

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

BY

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ABSTRACT

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

INTRODUCTION

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

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

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

METHODS

Seal Movement Data

Satellite tags were fitted to 24 adult FFS seals (males and females) between April and July during 1992–94 and 1996-1997 (median 87 days)(Abernathy, 1999). Although the distance and dive characteristics of the seals’ movements have been described (Abernathy and Siniff, 1998; Abernathy, 1999), at that time there were no data on seal-prey assemblages with which to compare. Activity patterns for each seal were plotted on a base map in a raster-based geographic information system (GIS)(IDRISI) representing the 600² - km area (0.13 km²/raster cell) section of the Archipelago from Necker Bank to Gardner Bank - the extent of travel documented for the FFS seals. Isobaths from National Ocean Survey charts were used to delineate the four depth/habitat zones, reef (0-30 m), bank (31-50 m), slope (51-300 m), and subphotic (301-500 m) as the primary test categories (Fig. 1).

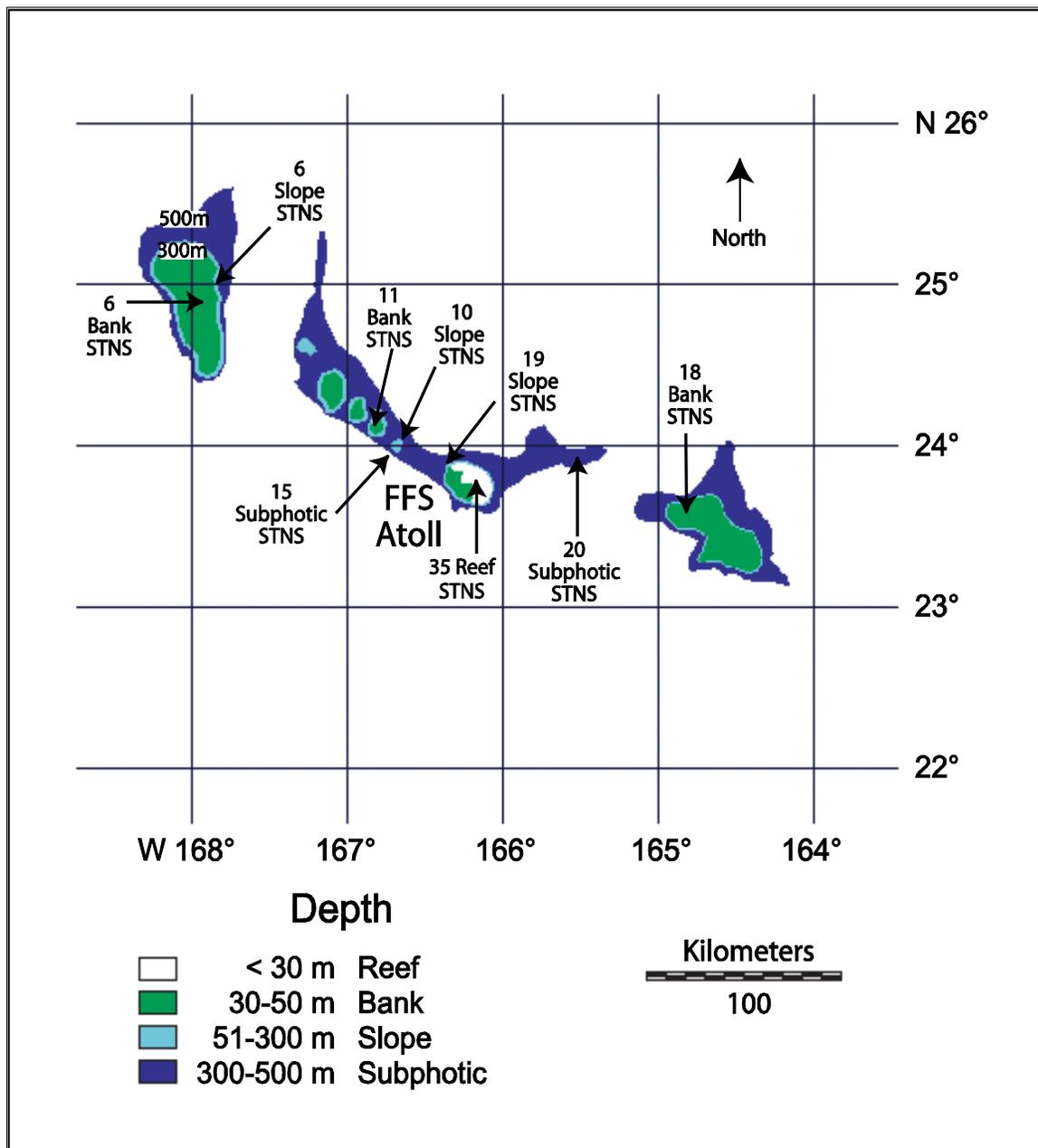


Figure 1. Base GIS coverage of the French Frigate Shoals region with each of the four habitat zones represented. Arrows indicate the location of the fish surveys.

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

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

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

Fish (Prey) Community Surveys

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

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

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

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

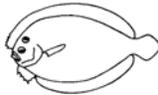
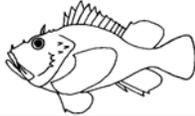
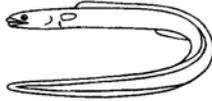
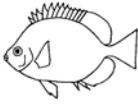
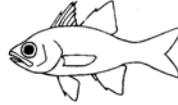
Monk Seal Diet

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

Analysis

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

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

Evasion Guild	Taxa found in seal scat	Example taxa morphology	
Bottom Camouflage	<i>Synodontidae</i>		
	<i>Cirrhitidae</i>		
BC	<i>Bothidae</i>		
	<i>Scorpaenidae</i>		
	<i>Octopodidae</i>		
Bottom Fleer	<i>Labridae</i>		
BF	<i>Scaridae</i>		
	<i>Acanthuridae</i>		
	<i>Muraenidae</i>		
	<i>Congridae</i>		
	<i>Kuhliidae</i>		
	<i>Ophichthidae</i>		
	<i>Mullidae</i>		
<i>Lutjanidae</i>			
Bottom Hider	<i>Pomacentridae</i>		
BH	<i>Tetraodontidae</i>		
	<i>Pomacanthidae</i>		
	<i>Chaetodontidae</i>		
	<i>Holocentridae</i>		
	<i>Pricanthidae</i>		
<i>Apogonidae</i>			
Midwater Fleer	<i>Kyphosidae</i>		
MF	<i>Monacanthidae</i>		
	<i>Balistidae</i>		

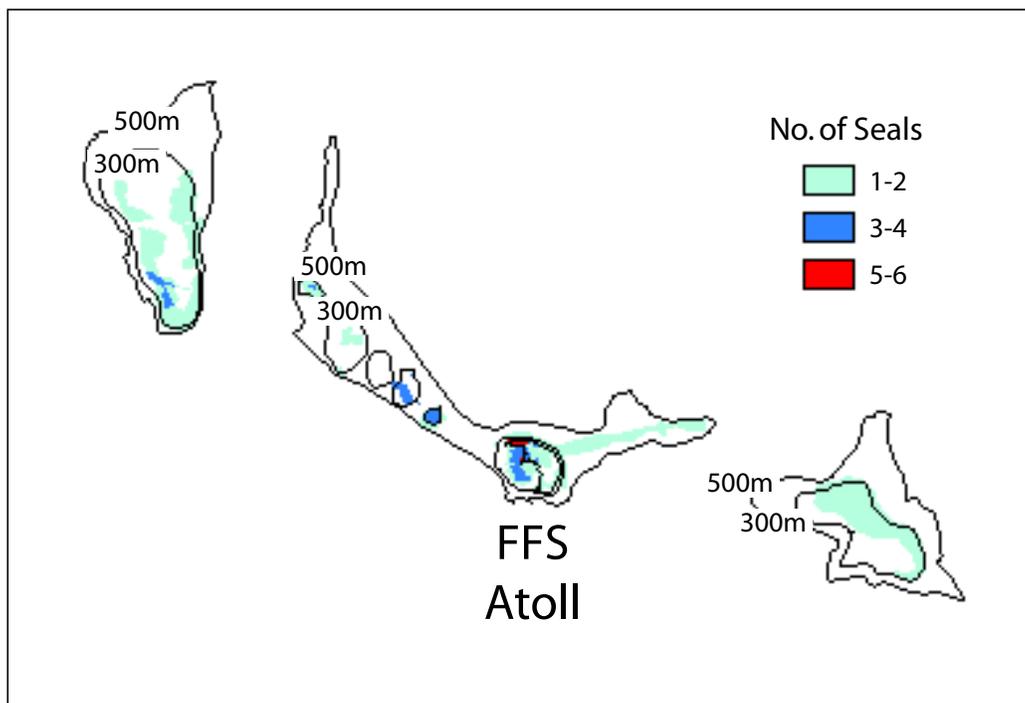


Figure 2. Movement of monk seals within the French Frigate Shoals region.

RESULTS

Seals' Use of Foraging Grounds

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

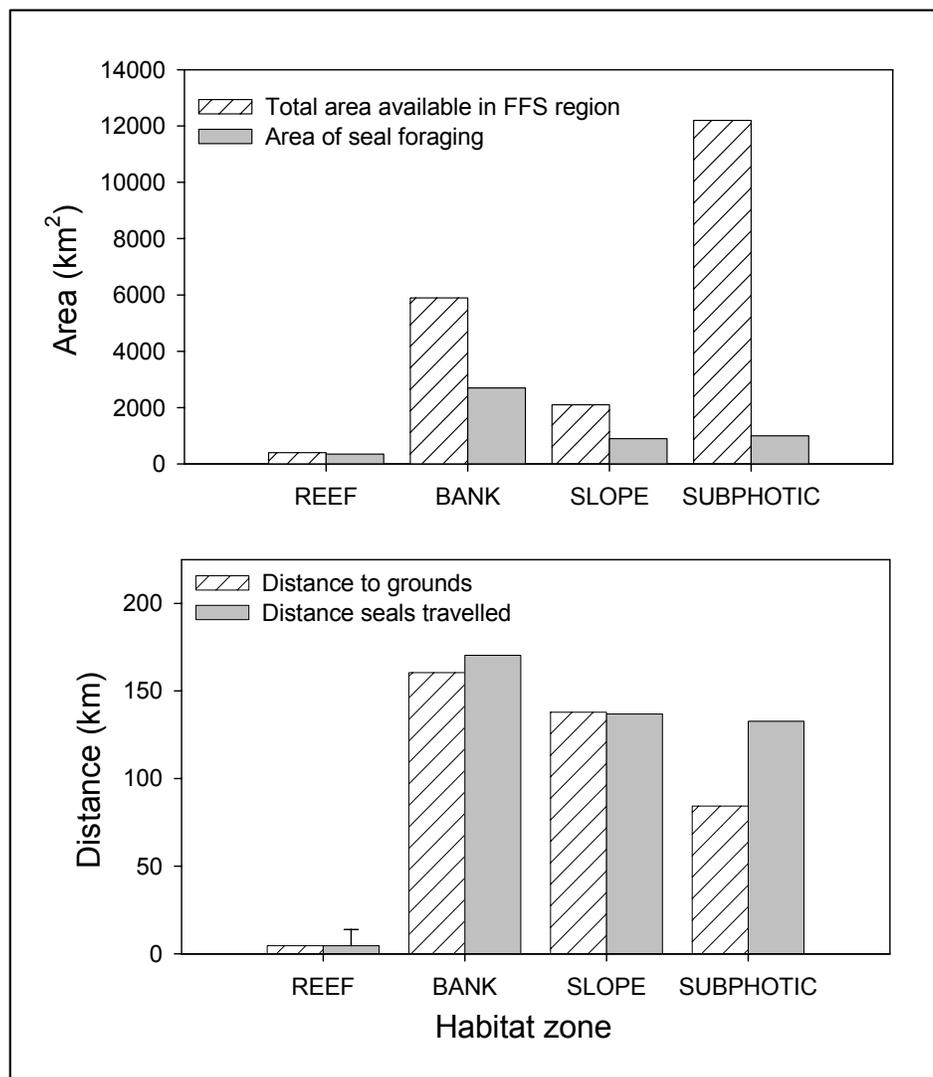


Figure 3. GIS derived mean area and distance (from FFS) for each of the habitat zones in the FFS region. The diagonal bars indicate the available habitat and the grey bars are the seals' movements.

Fish Community Structure

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

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

Fish Surveys	Median values <i>Habitat Zone</i>				P	Tukey <i>a posteriori</i> comparisons 0.05 threshold
	Reef (rf)	Bank (bk)	Slope (sl)	Subphotic (sp)		
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

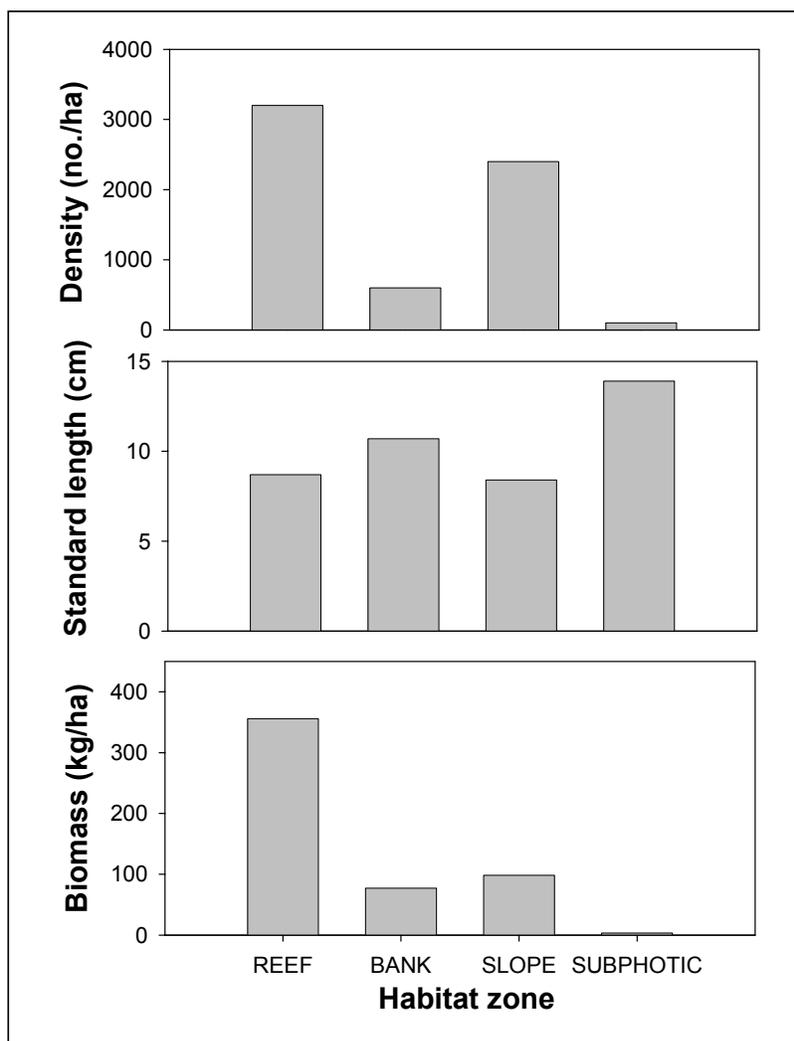


Figure 4. Numerical density, standard body length, and biomass density of fish for the four habitat zones in the French Frigate Shoals region.

Prey-Evasion Guilds

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

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

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

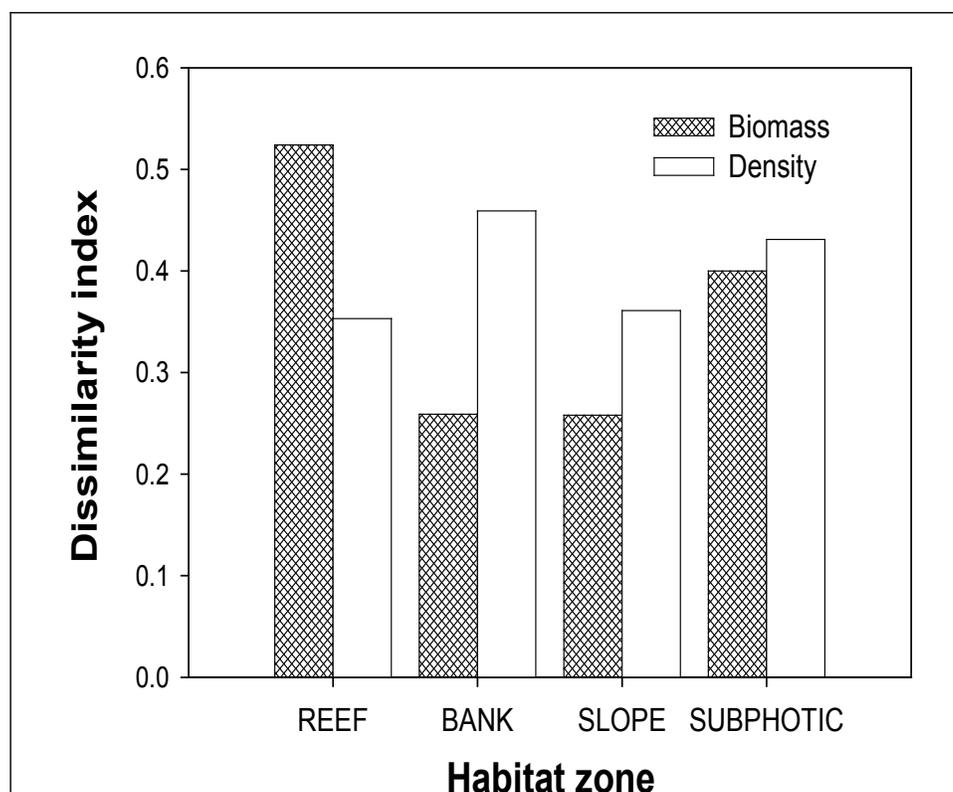


Figure 5. Scores from a dissimilarity analysis of each habitat's fish density and biomass density in the French Frigate Shoals region. Biomass density of the bank and slope zone differ the least from the seal diet (derived from scats).

DISCUSSION

Seal Movements

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

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

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

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

Fish Community Structure

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

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

Prey Preferences

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

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

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