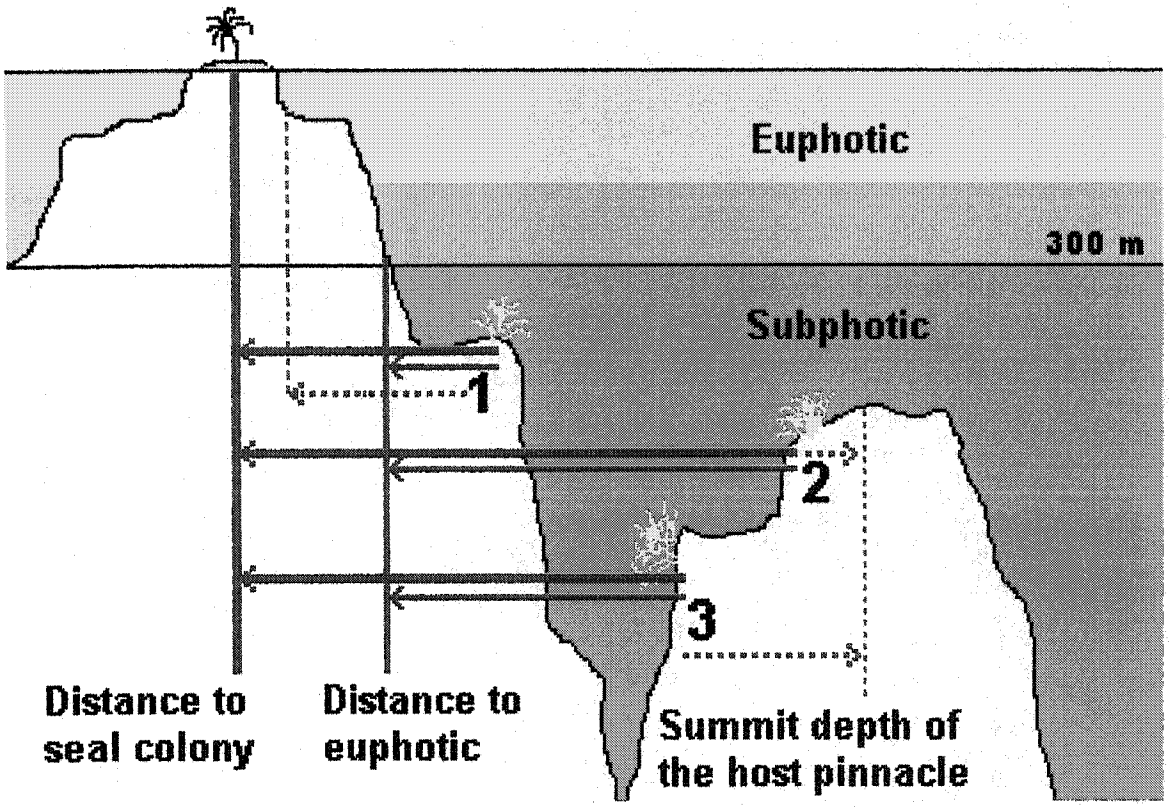


Figure 4.2. Diagram of the three measures used in the predation pressure analysis; distance to seal colony (thick line), horizontal distance to euphotic habitat (thin line), and summit depth of host pinnacle (dotted line). The numbers are hypothetical stations.

Table 4.2. Values for each survey station used in predation pressure analysis. Included are nearby seal colony population, distance to seal colony, distance to euphotic habitat and host summit depth.

Region	Survey station	Latitude (decimal)	Seal Pressure			Euphotic Pressure	
			Population of adjacent colonies		Distance (km)	Distance to euphotic habitat (km)	Host summit depth (m)
South	WestPac Bank	23.25	Nihoa	20	83	37	200
			Necker	18	204		
	East FFS	24.00	Necker	18	83	74	350
			FFS	342	63		
	Brooks	24.00	FFS	342	37	3	80
			Laysan	315	555		
Central	E. Northampt.	25.33	Laysan	315	42	1	35
			Lisi.	204	194		
	W. Northampt.	25.41	Laysan	315	55	1	35
			Lisi.	204	166		
	Bank 8	26.16	Lisi.	204	56	1	55
			P&H	239	222		
North	Pearl & Herm.	27.50	P&H	239	46	1	109
			Mid.	71	83		
	Ladd	28.50	P&H	239	101	1	64
			Mid.	71	46		
	Nero	27.98	Mid.	71	64	1	75
			Kure	129	74		
	Bank 10	28.96	Mid.	71	166	1	194
			Kure	129	111		
	Bank 11	28.88	Mid.	71	259	1	186
			Kure	129	75		

Analysis

Differences in organic matter and fish data were evaluated for the three productivity regions using a K-W test. For this analysis, the sample size permitted the detection of medium effect size (f=0.20) at a power of 0.80 with a significance of 0.01. Spearman correlations were used to assess the strength of association between organic data, chlorophyll data, fish data, and euphotic predators. Because there was no nonparametric alternative, fish data, chlorophyll data, and indices of predation pressure were assessed together for all NWHI stations in a linear backward regression. For correlation and regression statistics the sample permitted detection of small effects (f^2=0.02) at a power of 0.80 with a significance of 0.01. This analysis was then rerun pooling all pseudo replicates into 11 grand means representing each of the subphotic survey stations. For all regressions the adjusted R^2 was reported. Medians were used for all graphical representation of fish data except for the parametric regression which used means.

RESULTS

Organic fraction of sediment

The loss on ignition (LOI) analysis of the organic fraction of sediment samples (N=20) varied between 0.6 and 2.3 % . The only samples collected on a summit were at FFS, the rest of the samples collected at other stations were taken from the slope. No relationship was evident between measured organic values and the three Schmelzer's regions (KW χ^2=5.6 P=0.061) despite good correspondence of the three regions with the density of the chlorophyll layer (r_s=0.65 P<0.01). Finally, there was no relationship between organic values and the chlorophyll density data (r_s= 0.11 P=0.482)(Fig 4.3). Reasons for the lack of correlation are covered in the discussion section.

Fish community differences

A total of 887 psuedo replicates (the 5 min survey segments) were collected from all stations pooled. Samples sizes ranged from 25 pseudo replicates at the most remote stations to 287 at stations with multiple dives. These surveys covered a cumulative distance of 266 linear km (~319 ha). Most of the pseudo replicates were in the southern region (N=541), which was close enough to Honolulu to be sampled multiple times. The central region (N=166) and the northern region (N=188) had roughly equal numbers of pseudo replicates. Generally, fish numerical densities were low and variable. Numerical density, body size and biomass density of NWHI stations all differed significantly among the three productivity regions (Table 4.3). Median body sizes of fish in the northern and southern regions were indistinguishable, whereas fish in the central region were

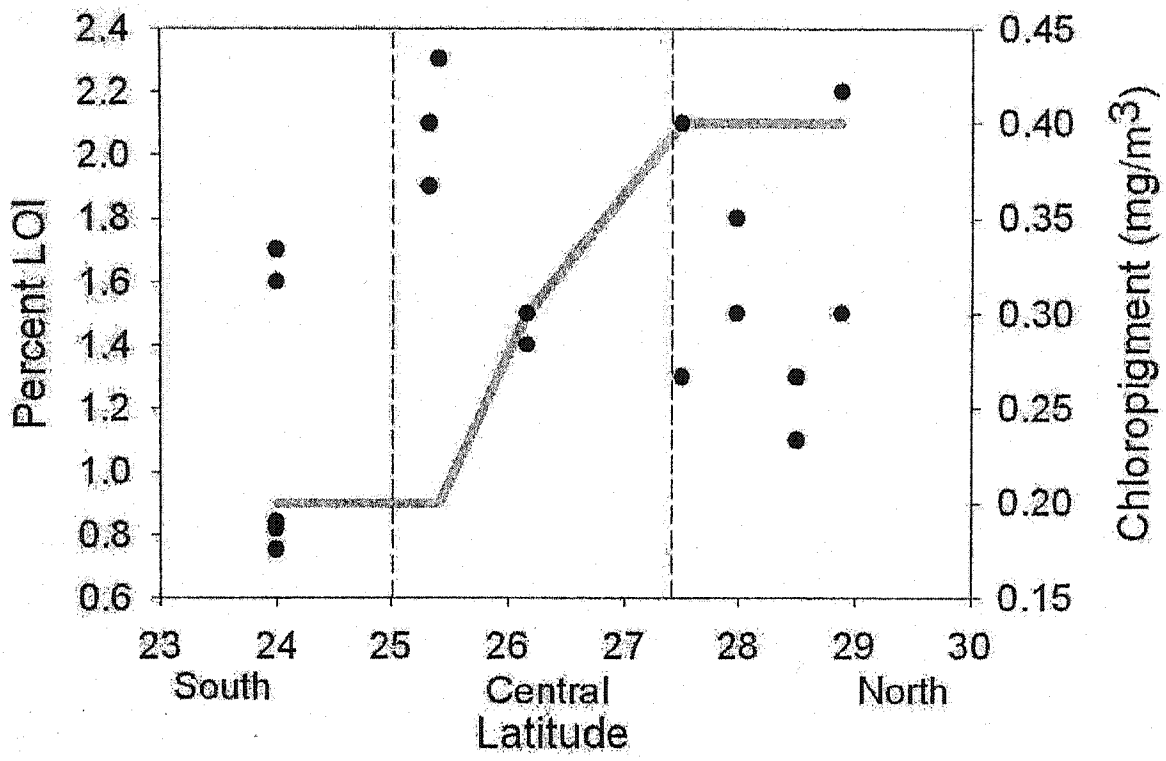


Figure 4.3. Plot of the percent organic fraction (LOI) in sediment by latitude (points) with the areas of the three productivity regions separated by dotted lines. Also plotted is the density of the chlorophyll maximum collected from ship transects (gray line). There are no obvious relationships between the different data types.

Table 4.3. Kruskal-Wallis values for fish numerical density, size and biomass density. Independent *post hoc* comparisons (0.05 threshold) indicate greater fish numbers in the central and northern regions, smaller fish in the central region and highest biomass density in the northern region.

Variable	Chi Square	*df*	P	Tukey *Post hoc* differences
Fish numbers	38.2	2	<0.001	north, central > south
Fish size	54.1	2	<0.001	north, south > central
Fish biomass	20.6	2	<0.001	north > central, south

significantly smaller (Fig 4.4). Fish numerical density in the northern and central regions were significantly greater than in the southern region (Fig 4.4). Finally biomass density of the northern region was statistically significantly greater than in the central and southern regions (Fig 4.5).

Comparing the chlorophyll values to the fish data, significant but weak associations with fish numerical density (r_s=0.20, P<0.01) and fish biomass density (r_s=0.20, P<0.01) were evident. No association was evident with fish body size. Fish taxa varied in abundance throughout the archipelago, and differences in their body shapes might confound attempts to detect patterns in the sizes of fish between the three regions. Table 4.4 lists some examples of taxa that exhibit clear biogeographic patterns and other taxa that do not. To isolate the effects of varying taxa between stations, body size of fishes that were present in each of the three regions was used with chlorophyll density in a correlation analysis. *Symphysanodon maunaloae* (r_s=0.48 P<0.01), *Laemonema rhodochir* (r_s=0.11 P<.01), *Antigonia eos* (r_s=0.30 P<0.01), and *Epigonus* sp. (r_s=0.52 P<0.01) all exhibited weakly significant associations with chlorophyll. Plots of body

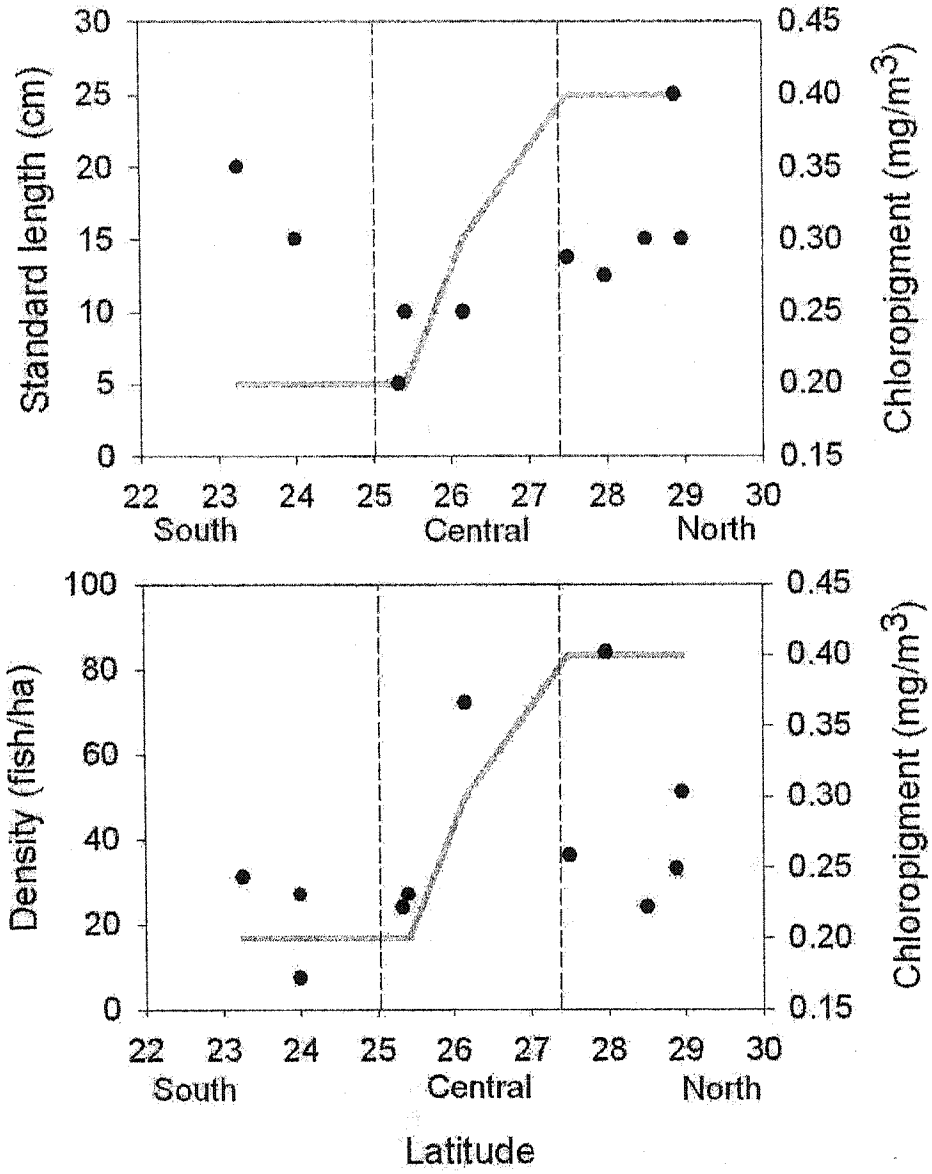


Figure 4.4. Fish body length (top) and numerical density (bottom) plotted by latitude with the three productivity regions (dotted lines) and density of chlorophyll (gray line) indicated for comparison. Significantly smaller fish are evident in the central region, and the two northern regions have more fish than the southern region

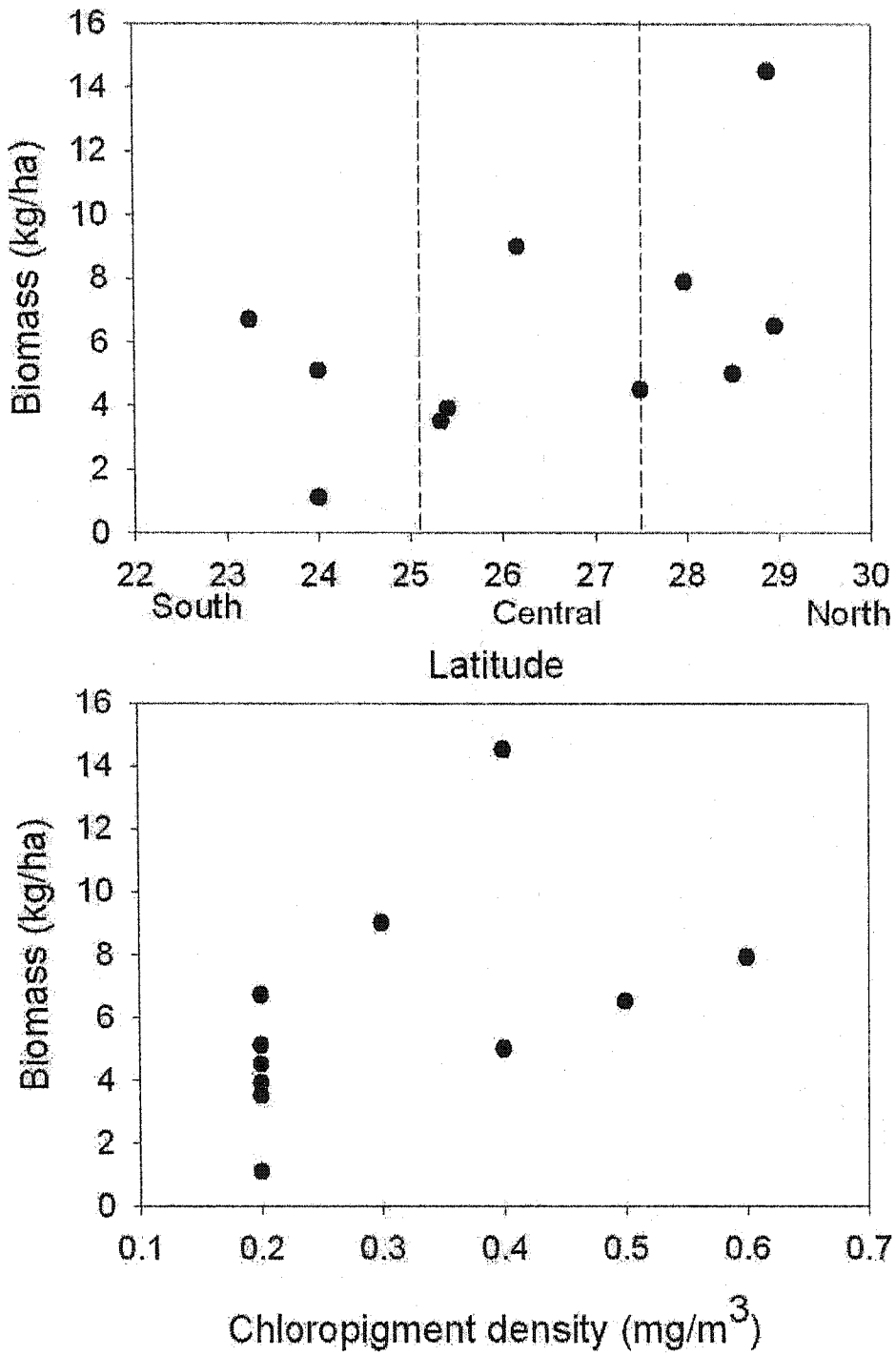


Figure 4.5. Top- Fish biomass density plotted by latitude and the three productivity regions showing at most weak agreement with the regions. Bottom-Biomass density plotted with chlorophyll density exhibiting, a diffuse relationship.

Table 4.4. List of the14 taxa that were represented across the three regions (vertical dotted lines denote the regions). Values are the decimal fraction of the total fish community at the station. No value indicates that the taxon was not observed on the surveys. Taxa highlighted in bold had fairly even representation across the archipelago and were used for the taxa specific size structure analysis.

Taxa	Bank 11	Bank 10	Ladd	Nero	P&H	Bank 8	W. Namp	E.Namp	Brooks	FFS	WestPac
Grammicolepis brachiusulus		0.16			0.06	0.45	0.3		0.02	0.01	0.01
Symphysanodon maunaloae	**0.33**	**0.47**	**0.18**	**0.35**	**0.21**	**0.02**	**0.11**	**0.75**	**0.02**	**0.67**	**0.01**
Polymixia sp.	0.01		0.01	0.01		0.01	0.01		0.04	0.03	0.58
***Epigonus* sp.**	**0.03**	**0.03**	**0.42**	**0.27**	**0.31**	**0.4**	**0.47**	**0.12**	**0.04**	**0.02**	**<0.01**
Pseudopentaceros wheeleri	0.13	0.04	0.01	<0.01							<0.01
Glossanodon struhsakeri	0.05			<0.01	0.05	<0.01	<0.01		0.12	0.01	0.01
Zenopsis nebulosus	0.01	0.11	0.05	<0.01		0.08				<0.01	
Antigonia eos	**0.01**	**<0.01**	**0.01**	**<0.01**		**0.01**		**<0.01**	**<0.01**	**0.03**	**0.09**
Beryx decadactylus	0.01		0.01		0.01	<0.01	<0.01		0.07		0.02
Ijimaia plicatellus				<0.01		<0.01			0.06	<0.01	0.01
Hollardia goslinei						0.01	0.01		0.04	<0.01	0.04
Laemonema rhodochir	**0.01**	**0.02**	**0.02**	**<0.01**		**<0.01**	**0.01**		**0.02**	**0.04**	**0.04**
Meadia abyssalis		0.02		<0.01				<0.01	0.01	<0.01	<0.01
G. macrophthalmus	0.05		0.02	0.04		<0.01			<0.01	<0.01	

size of these species by latitude are presented in Figure 4.6. Despite the statistically significant associations, the regional trends in these plots vary quite a bit, and their significance is probably an artifact of the large sample size. *Epigonus* sp. best exhibits a trend of increasing size to the north where productivity is higher. But the size of *Laemonema rhodochir*, *Antigonia eos* and *Symphysanodon maunaloae* seems relatively constant across the three regions. Dips in this size structure were evident in the central region for *Laemonema rhodochir* and *Symphysanodon maunaloae*. Finally two of the taxa (*Laemonema rhodochir, Antigonia eos)* were not seen at all at Pearl and Hermes (latitude 27.5) and Nero (latitude 28) stations and *Antigonia eos* was missing from the Brook's Bank station (latitude 24).

Dividing the fish community into the four seal prey functional groups revealed benthic hoverers as the dominant group for numerical and biomass density in all three regions (Fig. 4.7). The central region had an exceptionally large fraction of benthic hoverers with a corresponding reduction in the benthic ambush and benthic searcher categories. This difference in the fish assemblage may reflect habitat differences. However the fraction of substrate and relief recorded on these surveys did not indicate any pattern that would explain a spike of benthic hoverers in the central region. The two obvious habitat trends are the dominance of carbonate substrate across all regions and increasingly steep relief to the north (Fig. 4.8). If steep relief were most extensive in the central region, then perhaps the abundance of the benthic hoverers there could be attributed to habitat. Based on actual habitat data , no explanation for the different composition of prey functional groups in the central region is evident.

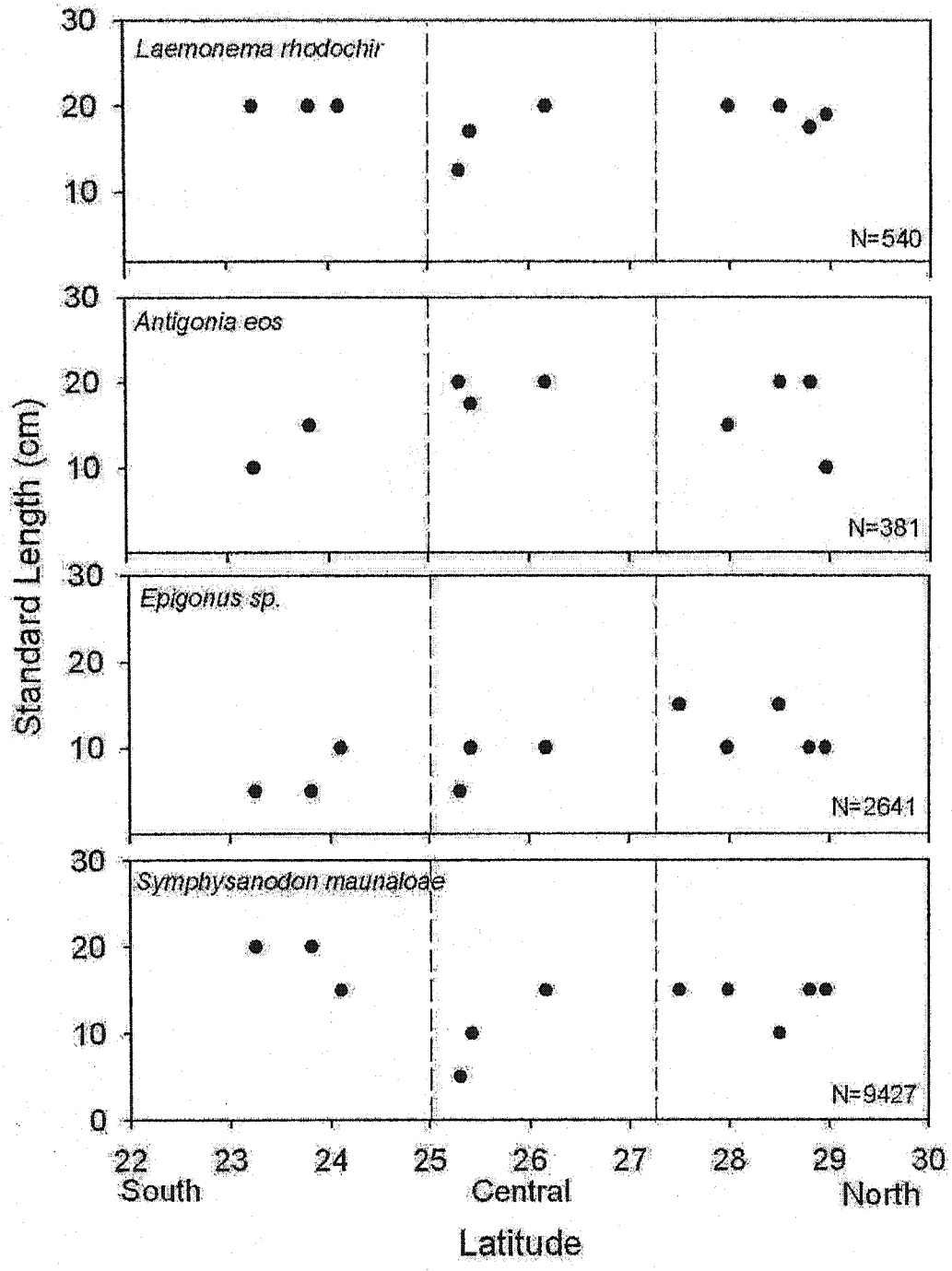


Figure 4.6. Plots of fish body size by latitude for four fish taxa that occur in each of the 3 productivity regions. The three regions are denoted with dotted lines, and the sample sizes of fishes are indicated in the lower right corner of each plot.

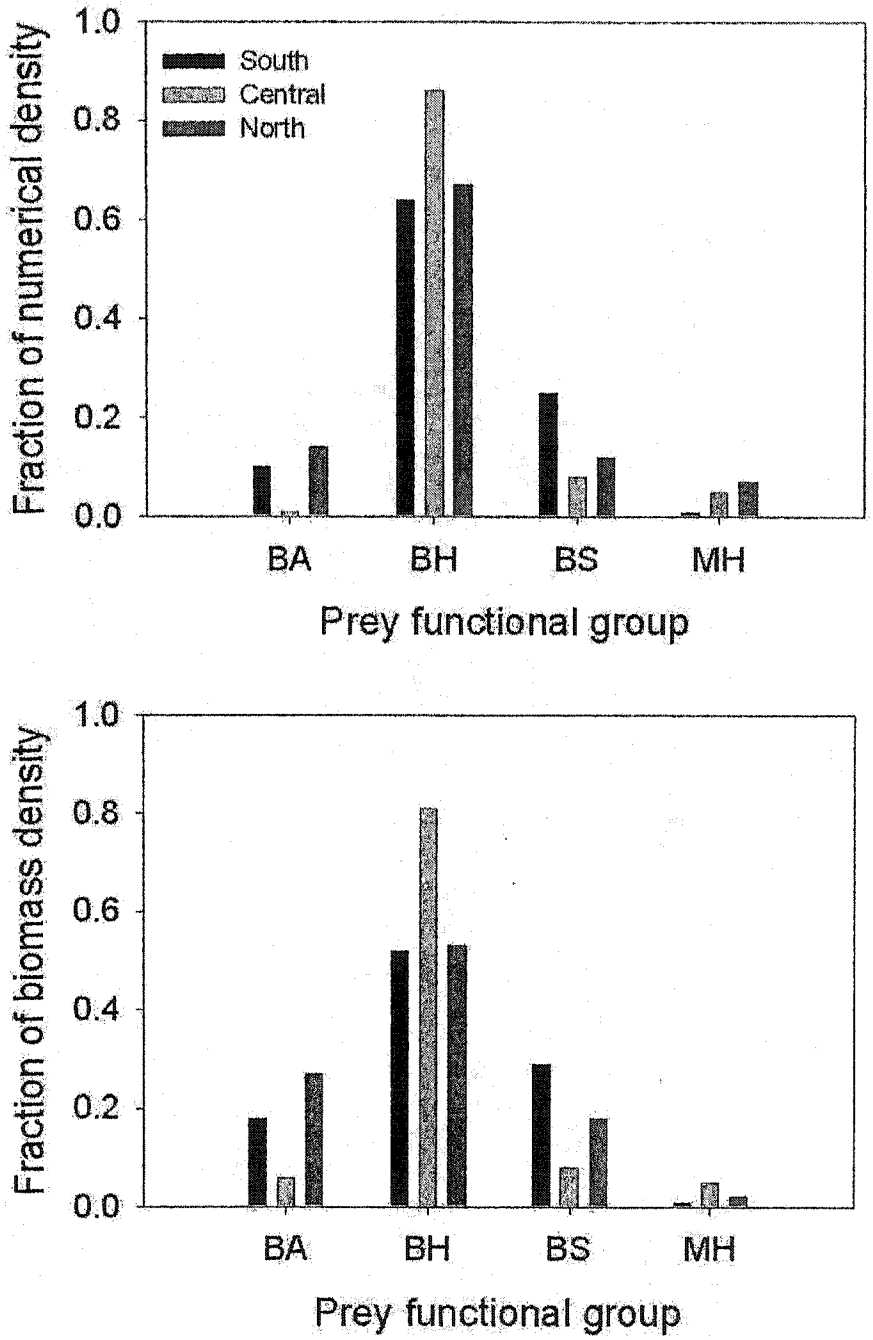


Figure 4.7. Proportion of fish numerical and biomass density by the four seal prey functional groups for each productivity region (BA=benthic ambush predator, BH=benthic hoverer, BS=benthic searcher, MH= midwater hoverer). A higher proportion of benthic hoverers is evident in the central region.

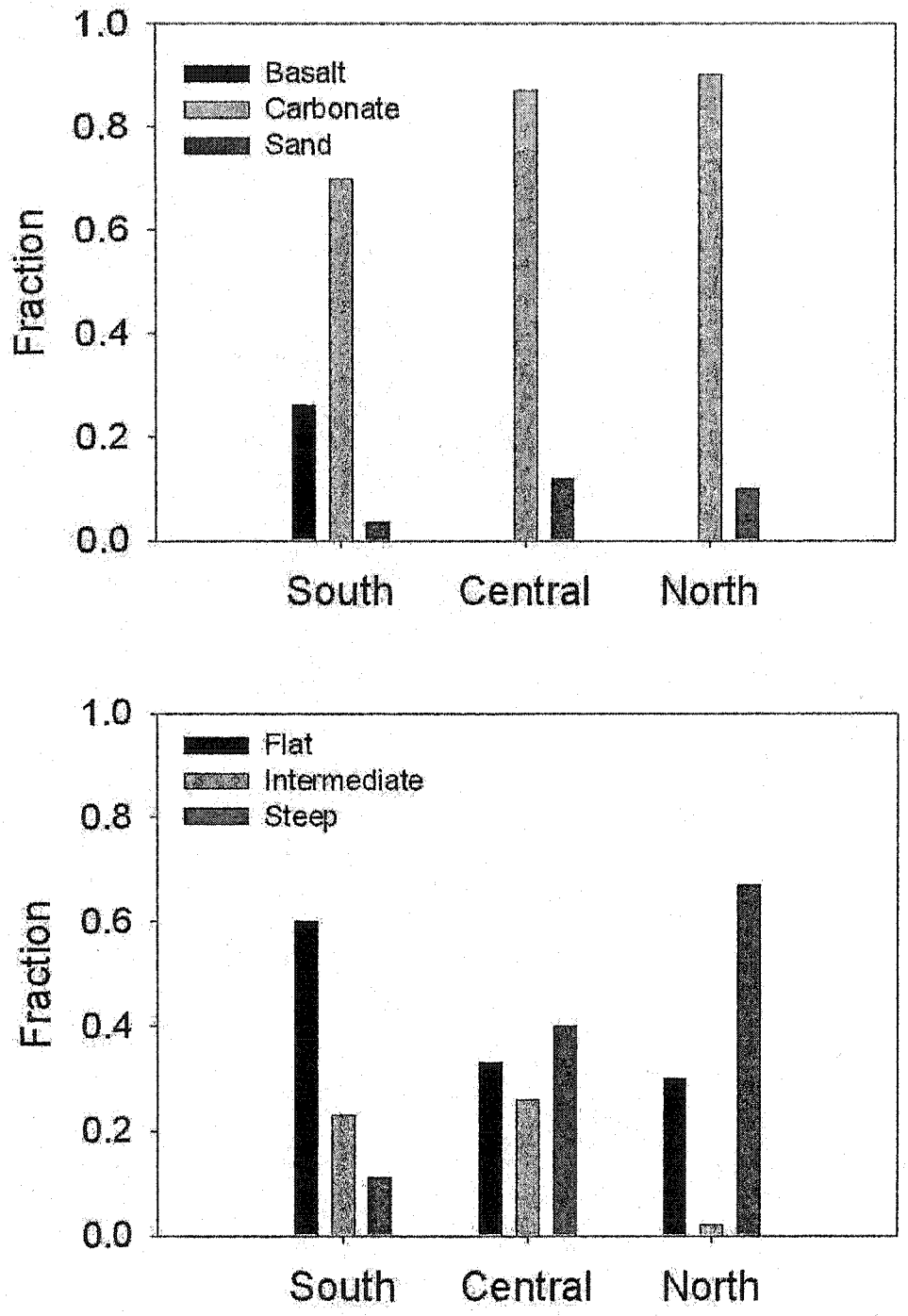


Figure 4.8 Proportion of habitat type (top-substrate type, bottom-relief type) for the three productivity regions. Substrate is primarily carbonate across all regions, and bottom relief becomes increasingly steep to the north

Connectivity with predator populations

All four indices of euphotic predation pressure were significantly but weakly correlated with some of the fish variables. The specific values are presented in a Spearman correlation matrix in Table 4.5. Fish length was significantly explained by all the predation pressure indices. Population size of the seal colony and its distance from the station were the two indices that exhibited the strongest association with the fish variables, showing significant correlation and appropriate sign with fish size, numerical density and biomass density.

Table 4.5. Correlation matrix of fish variables and indices of predation, showing significance for all fish variables with distance to seal colony's seal population size. Fish standard length was significantly correlated across all indices.

Predation index	**Biomass** (N=887)		**Density** (N=887)		**Standard length** (N=880)	
Summit depth	r_s=0.12	P <0.01	r_s=0.01	P =0.35	r_s=0.16	P <0.01
Distance from euphotic habitat	r_s=0.01	P =0.37	r_s=-0.07	P =0.02	r_s=0.09	P <0.01
Distance from seal colony	r_s=0.28	P <0.01	r_s=0.15	P <0.01	r_s=0.17	P <0.01
Seal colony population	r_s=-0.22	P <0.01	r_s= -0.21	P <0.01	r_s= - 0.12	P <0.01

The pseudo replicates for the 11 NWHI stations were subjected to a linear backward, multiple regression analysis, using all the predation indices to explain fish numerical density, body size, and biomass density. For the analysis of fish numerical density the variables of summit depth and distance to the seal colonies were retained in the analysis and explained almost 4% of the variance (R^2=0.037, P<0.01). Running the

regression analysis with fish size yielded a slightly improved model that retained the two seal predation indices of distance to seal colonies and seal population at the colonies (R^2=0.045, P<0.01). Proximity and population of the nearest seal colony was also retained by the biomass density analysis, which provided the best relationship of the three comparisons (R^2=0.091, P<0.01) explaining 9% of the variance. Adding chlorophyll density to the biomass density analysis explained no additional variance, and chlorophyll was excluded from the model.

Finally, collapsing the biomass density data into a single grand mean for each station, the data were plotted against weighted scores of seal predation pressure (colony population size/distance to seal colony) (Fig. 4.9). Re-running the biomass density regression using the grand means, with all the predation indices, again retained distance to the seal colony and size of seal colony as the most important variables in structuring the fish community and explained 80% of the variance of the grand means (R^2=0.80, P<0.01).

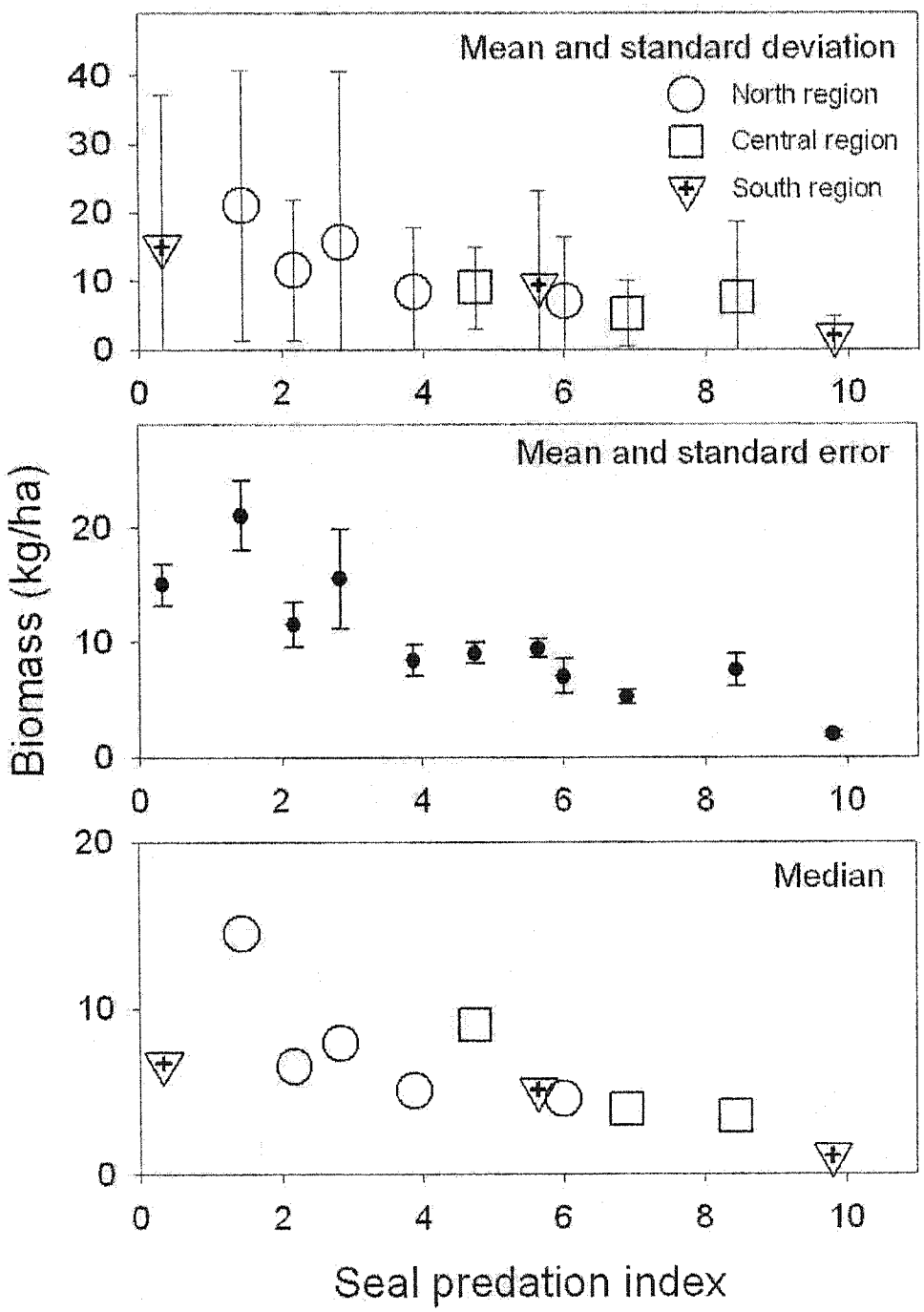


Figure 4.9. The negative relationship of subphotic fish biomass density with the monk seal predation index (population of nearby seal colonies divided by the distance from the subphotic station to the seal colony). Mean, standard deviation, standard error, and median are presented.

DISCUSSION

Regional productivity

Schmelzer's three productivity regions were derived from sea surface chlorophyll levels measured by satellite remote sensing. Comparing remotely sensed productivity data with monk seal survival, she proposed three statistically distinct regions. Regions with higher productivity meant more seal prey and better seal survivorship. However these regions are entirely based on surface values and failed to consider depth variations in the chlorophyll layer. The layer with the maximum chloropigment varies in density and depth with latitude; the maximum density is on the surface at northern latitudes and is layered well below the surface in southern latitudes (Seki et al. 2002). The chloropigment layer provides better resolution on the measurement of productivity than the satellite remote sensing. This is particularly so in the central region where the chlorophyll density levels are moderately high but are subsurface. Despite the variable depth of the chlorophyll layer, its general pattern in density (the degree of productivity) is consistent with the three productivity regions proposed by Schmelzer.

Organic fraction in sediment

The sediment LOI data exhibited no pattern in relation to the three productivity regions or the chlorophyll density data. It is likely that many of the sites sampled were not appropriate for detecting regional productivity differences in the organic rain. Ideally sediment should be collected on a horizontal surface such as a subphotic summit that accumulates organic rain. Sediment on the slopes of banks with summits at euphotic

depths are at an increased risk of enhancement from alluvial transport of organic material down slope. Except for FFS, all the sediment collections were taken on the slopes of banks with euphotic summits. The southernmost sediment collections (24° north latitude) may have had such a wide range because they were split between the subphotic summit of FFS (~0.8% LOI) and the slope of Brooks Bank (~1.6% LOI), which extends into euphotic depths. It is possible that organic material slid downslope and elevated organic values at Brooks Bank and the rest of the northern stations. Aside from problems with bank physiography, the flanks of the banks were generally swept by currents and it is likely that deeper sites, with lower flow rates, would accumulate more detritus and more accurately reflect regional differences in productivity. However, the effort and cost associated with these deeper sediment collections made them logistically infeasible. Given the uncertainty in the sampling for the LOI analysis, the findings are questionable.

Fish community differences

Higher productivity regions were expected to have greater fish numerical density, larger body size and higher overall biomass density. Of these three measures of the fish community, biomass density was expected to produce the best measurements because it incorporates the other two in a single value. Aside from the northern region having the highest numerical fish density, largest body size and biomass density, none of the fish variables conformed well to a model of successive increases with latitude across the three regions defined by Schmelzer. Fish numerical density was significantly greater in the northern and central regions and biomass density of the northern region was significantly

greater than the central and southern regions. The failure to detect differences in fish numerical density between the central and northern regions may highlight the inability of satellite data to detect moderately high subsurface chlorophyll density (Seki et al. 2002) for the latitudes in the central region. Given that the northern and central regions did not differ in fish numerical density, the significant difference in biomass density was attributable to the fish in the central region having a smaller body length than fish from the adjacent north and south regions. However, reasons for the reduced fish body length in the central region are not clear. The size structure analysis of individual species showed a weak positive correlation between fish body size and chlorophyll level but the pattern is inconsistent when examined by the few available individual taxa that span the three regions. Smaller body size in a fish community is often attributed to effects of predation and this will be discussed in the next section.

The fish data classified into seal prey functional groups also identified the central region as different from the north and south regions. The greater proportion of benthic hoverers in the central region suggests a local influence rather than something determined by a productivity gradient. If the productivity gradient were the only determinant of fish abundance across regions, the relative proportion of functional groups should also remain constant. The regional evaluation of the habitat data revealed no pattern in the prevalence of substrate or relief type that would explain the central region's unique composition of community functional groups. The peak in benthic hoverers is a cumulative reflection the region's smaller fractions of benthic ambush predators and benthic searchers. One possible explanation for the community structure is outside (e.g.

euphotic) predation pressure being exerted on the subphotic community at different intensities in different regions. Again, this will be addressed in the next section of the discussion.

Connectivity with predator populations

Euphotic predators that prey on the subphotic fish community can be divided into (1) monk seals and (2) other euphotic apex predators (e.g. sharks, jacks and snappers). Analysis of the fish data indicated that the primary effect of predators was related to the proximity to the seal colonies, and the size of the seal population. It seems likely that other euphotic predators' in addition to seals, were part of this predation index. However, it is not possible to separate them from the seals, because unlike seals, their abundances are poorly known. The summit depth of the host pinnacle was identified as marginally important only for fish numerical density. Distance to euphotic habitats from the subphotic stations was excluded from all multivariate models by the software's criteria of importance. This exclusion could indicate that euphotic predators (e.g. sharks, jacks and snappers) are of minor importance. Despite our observations of some deep feeding jacks, these predators are thought to stay close to shallow reef systems most of the time (Sudekum et al. 1991). The jacks seen feeding at subphotic depths may have followed the submersibles down on the submersibles descent to unusually great depth. They were clearly exploiting the fact that the lights of the vehicles revealed otherwise cryptic fish, which they chased and ate. Without the submersible for the jacks to follow, it is unknown whether the jacks would commonly feed at these depths. In contrast, seals are known to routinely make the oceanic transits to neighboring banks and visit subphotic

depths (Abernathy 1999, Stewart 1998, Stewart 2004). Consequently, it is possible that seal foraging pressure could be structuring subphotic fish assemblages, although it seems unlikely. The analysis of seal predation pressure considered only the closest seal colonies to the survey station. It is possible that seal foraging pressure could come from more distant colonies, but this would involve a considerable travel effort for the "commuting" seals, and the annual NMFS surveillance of the seal colonies indicates little movement between sites (Johanos and Baker 2000).

An immediate appeal of the predator pressure hypothesis is its ability to explain three inconsistencies that were encountered when the productivity model was employed. The first and most obvious of these was the high fish levels of the FFS and WestPac stations. Their location in the low productivity southern region is incompatible with the regional productivity hypothesis. These two stations are distant from surrounding seal colonies, which should lead to reduced seal foraging pressure. The WestPac station is particularly protected from predation pressure because the population of the nearest seals at Necker and Nihoa is very small (N=38), and because a sizable distance separates the station from the seals. In addition, WestPac is a subphotic summit, which probably conceals its location from the seals to some degree. Summits that extend into the euphotic are more likely to be discovered by traveling seals than those concealed at subphotic depths. The east FFS pinnacle, on the tip of the FFS platform, is the only other subphotic summit in the analysis, and satellite telemetry studies have documented seals routinely visiting it (Parrish et al. 2002). The east FFS station is closer to its'seal colony than WestPac, and the FFS colony is an order of magnitude bigger than the Necker and

Nihoa seal populations. Another important characteristic is the habitat "bridge" that connects the station with the FFS seal colony. Seals following this subphotic bridge are more likely to find the pinnacle than if it were topographically isolated.

The second inconsistency was the smaller body size of fish in the central region. Plotting the mean distance to seal colonies for all NWHI summits shallower than 100 m (NOAA 2003) revealed a range of mean distances from 172 to 263 km for the three regions. The mean distance by region for the stations surveyed in this work ranged between 63 and 72 km, but the stations in the central region were equal distant from the seal colonies (range 10 km) than the southern and northern stations (range 50-60 km) (Fig. 4.10). The stations' proximity to the larger seal population in the central region could explain the size of fish in this region. Finally, this geographic difference could explain the third inconsistency, which is the unique fish composition in the central region. Proximity to a large seal population probably increases predation pressure directed at the larger size fish prey in the benthic ambush (e.g. *Octopodidae*, *Chlorophthalmidae*, *Bothidae*) and benthic searcher (e.g. *Congridae Polymixiidae*, *Squalidae*) taxa (Goodman-Lowe 1998). Such pressure could explain the lower number of large fish and the reduced biomass density in the central region.

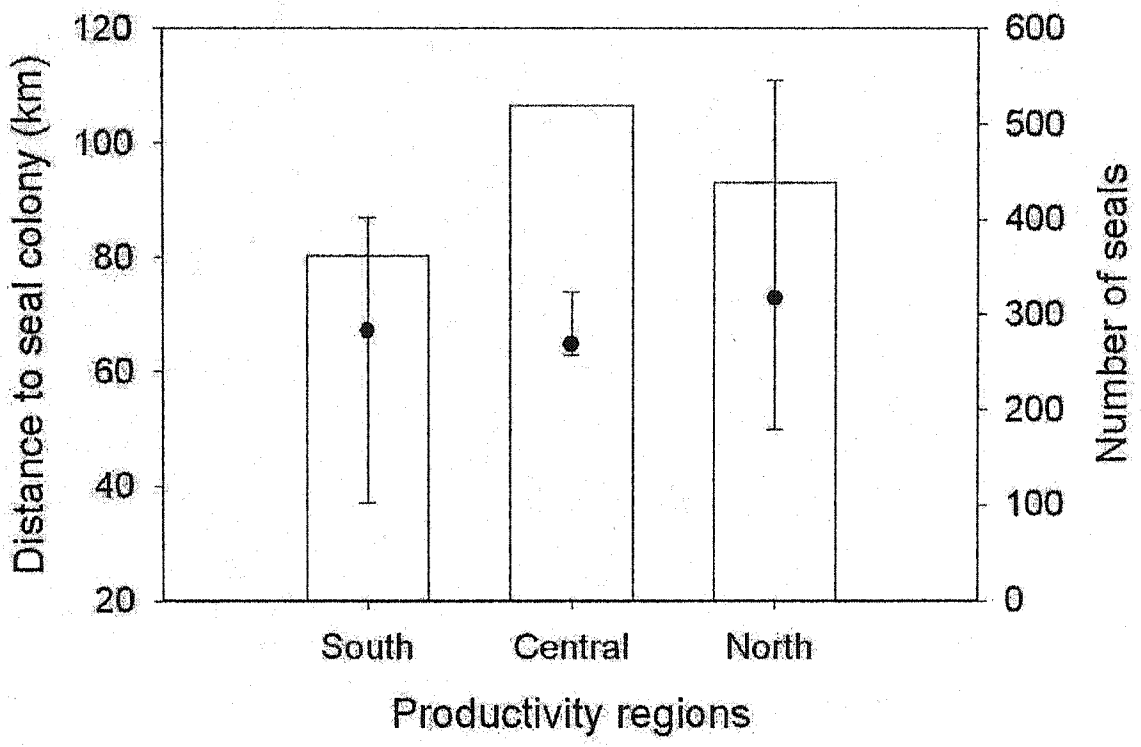


Figure 4.10. Plot of the means and range (dots with error bars) of distance from survey stations to nearby seal colonies for three productivity regions. Also shown for each region is the seal population (bars). The central region differs from the rest in that it has a larger seal population which is closer to the subphotic station

Dominant effects in the subphotic fish community

The three productivity regions proposed by Schmelzer correlate with survivorship of seals, but it seems likely that some other geographic variables contributed to the spatial pattern of the seal populations. Productivity (represented by chloropigment), explained 2% of the variance in the regression with fish biomass density. The large sample size gave this analysis the power to detect effects as small as 2%, so the effect of productivity level (chlorophyll) may have been detected. However, a multiple regression using productivity and predation pressure with fish biomass density indicated that predation pressure was consistently stronger (pseudo replicate level R^2=0.08, grand median R^2=0.80) than the relationship with productivity (pseudo replicate level R^2=0.014, grand median R^2=0.24), which was dropped from the model by the algorithm. Primary productivity probably plays a role in the community, structure as suggested by the general correlative patterns in the species specific analysis. The fact that the available forage area per seal (within the 100-m isobaths) is less in the central and northern regions (south=18 km^2, central=10 km^2, and north=4 km^2) (NOAA 2003) indicates northern seals actually use less forage area than seals in the southern region. It may be that forage grounds are more productive in the north, but their positive effects on the seals' population are mitigated by lack of suitable habitat.

The idea that seals may alter the structure of subphotic fish assemblages (biomass density, size distributions and species composition) by their foraging is supported by recent satellite telemetry work completed at all the NWHI seal colonies. Foraging seals were documented visiting all the islands, banks and seamounts in each of the regions

(Abernathy 1999, Stewart 2004). Preliminary assessments of diving behavior indicate that subphotic (>300-m) visits were made primarily by adult males and females (Abernathy 1999; Stewart 2004; Stewart and Aecium 2004a; Stewart and Aecium 2004b), although some limited subphotic diving was documented for juvenile seals. Seals that dove deep appear to be specializing in subphotic foraging. Of the 37 adults instrumented in these studies, 17 seals (46% of the sample) used subphotic depths. Extrapolating this percentage across the NWHI seal population yields a minimum estimate that 310 seals, or roughly a fourth of the entire population, do some feeding at subphotic depths. Given the very low biomass density at subphotic depths, it is reasonable to expect that we could detect the impact of feeding seals on the fish community. Structuring of the fish communities by apex predators in the NWHI is well documented at shallower depths (Friedlander and DeMartini 2003, Parrish and Boland, 2004), and typically it is attributed to a combination of predators including sharks, jacks and seals. This is the first analysis that identifies the monk seals as a primary predator in shaping the structure of an identified fish community.

Implications

It is not known whether subphotic fish communities have always been a component of the seals' foraging grounds. Foraging studies have focused on the FFS population and have consistently discussed the possibility that the subpopulation at FFS is at or near carrying capacity, which implies that hunger is driving the seals to forage deeper and deeper. A confirmation of such a behavioral adjustment might be a

determination that "healthier" seal populations at the north end of the chain are feeding shallow and not using subphotic depths. However, it is clear from satellite tag data (Stewart 2004) and the fish surveys that seals in the central and northern colonies are using subphotic depths. Because there is no prior telemetry data for seal activity patterns in earlier decades, it is not possible to do a temporal comparison and possibly resolve the carrying capacity question. It appears that either (1) the seals of the NWHI always fed on the subphotic community, or (2) all NWHI seal colonies are approaching carrying capacity and the seals are compensating by feeding deeper. Regardless, the relationship of subphotic fish abundance to seal predation pressure suggests that seals routinely use these deep fish communities, and raises concern that northern seal populations may be closer to carrying capacity than previously thought. Prior to Stewart's work, seal feeding at subphotic depths was always thought to represent a very small percentage of the seals' total effort. At FFS, the available data suggested that seals that feed at subphotic depths number around 10% of the FFS population (Parrish et al. 2002). This number was based on the fact that the FFS study (Abernathy 1999) instrumented mostly males with satellite tags, and only males were documented to dive deep. So the estimate was projected for only the male segment of the population. Stewart's work shows females diving deep as much as males, so estimates of seals using subphotic depths must be adjusted upward considerably.

This work focused its efforts at 300 to 500 m, the maximum depth at which seals have been documented to forage (Stewart 1998, Abernathy 1999, Baco-Taylor pers comm). However, it is possible that monk seals are capable of diving deeper. Seals have

been documented exceeding the maximum limits of their depth recorders (Abernathy 1999, Stewart 2004). The slopes of the NWHI are steep (often cliff faces) permitting the seals to search for prey at intermediate depths as they descend to and ascend from greater depths. When possible, our the submersible transects were extended deeper, sometimes reaching 1000 m, and in a number of cases, more fish were seen than at the 300-500 m target depth. Finding more fish deeper is unexpected, and it is unknown whether this is an artifact of the seals' depleting fish at shallower depths. The maximum depth at which monk seals can feed remains a unknown.

CONCLUSION

Attempts to verify regions with various levels of productivity (and chloropigment density) by examining the organic fraction in sediment samples were unsuccessful. It is likely that the steepness of slopes at many of the stations with summits, at euphotic depths, caused elevated organic levels due to alluvial transport of shallower materials. Fish numerical densities were generally low and variable, and representation of some taxa diminished and others increased with latitude. Fish numerical and biomass density, and size, correlated poorly to Schmelzer's three productivity regions (derived from remote sensing) and the chlorophyll density data (derived from ship transects). Unexpectedly, seal predation pressure, and size and distance to the nearest colony best explained the observed structure of subphotic fish assemblages.

CHAPTER 5. GEOGRAPHIC SYNTHESIS

THE SEALS' SUBMARINE LANDSCAPE

Discussions about the Hawaiian monk seal inevitably lead to talk of the FFS colony and its poor survivorship, in particular it's greater number of starving seals (since early 1990's), compared to seal colonies at the north end of the archipelago. Linking the apparently malnourished FFS seals to a shortage in the region's prey base has been difficult to show with any single study. A better approach may be to look for consistent patterns in data using a number of research methodologies. Given the many studies focused on FFS, it is an excellent starting place for a geographic analysis of the monk seals' foraging landscape. Satellite telemetry, scat analysis, and satellite oceanography were used to make inferences about the monk seals' forage base but without the benefit of information on the fish (or seal prey) assemblages for the different habitats and regions. This dissertation presented data on fish assemblages in four conspicuous habitat zones, (with an emphasis on the subphotic zone) and considered them in relation to prior studies. The second chapter employed these zones to examine depth differences in the seals' submarine landscape, the third chapter examined fish associations with deepwater habitats including corals, and the fourth chapter compared subphotic fish assemblages across the NWHI to test prevailing hypotheses about regional productivity differences.

The four habitat zones provided a crude method of evaluating the potential contribution of different depth-specific fish assemblages (the vertical landscape) to the seals' forage base. Comparing fish data with Abernathy and Siniff's (1998) satellite tag study, indicated that the seals' effort was not directed at any single habitat, and their

foraging was spread throughout the FFS region. The habitat zone with the greatest number, size and biomass density of fish was not visited more frequently by seals. The only persistent spatial pattern was that the seals foraged along the edges of the banks, often overlapping multiple habitat zones. Differences were only evident for the subphotic zone, where monk seals location data on average exceeded the median distance to the available grounds, suggesting seals were traveling to a specific feature in the habitat zone. Using functional groups, the composition of fish in the seals' diet (derived from Goodman-Lowe's 1998 analysis of scat) was compared to the composition of the fish assemblages in each of the four habitat zones. The biomass density of the fish assemblage in the bank and the slope habitat zones best conformed to the seals' diet as reported by Goodman-Lowe (1998).

The seals are clearly able to transverse the distance (300 km) to feed on the banks and the slopes northwest and southeast of their atoll. However, subphotic diving requires more effort, and as a result, subphotic depths are near the edge of the seals' foraging range. Because the choice to dive deep is presumably costly (is a physiologic sense), the pattern of the seals subphotic foraging may better reflect differences in the forage base than do the seals' foraging patterns at shallower depths. We would expect to see focused feeding around deepwater corals with the hypothesis that deepwater corals aggregate fish and improve the seals foraging success.

The evaluation of subphotic fish assemblages with deepwater corals (Chapter 3) indicated a co-occurrence of deepwater coral and fish at sites of high water flow. Sites with high bottom relief tended to support the tallest types of corals, and they were used as

shelter by fish (mostly benthic hoverers). However, no significant increase in fish could be attributed to the presence of corals, because areas of high bottom relief without corals often supported a comparable fish assemblage. The seals may feed on the fish hiding around relief features, and corals may colonize those features because of the improved water flow characteristics created by the relief. Alternatively, there may be some undetected ecological component that improves the seals' foraging success around corals. This remains a possible direction for future research.

The studies reported in Chapter 4 shows that regional differences in NWHI oceanic productivity poorly explain the observed spatial differences in the numerical and biomass density or body size of subphotic fish assemblages. A better explanation of the character of fish populations was the variable predation pressure exerted by the size and proximity of seal colonies to the subphotic survey stations. There was evidence for greater primary productivity at the north end of the chain, including the increased chlorophyl levels. Here seals survive in areas with less forage grounds, and there is a weak statistical association between fish biomass density and in-situ measures of subsurface chlorophyll maximum (Seki et al. 2002). Statistical tests of fish variables using Schmelzer's model, indicated that the north region has significantly greater numerical fish density, larger body size, and biomass density than the southern region (Table 4.3). The central region emerged as unique only for a smaller fish body size. The analysis showed the central region was similar to the north region for fish numerical density and to the south region for biomass density. Overall, the patterns in the fish data conform weakly at best to Schmelzer's three-region model. Proximity to the seal

colonies seemed a more important influence. Fish biomass density was negatively correlated with proximity and size of seal colonies. The significantly smaller size of fish (and low biomass density) in the central region was attributed to their proximity to seal colonies and presumably more intense foraging pressure than the northern and southern stations. Unfortunately the probable effect of the predation pressure confounds the ability to firmly resolve the effect of productivity using fish assemblages. Had suitable stations for sediment collection been located, the LOI analysis could have proved valuable in establishing regional differences in the levels of organic rain.

FUTURE STUDY

The seals' predatory activities clearly affect the subphotic fish assemblages. The study of subphotic fish patterns may be a new way to evaluate the foraging success of monk seal populations. Areas with high subphotic biomass density close to a seal colony could be an indication that the seal population is getting sufficient food from shallower depths and is probably not at carrying capacity. Effective interpretation of these patterns will depend on being able to discern between seal predation pressure and pressure from other predators. Sharks, jacks, and snappers are known to be abundant in the reefs of the NWHI (Setaceum et al. 1991; Friedlander and DeMartini 2002), and their ability to cross channels to neighboring peaks is established for large predators (Holland et al. 1999) but uncertain for smaller ones. Perhaps seal predation could be isolated by comparing NWHI stations with subphotic stations free of seal predation pressure. Surveys conducted in the main Hawaiian Islands (MHI) or the Line Islands where there are no seals could provide

insight. However, effects of extensive fishing pressure on sharks, jacks and snappers, which eat the fish types recorded in these surveys (Fig. 3.8), could confound the comparison. All that can be reliably said is that the absence of seals, sharks, jacks and snappers in the MHI means much lower predation pressure than the NWHI.

Less predation pressure in the MHI is consistent with the finding that deepwater corals do not aggregate fish. Knowing that seals feed at subphotic depths, and that some focus their activity in the area of deepwater corals, raises concerns that seals may have depleted any enhanced fish numbers in the coral beds before these surveys were conducted. If this is true, then the findings reported in Chapter 3 of this dissertation may have to be reconsidered. In the MHI, subphotic fish are not exposed to seals or large numbers of sharks, jacks, and snappers. Furthermore, none of the survey taxa (Fig. 3.8) appeal to fishers and they are rarely caught as by catch, so there should be no loss of survey taxa to fishing. The lack of predation (seal or otherwise) and fishing pressure should leave any MHI aggregations of fish around deepwater corals unmolested. Consequently if fish do aggregate to deepwater corals in the MHI, surveys should have detected more fish in the deepwater coral beds than out of it - and this was not seen.

Other sites without seals and with less fishing could be surveyed and compared with the NWHI data. Places like Johnston Island or the Line islands are likely to have similar subphotic fish assemblages and a more intact euphotic predator population (sharks, jacks, snappers). Findings of studies further from Hawaii are arguably less relevant, but there are few alternatives. Subphotic work in the NWHI should be continued. Any study undertaken should employ a study design that accounts for the

proximity to seal colonies. These types of studies will bring new insight to the issues of monk seal carrying capacity and possibly suggest the reason for recent immigration of NWHI seals to the MHI (Johanos and Baker 2000).

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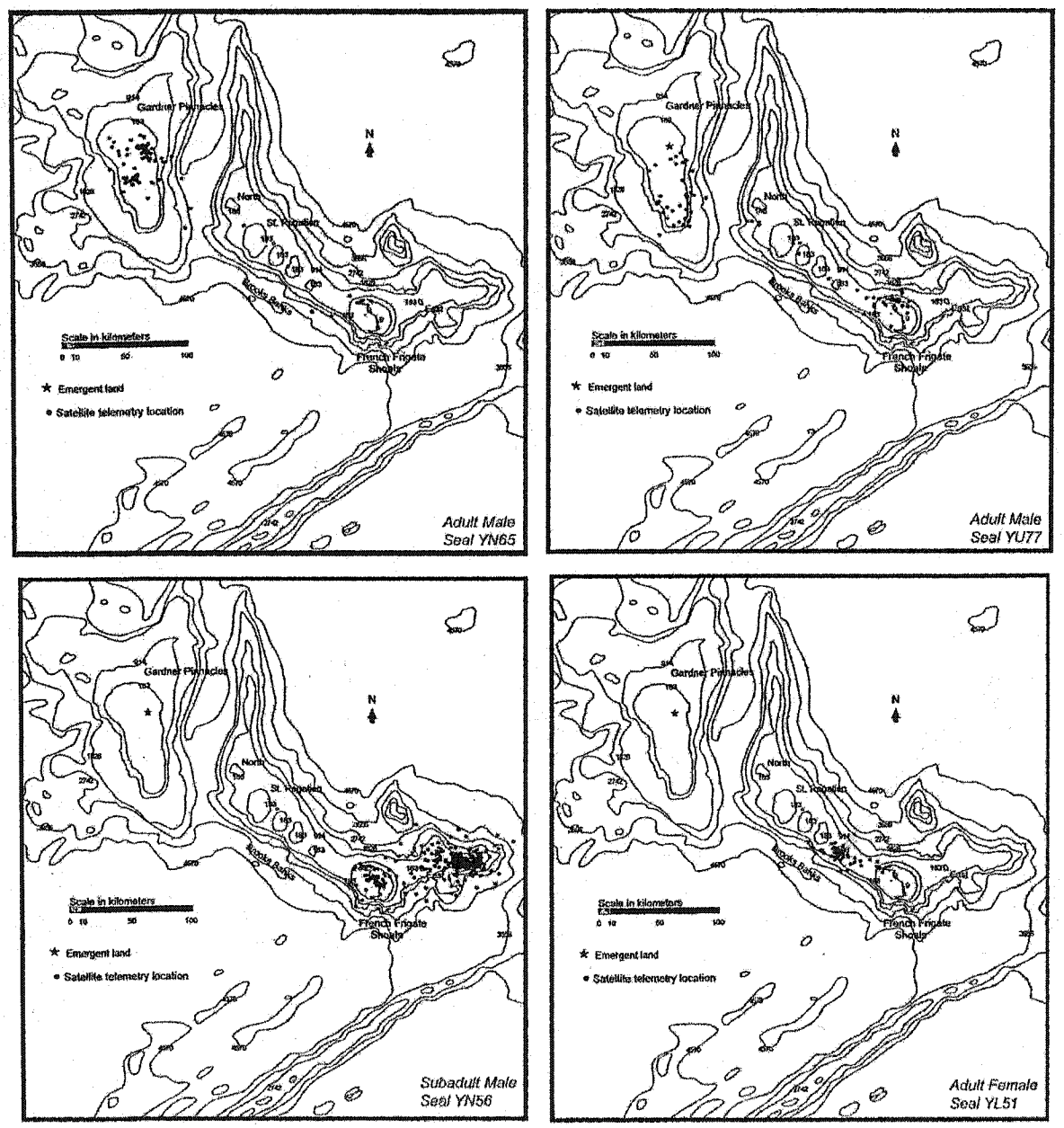
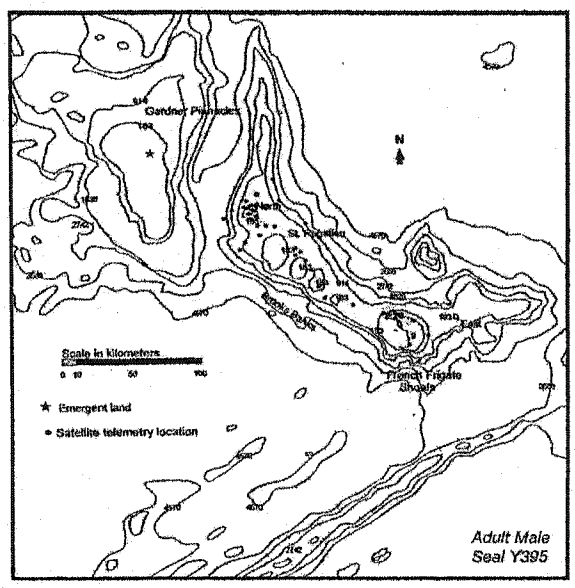
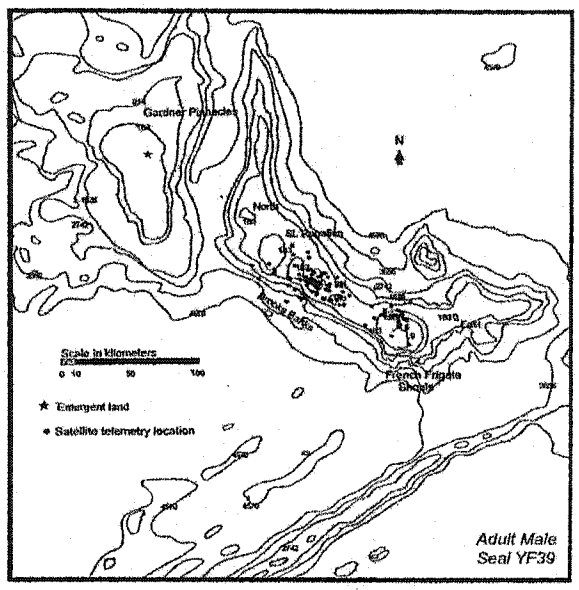
APPENDICES

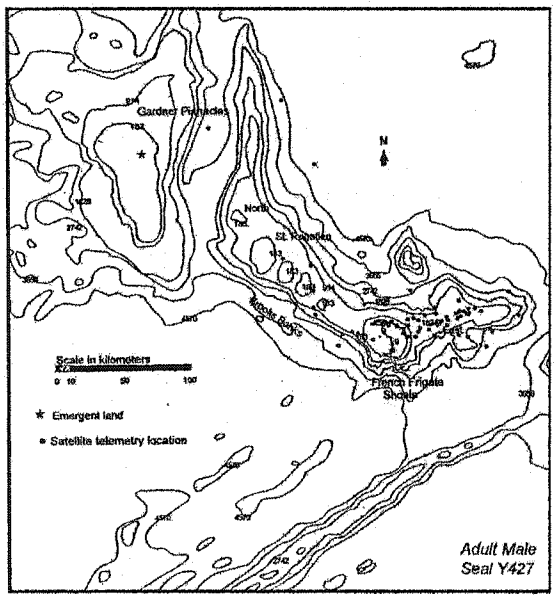
Appendix A. Plots of satellite tag positions for each of the seals tagged in Abernathy and Siniff (1998).

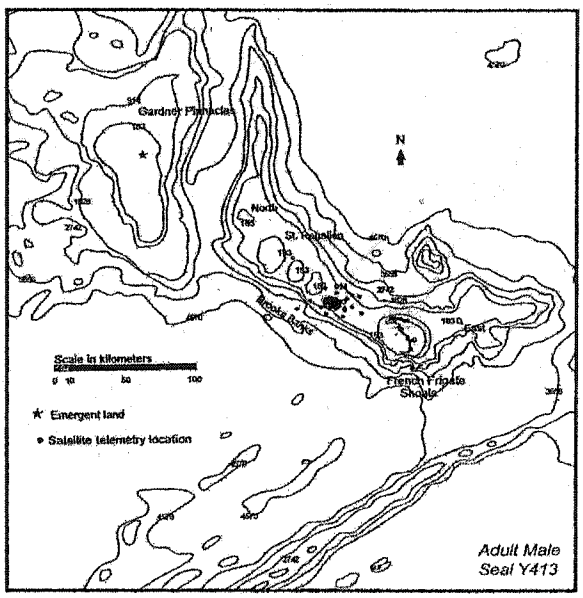


Appendix A - continued.

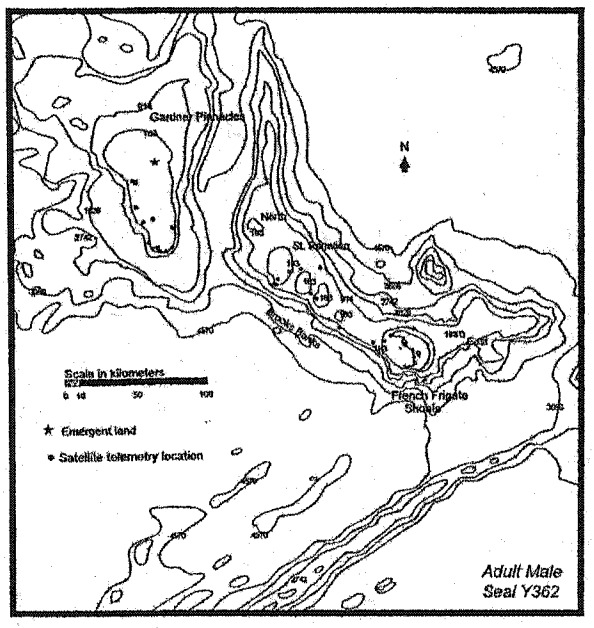


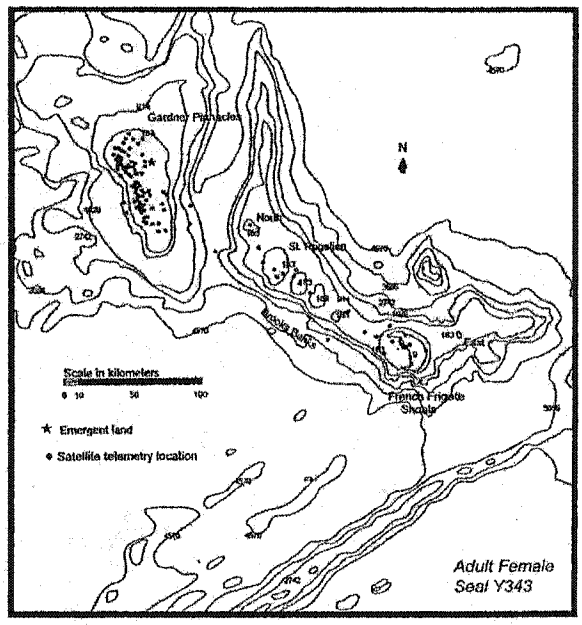


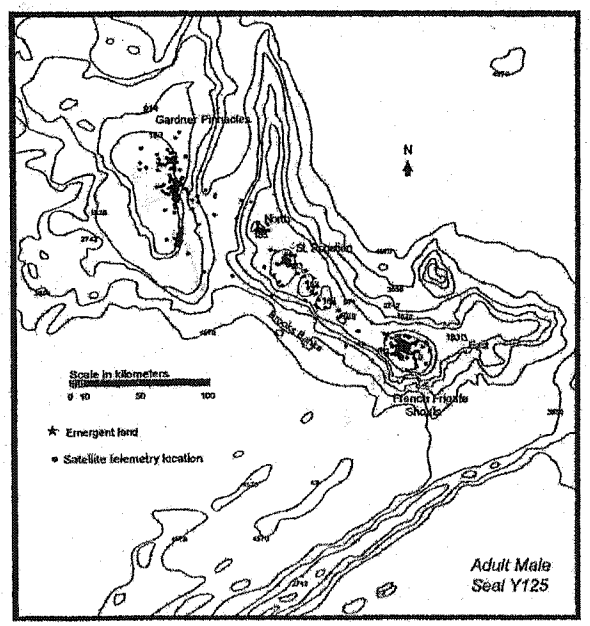


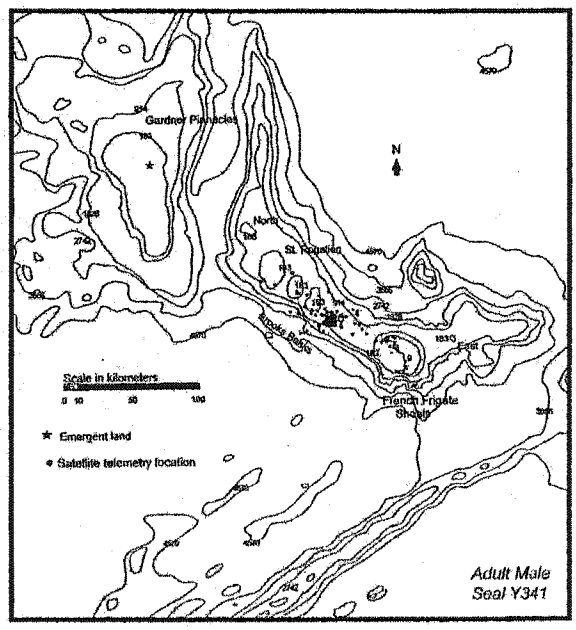


Appendix A - continued

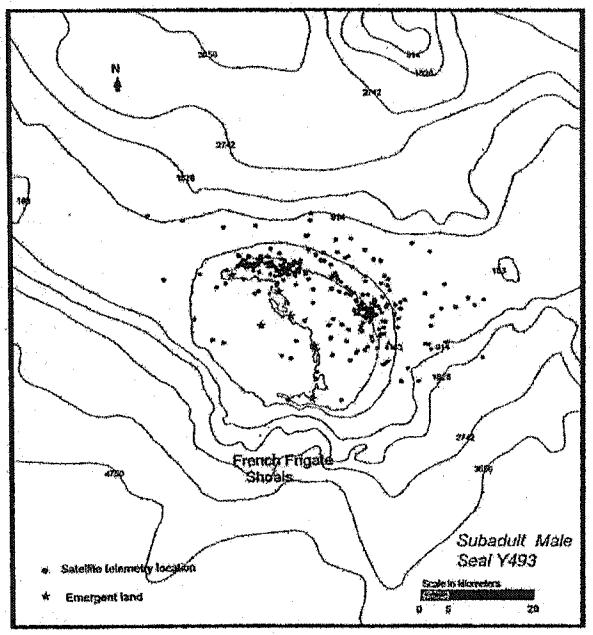


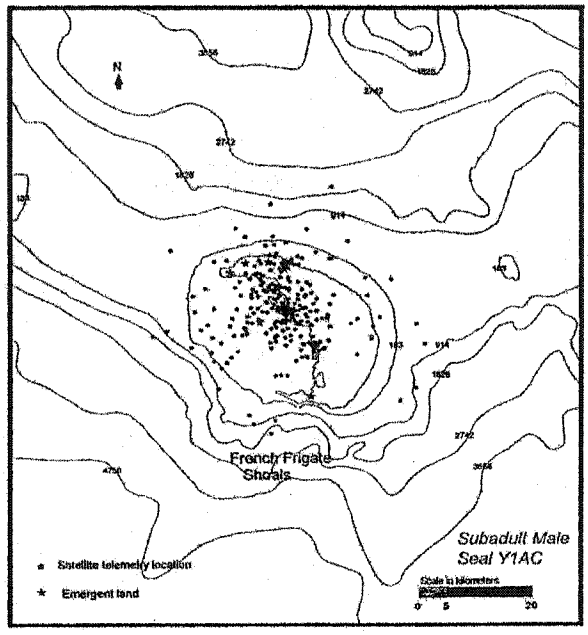


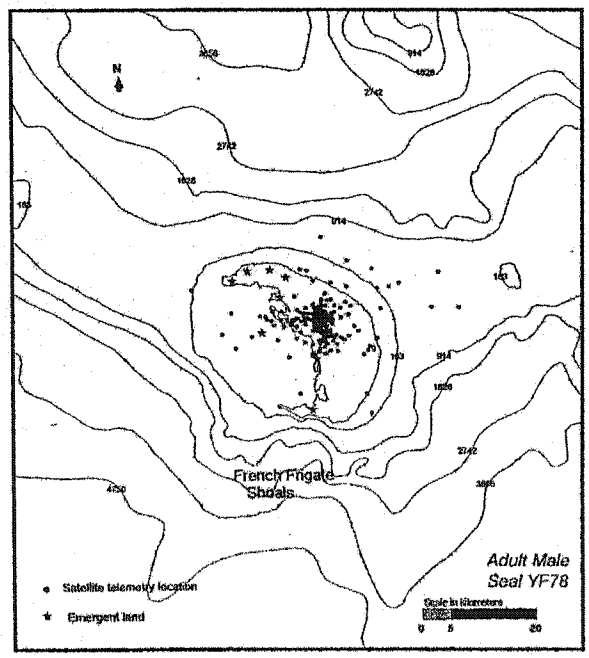


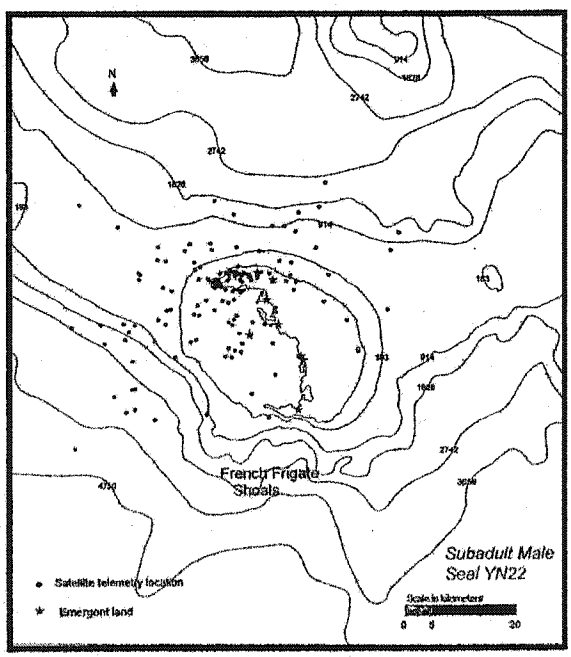


Appendix A - continued.

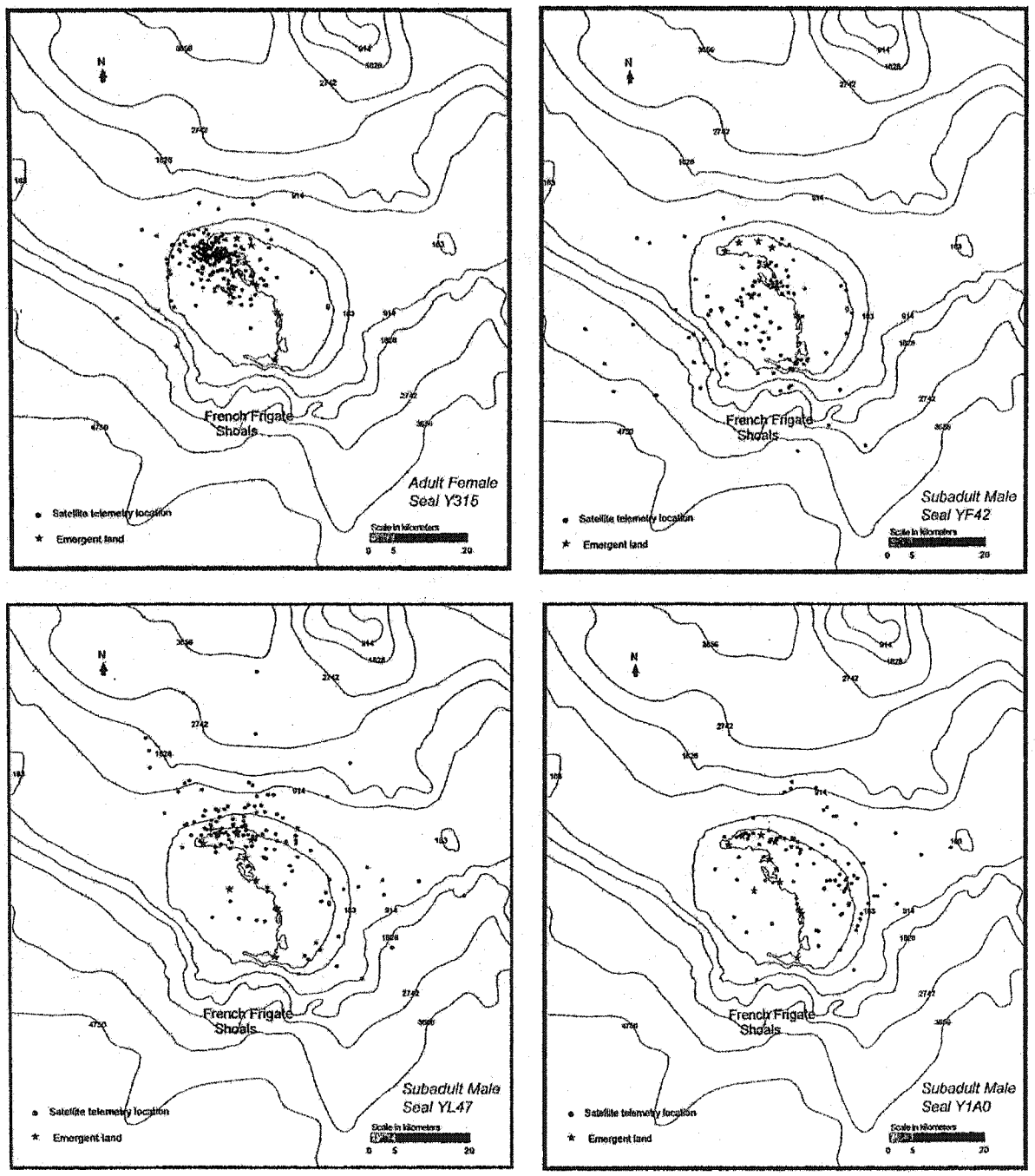








Appendix A - continued.



Appendix B. List of all dives made by year, submersible, depth range, position and closest monk seal colony. FFS stands for French Frigate Shoals, NA means no recognized seal colonies present in the area .

Year	Dive no.	Station	Depth (m)	Position		Seal colony
1998	R-019	WestPac	339-481	23° 14.2	162° 38.849	Nihoa
1998	PV-380	WestPac	355-500	23° 14.2	162° 38.849	Nihoa
1998	R-020A,B	FFS	351-462	23° 55.085	165° 22.702	FFS
1998	PV-382	FFS	351-576	23° 55.000	165° 23.100	FFS
1998	R-021A,B	FFS	339-379	23° 56.948	165° 41.385	FFS
1998	R-022A,B	Brooks	352-549	23° 58.6	166°40.6	FFS
1998	PV-384	Brooks	352-499	23 °58.645	166° 44.324	FFS
2000	R-072	Kaena	339-456	21°37.00	158°23.88	NA
2000	PV-446	Kaena	381-635	21° 37.00	158°23.00	NA
2000	PV-450	WestPac	341-422	23°14.760	162° 37.924	Nihoa
2000	R-075	FFS	374-504	23°55.23	165°23.28	FFS
2000	PV-451	FFS	352-410	23°55.00	165° 23.22	FFS
2000	PIV-014	Cross	336-420	18°43.833	158°15.55	NA
2000	PIV-016	Keahole	368-485	19°47.78	156°06.97	NA
2000	PIV-017	Pohue	390-593	19°00.06	155°48.82	NA
2001	R-086	FFS	470-780	23°55.15	165°20.24	FFS
2001	PV-455	FFS	353-365	23°55.06	165°23.15	FFS
2001	PV-456	FFS	353-675	23°55.06	165°23.15	FFS
2001	PV-457	Brooks	59-552	23°58.65	166°44.33	FFS
2001	R-087	Brooks	50-436	24°.04.70	166°45.78	FFS
2001	PIV-031	Keahole	380-400	19°48.02	156°07.21	NA
2001	PIV-032	Cross	353-425	18°43.79	158°15.54	NA
2001	R-119	Cross	382-480	18°42.50	158°15.43	NA
2001	PIV-033	Cross	349-417	18°43.33	158°15.70	NA
2001	PIV-034	Cross	342-405	18°43.33	158°15.7	NA
2001	R-120	Makapuu	315-485	21°17.10	157°32.84	NA

Appendix B - continued

2001	R-121	Makapuu	331-468	21°17.85	157°32.60	NA
2001	PIV-035	Makapuu	390-424	21°17.50	157°32.00	NA
2001	PIV-036	Makapuu	372-418	21°19.5	157°33.5	NA
2002	R-175	E. Northampton	258-457	25°17.49	172°03.14	Laysan
2002	R-176	E. Northampton	422-531	25°18.20	172°01.34	Laysan
2002	PIV-054	E. Northampton	339-1043	25°19.90	171°59.90	Laysan
2002	PIV-055	E. Northampton	296-876	25°16.76	172°01.36	Laysan
2002	R-177	W. Northampton	104-392	25°21.60	171°59.60	Laysan
2002	PIV-056	W. Northampton	314-862	25°33.35	172°17.79	Laysan
2002	R-178	W. Northampton	447-515	25°33.95	172°18.45	Laysan
2002	PIV-057	W. Northampton	319-734	25°31.62	172°19.32	Laysan
2002	R-179	W. Northampton	308-433	25°28.10	172°22.85	Laysan
2003	R-223	FFS	376-428	23°53.38	165°24.00	FFS
2003	PIV-096	FFS	348-360	23°55.01	165°23.13	FFS
2003	PIV-103	Bank 8	327-760	26° 13.32	174° 30.92	FFS
2003	PIV-104	Pearl & Hermes	350-754	27° 42.210	175 36.155	Pearl & Hermes
2003	PIV-105	Ladd Seamount	365-883	28 30.69	176 36.54	Midway
2003	PIV-106	Bank 10	1265	28 53.070	178 29.636	Kure
2003	R-230	Bank 10	128-527	28 54.748	178 37.000	Kure
2003	R-231	Bank 10	194-550	28 55.98	178 37.169	Kure
2003	PIV-107	Bank 11	350-595	28 58.048	179 32.592	Kure
2003	PIV-108	Nero Seamount	344-734	27 56.613	177 53.532	Kure

Dive Codes
R - stands for remote controlled vehicle
PIV - stands for *Pisces* IV submersible
PV - stands for *Pisces* V submersible

September 16, 2003

Terry Kerby
Operations Director
Hawaii Undersea Research Laboratory,
School of Ocean and Earth Science and Technology
University of Hawaii

Aloha Terry

In place of using photos, I would like to use two of your artist renditions of the *Pisces* submersibles in my dissertation "Vertical and horizontal patterns in the foraging landscape of Hawaiian monk seals." The two images I would like to use include the one of the *Pisces V* at the French Frigate Shoals gold coral bed and the *Pisces IV* at Cross Seamount surrounded by sharks. You will be credited as the artist in the figure caption and will maintain all rights and authority concerning your work. If this is agreeable to you please sign in the space provided below.

Sincerely,

Frank Parrish

I approve of the use of my art work in the manner described above.

Terry Kerby