PRECIOUS CORALS AND SUBPHOTIC FISH ASSEMBLAGES

BY

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ABSTRACT

Telemetry studies of monk seal movements at French Frigate Shoals identified two areas where seals were focusing their foraging at subphotic depths. Submarine surveys (1998, 2000, and 2001) were used in these areas to locate beds of deep-water corals. In an attempt to link the density, size, or biomass of subphotic fish (potential seal prey) with the presence of deep-water corals, a comparison of areas with and without deep-water corals was conducted. Areas with tall morpho-types of deep-water corals (e.g., *Gerardia* sp.) often supported greater fish densities than adjacent areas without deep-water corals. The prey-evasion guild of "bottom hiders" was the fish group most commonly seen using the coral branches as shelter. However, an analysis of fish and coral data accounting for habitat effects indicated fish and deep-water corals co-occur in areas of high relief, each likely exploiting improved flow conditions, with little inter-dependence.

INTRODUCTION

Recent documentation of monk seals (*Monachus schauinslandi*) visiting beds of deep-water corals prompted a hypothesis that seals may have more success in obtaining subphotic prey around deep-water coral beds, because the shelter afforded by the corals continually aggregates fish from the diffuse surroundings. This notion is an extension of findings from foraging research conducted at shallower depths where seals were found to repeatedly target specific foraging habitat types (Parrish et al., 2000), including filamentous deep-water black coral colonies (Parrish et al., 2002). If the French Frigate Shoals (FFS) seal colony is at or approaching carrying capacity for foraging as suggested by some research (Gilmartin et al., 1993; Gilmartin and Eberhardt, 1995), seals may be choosing to dive deeper to explore nearby subphotic depths rather than swim to distant, neighboring banks to feed. Habitats at depths below the photic boundary are understandably less diverse than shallower sites. The lack of scleratinian corals and macroalgae generally leaves only the geologic composition of the substrate and the scale of bottom relief to provide habitat. Patches of deep-water corals are one of the few exceptions that diversify the substrate. It is unknown whether fish (seal prey) are associated with the coral "trees," using them facultatively. This work explores potential links between deep-water corals and the fish assemblages that could be prey for monk

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seals. In particular, two deep-water corals, *Corallium* (pink coral) and *Gerardia* (gold coral) which are targeted commercially, were used to represent the two primary forms of coral trees found among deep-water corals (Fig.. 1). *Corallium* is a crustose octocoral

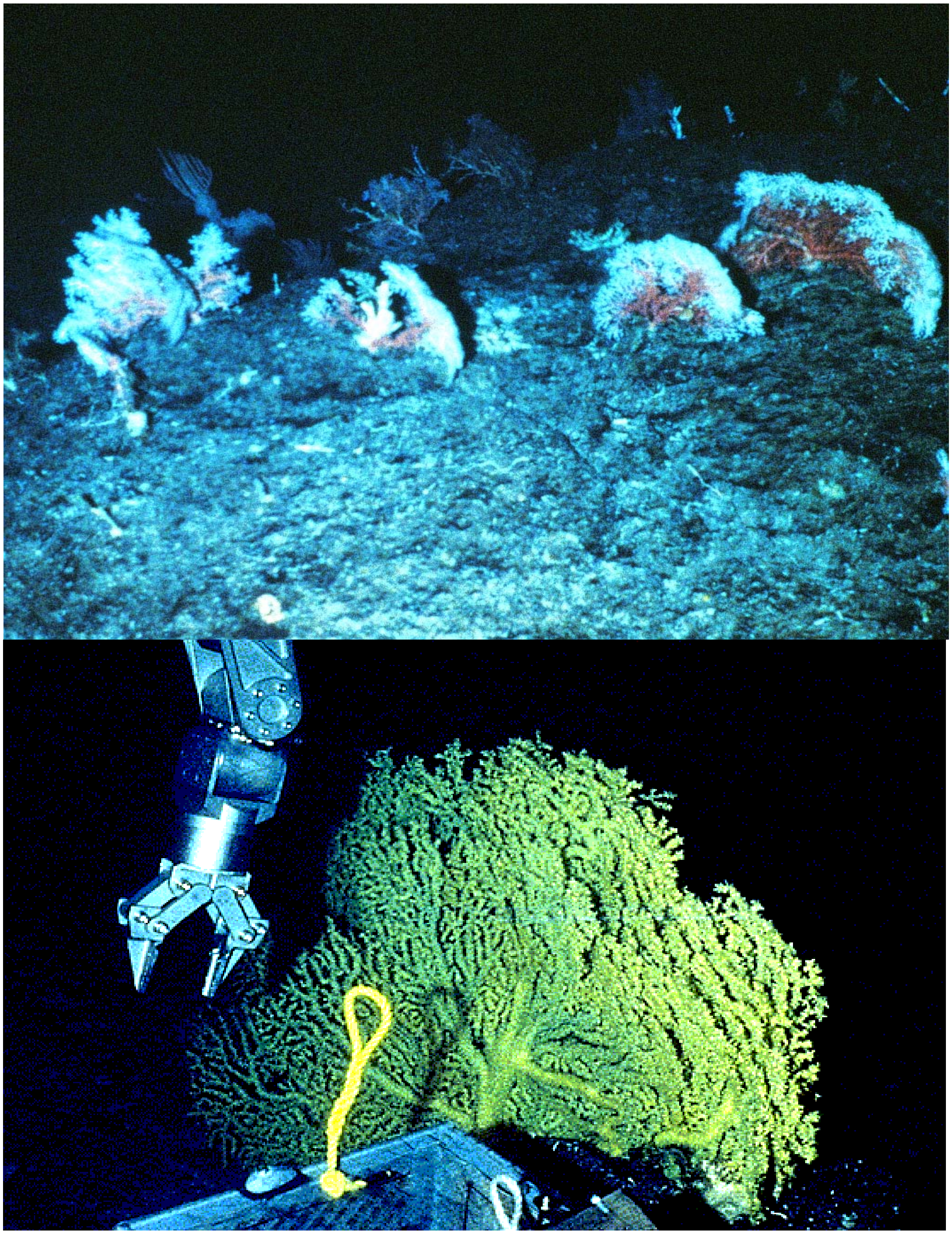

Figure 1. Representative morphology of the two genera of deep-water corals assessed in this work. *Corallium* sp. (pink coral) form colonies less the 30 cm in height (top) whereas *Gerardia* sp. (gold coral) grows to 150 cm in height (bottom).

which occurs in pink (*C. secundum*) and red (*C. lauuense*) species reaching heights of 30 cm. For the purposes of this work, I will refer to all *Corallium* (pink and red) as pink coral. *Gerardia* sp. is an imposing hexacoral with flexible branches that grows to heights of well over 100 cm. Both genera are known to colonize locations of high flow (Grigg, 1993) and were found at the two subphotic sites visited by FFS seals.

METHODS

Submersible Survey Methodology

All the subphotic data were collected in a series of submersible dives using the *Pisces V*, *Pisces IV,* and *RCV-150* to survey depths between 300 and 500 m (1998, 2000, and 2001). Dive sites, hereinafter referred to as stations, included Makapuu, Keahole, and Cross Seamount in the Main Hawaiian Islands (MHI) and Brooks Bank, East French Frigate Shoals (FFS) Platform, and WestPac Bank in the Northwestern Hawaiian Islands (NWHI) (Fig. 2). Submersible surveys at each station consisted of four transects covering a 3,600 m^2 swath of bottom along the 350 m, 400 m, 450 m, and 500 m contours. However, the physiography of the slope varied considerably and often dictated restructuring of transects within the depth range. The submersibles were three-person vehicles with the pilot situated in the center and observers on either side. Each person can see an illuminated bottom area of ~55 m^2 through view ports directed diagonally forward and down. The cumulative view from the three view ports (adjusted for overlap) provides an effective illuminated survey area of ~120 m^2. A video camera on each side of the submersible was operated continuously, and the edited video feed from the cameras was recorded throughout the dive. The *RC-150* is a remotely operated vehicle (ROV); the pilot and observers watch a live video feed aboard the ship while the tethered vehicle navigates below. This camera views a bottom area of ~46 m^2 .

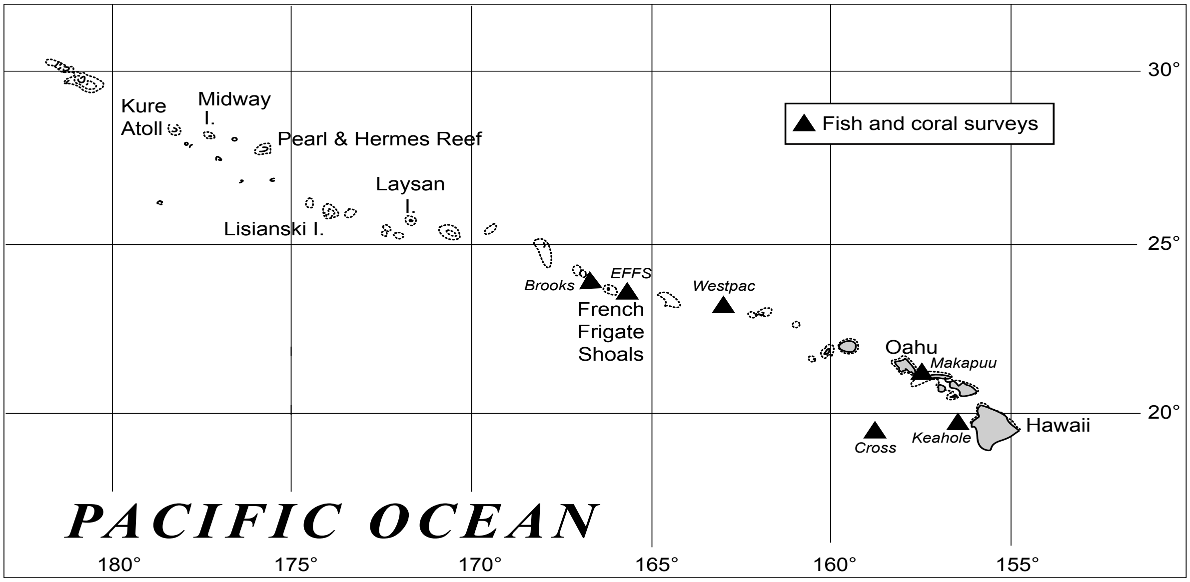

Figure 2. Map of the Hawaiian Archipelago with locations of dive stations.

Fish and corals were identified to genus, if not species, and visual counts of fish with their lengths and corals with their heights were recorded cumulatively for 5-min segments to obtain numerical density and size structure information. A brief break (~30 sec) was taken between each segment. This pseudo replication technique is common in ecological sampling (Oksanen, 2001) and has been used effectively to survey fish assemblages from *Pisces* and *RCV-150* submersibles in prior studies (Moffitt and Parrish, 1992; Parrish et al., 2002). A laser reference scale was projected on the bottom within the view of the video cameras used on each of the submersibles to assist the observers in estimating the lengths of fish and height of corals. In addition to the fauna, the surveys logged substrate type and relief scale using three categories. Substrate was divided into categories of sand, carbonate hard bottom, and basalt/manganese. Relief was divided into categories of flat, even bottom called "hardpan" (< 15 cm relief); uneven bottom "outcrops" (15- 90 cm); and steep surfaces such as "pinnacles" or cliffs (>90 cm). Any fish seen orienting close to a coral tree (presumably using it as shelter) was recorded. All fish taxa were divided into one of four prey-evasion guilds including bottom hider, bottom fleer, bottom camouflage, and midwater fleer.

The opportunistic nature of these submersible surveys and modifications to the study design because of weather and mechanical problems resulted in a temporally unbalanced data set. Surveys were conducted in 1998, 2000, and 2001 during the fall of each year (September to November). For some stations, multiple dives were made in the same year; at other stations dives were separated by years. For this reason, "year" was not included as a variable in the analysis.

Analysis

The fish and coral data were nonnormally distributed, and could not be normalized by conventional transformations. For this reason, all analyses relied on nonparametric techniques. Coral preferences for substrate and relief were assessed using Mann-Whitney (M-W) and Kruskal-Wallis (K-W) tests, respectively. The association of fish with each of the two coral genera was assessed individually. To test the null hypothesis for fish numerical density, fish length, and fish biomass density, all pseudo replicates of sites with corals were pooled and compared to those without corals using a Mann-Whitney test. A Wilcoxon related samples test was run using the variable station to compare pseudo replicates with and without corals. Spearman correlations were used to determine the degree of association between variables identified as relevant in the prior analyses. In circumstances where there was reason to suspect colinearity between explanatory variables, a parametric partial correlation analysis was used to describe the linear association between two variables while controlling for the effects of a third. The size structure of trees that had fish hiding in them was then compared to the size structure of trees without fish to see whether fish preferentially sheltered in the largest trees. Descriptive statistics were computed to describe the species and seal-evasion guilds that comprise the fish assemblages found in the trees. Sample sizes for all analyses were adequate to detected differences at large-effect sizes with alpha at 0.01 and a power of 0.80.

RESULTS

Habitat Description

The stations varied in their topography, habitat and corals. Details of the substrate, relief, and coral type for each of the stations are presented in Table 1. Some stations were on summits, such as Cross Seamount, whereas others were on the flanks of islands and shallow banks, such as Brooks Bank or Makapuu Point. The bottom substrate and relief at these sites ranged from a homogenous continuum of one type to a combination of all types at a single site, such as the FFS Platform.

Table 1. Number of pseudo replicates, mean depth, prevalent substrate type, relief type and coral type for each of the known coral beds at various stations in the Hawaiian Archipelago during 1998, 2000, and 2001. FFS stands for French Frigate Shoals.

Station	No. pseudo replicates	Mean Depth (m)	Primary substrate	Primary relief	Coral type
Brooks	127	485	Carbonate/basalt	Pinnacle	Pink-R* / gold
FFS	275	379	Basalt	Pinnacle	Gold
WestPac	141	368	Carbonate	Hardpan	Pink
Makapuu	126	398	Carbonate	Hardpan	Pink
Keahole	70	387	Carbonate/basalt	Outcrop	Pink-R* / gold
Cross	158	389	Basalt	Pinnacle	Gold

* Pink-R indicates *Corallium lauuense*.

Other than a general depth range and the assumption that areas of high water flow over exposed bottom were needed for successful coral growth, there was no basis found for predicting where the coral beds would occur. Coral composition varied among stations. Some stations had more gold coral (*Gerardia* sp.) or more pink coral (*Corallium* sp.). A few stations had the two taxa intermixed (Table 1). Density of coral colonies in the beds was higher for pink coral (mean 88±(sd)149/ha) than for gold coral (mean 42±(sd)54/ha). When a submersible transect first encountered a coral bed, the initial sightings of individual corals would increase quickly to a high numerical density within the span of a single pseudo replicate, making coral presence-absence type analyses viable. Gold coral was found in significantly greater density on manganese/basalt substrate (MW $Z=-6.18$ $P<0.01$) and differed by relief type (KW, $\chi^2=164.9$ df=2 $P<0.01$). *Post-hoc* multiple comparisons attributed the relief significance to greater densities of gold corals encrusting "pinnacle"-type relief versus the flat or outcrop relief types (Tukey $Q=11.5$ & 12.1, $P<0.05$). Most of the pinnacles surveyed were composed of manganese/basalt which probably explained the substrate differences identified above. In contrast, the density of pink coral was significantly higher on carbonate substrate (MW, $Z= 83.4$, $P<0.01$) and flat bottom (KW, $\chi^2=54.9$, $P<0.01$; Tukey $Q=5.5$ & 6.2, $P<0.05$).

Fish Diversity, Density, and Biomass

The surveyors counted and sized 13,295 fish in a total of 897 pseudo replicates. Depth was positively correlated with fish size ($r_S = 0.154$, $P<0.01$) but negatively correlated with fish numerical density ($r_S = -0.303$, $P<0.01$). A total of 42 taxa were identified. Many of these fish were eel-shaped and moved more slowly than shallow-water species. The number of taxa did not change appreciably between areas with coral (w/gold n=41, w/pink n=39) and those without (w/o gold n=42, w/o pink n=40). The top 20 taxa identified in this analysis comprised 94% of the total number of fish sampled and are listed in Table 2. Eleven of these taxa were present at all stations. The absence of some taxa from some stations did not fit any obvious latitudinal or physiographic pattern. All taxa were used in the analysis of fish and coral association, because it is not known which of the fish taxa are eaten by seals. Multiple dives at each station generated a median of 150 pseudo replicates for each station. As with many field studies, it was not possible to balance sampling across substrate, relief, and coral type for all stations, but all types were well represented in the data.

Effect of *Gerardia* Sp. (Gold Coral)

Table 2. The top 20 fish taxa ranked by the number of pseudo replicates in which each taxon was seen. Also included is the mean number of fish per pseudo replicate where each taxon was sighted and the seal prey-evasion guild (BC=bottom camouflage, BF=bottom fleer, BH=bottom hider, MF=midwater fleer).

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

Gold corals were found at depths from 350 to 516 m (N=199 replicates), and supported significantly greater fish densities (MW, Z= -2.9, $P<0.01$) than tracts of bottom in the same depth range without gold coral (N=399 replicates). An analysis comparing across related samples (within station) of coral (N=191) to non-coral (191) pseudo replicates similarly indicated significantly greater densities of fish around gold coral (Wilcoxon Z=-3.34, $P<0.01$). However, persistent high counts of *Symphysanodon maunaloae* at the east FFS station strongly influenced the analysis. If the FFS station is excluded, no difference in numerical density is evident in either the pooled (MW Z= -3.1, P=0.76) or related sample comparison (Wilcoxon Z=-0.316, P=0.75). Fish body size did not differ significantly between sites with gold coral and sites without (MW, Z= -1.0, P=0.312 or Wilcoxon Z=-1.35, P=0.17).

Relief type significantly affected fish numerical density (KW, 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. Significantly more fish were found around pinnacles (Tukey, Q= 5.0 & 3.5, $P<0.05$), and these fish were on average smaller (Tukey, Q= 52.0 & 60.7, $P<0.05$). A potential for covariance with sources of high relief existed between the fish data and gold coral data, so all the variables with depth were assessed using Spearman correlations. Weak correlations were evident between the density of gold coral and fish numerical density (r_s=0.12, $P<0.01$) and relief scale (r_s=0.37, $P<0.01$). However, the positive association between coral density and fish numerical density was lost (r_s=0.02, P=0.34) in a partial correlation when the effects of relief were controlled.

Effect of *Corallium* Sp. (Pink Coral)

Pink coral was documented at depths of 328-573 m. Fish numerical density, length, and biomass density in areas with pink coral (N=312 pseudo replicates) were not significantly different from those without pink coral (N=557 pseudo replicates) within this range (MW, Z= -0.016 to -1.6, P=0.093 to 0.98). Comparing across related samples (within station) of coral (N=215) to non-coral (215) pseudo replicates similarly indicated no significant differences associated with the presence of pink coral (Wilcoxon Z= -0.26 to 1.06, P=0.28 to 0.79). In some beds, the relatively small pink corals are intermixed with the much larger gold corals (Brooks Bank, Cross Seamount, Keahole Point), potentially confounding the comparisons. The analysis was rerun using only data from the stations of WestPac Bank and Makapuu Pt. to address exclusively beds of pink coral, and still no effect was detected for any of the fish data (MW, Z= -0.89 to -3.8, P=0.37 to 0.55). Similarly, follow up correlations indicated that pink coral had no significant effect on fish numerical density, body length or biomass density (r_s= -0.03 to -0.01, P=0.62 to 0.85).

Evasion Guild Comparison

The numerical density of the seal prey was compared between areas with and without corals. Areas with gold coral were found to have significantly more bottom hiders (MW, Z= -4.03, $P<0.001$)(Fig. 3). However, again this finding lost significance when the FFS site was excluded (MW, Z= -1.4, P=0.14). The body lengths of evasion guilds were indistinguishable between areas with and without gold coral (MW, Z=-0.027 to -0.205, P=0.10 to 0.98) except for the bottom camouflage guild (MW, Z= -2.8,

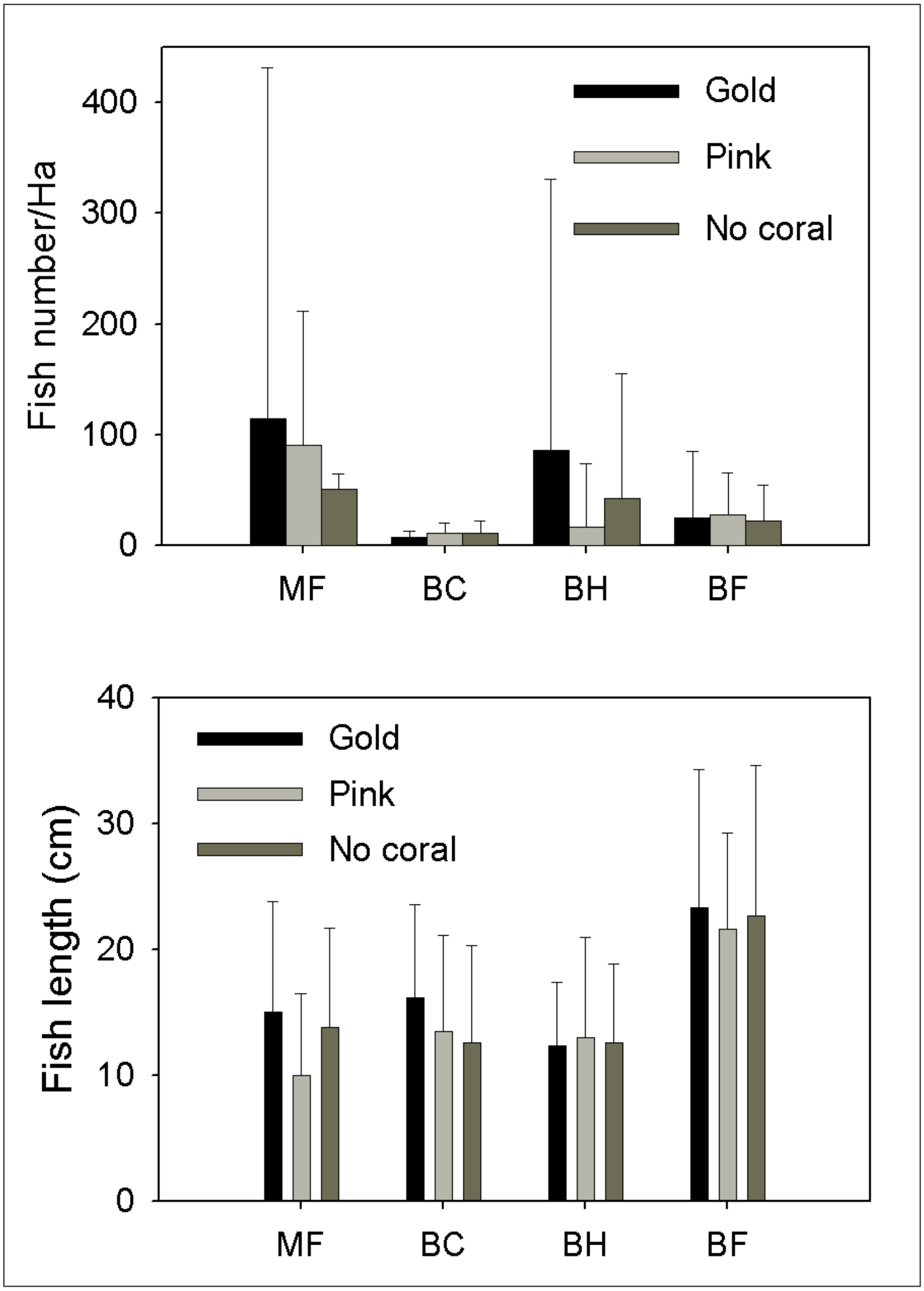

Figure 3. Numerical density (top) and body length (bottom) of fish data divided into seal prey evasion guilds with values for sites with gold, pink, and no coral (MF=midwater fleer, BC=bottom camouflage, BH=bottom hider, BF=bottom fleer). The error bars indicate the standard deviation.

P<0.01). 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 guilds differed significantly between sites with and without pink coral (MW, Z= -0.44 to -1.85, P=0.064 to 0.66).

Corals as Shelter for Monk Seal Prey

Using data from all stations surveyed Archipelago-wide (N=1,452 pseudo replicates), only 93 pseudo replicates documented fish using coral trees as shelter. These 286 fish represented 13 taxa and are listed in Table 3. All these taxa were seen commonly using abiotic sources of benthic relief, so none are thought to be exclusively dependent on coral colonies. Almost all were bottom hiders (>90%). Based on the survey counts, an estimated 2,900 gold coral colonies, 11,916 pink colonies, and 79,397 colonies of other coral types (ranging from single filamentous whips to tall branched trees) were inspected during these surveys. The survey counts above should not be construed as actual numbers of coral colonies, because they probably include counts of some of the same colonies on successive survey years. The height of coral colonies ranged from 5 to 180 cm for gold coral and 5 to 60 cm for pink coral (Fig. 4). Most of the fish (73%) were seen with the taller gold coral colonies.

Table 3. List of taxa that used coral colonies as shelter, with the number of pseudo replicates in which they were observed, the mean number of fish counted, the mean standard length of the fish, and the mean height of the host colonies in centimeters.

Taxa	Pseudo replicates	Mean No. fish (sd)	Mean size (cm)	
			Fish length	Coral height
Symphysanodon maunaloae	98	16.3 (19.8)	13.6	100
Antigonia sp.	62	1.6 (0.8)	11.9	75
Hollardia goslinei	36	1.2 (0.4)	11.1	108
Grammicolepis brachiusculus	7	1.2 (0.4)	25.7	103
Moridae	6	1.0 (na)	18.0	100
Stethopristes eos	6	1.0 (na)	9.1	150
Epigonidae	5	6.5 (6.9)	5.0	100
Beryx spp.	5	5.0 (na)	15.0	120
Congridae	5	2.5 (2.1)	28.0	132
Scorpanidae	4	1.3 (0.6)	16.2	103
Cytonemis	4	1.0 (na)	7.5	64
Macrouridae	1	1.0 (na)	40.0	135
Synaphobranchidae	1	1.0 (na)	40.0	70

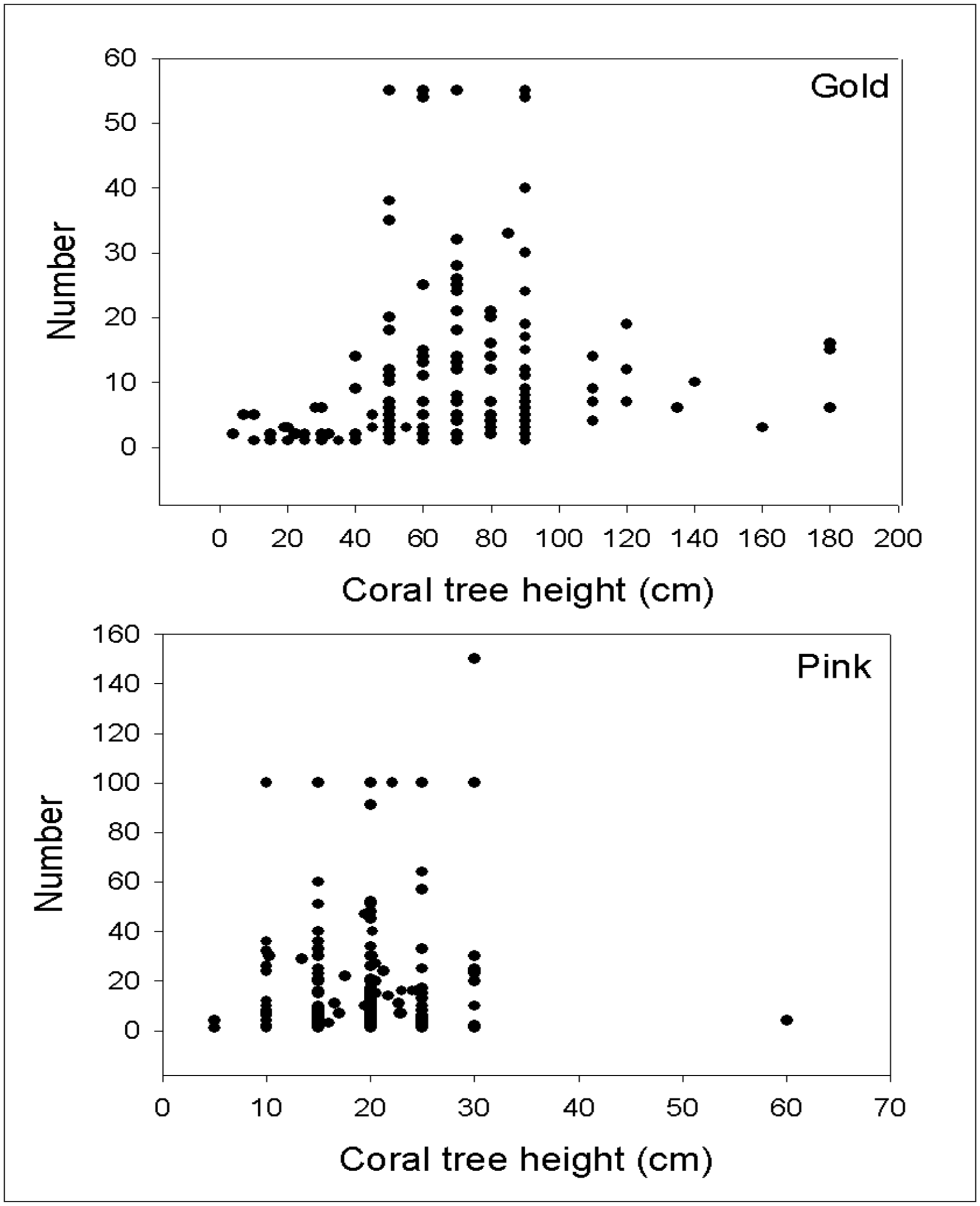

Figure 4. Median height of gold (top) and pink (bottom) coral trees for each 5-min survey segment with coral.

DISCUSSION

Substrate and Relief

There were obvious differences among the substrate, relief type, and corals at each of the stations. It appears that the two coral types prefer different habitat configurations. Habitat measures used in this work were limited to three types of substrate (sand, carbonate, basalt/manganese) and three relief categories (hardpan, outcrops, and pinnacles). Even with this crude resolution, it was clear that the carbonate hardpan of the Makapuu station looked the same as that at the WestPac station, and that both supported dense populations of pink coral. The basalt pinnacles on the summits of Cross Seamount and the FFS Platform were similar, and each was encrusted with gold coral. Brooks and Keahole were a mix of basalt and carbonate outcrops, and both supported gold and the *Corallium lauuense* variety of pink coral. Although these habitat associations were for the most part consistent, coral success also is related clearly to localized water flow, a variable not measured in this study. High-relief features can divert water movement and enhance localized water flow, in which corals thrive. This would explain why the scale of relief was the only bottom variable that significantly influenced gold coral. Gold trees were grouped on the tops of pinnacles, on the top edges of cliffs, and along sharp bends in walls. All these bottom features intensify water flow and probably improve the corals' growth. Indeed, on a number of dives working in gold coral beds, the submersible was forced to hide from the current until the flow abated, and on one occasion the submersible was pinned against a cliff face by the strength of the local current.

An association with topographic features and flow was not identified for pink coral. The two largest beds (Makapuu and WestPac) were on hardpan, nearly devoid of relief. It may be that the low-standing, crustose fan of pink coral is better suited to more unidirectional or lower-speed flow than the more intense and perhaps multi-directional flow in which gold corals thrive. Future work is planned to determine the water flow characteristics with which the two corals associate.

Fish Assemblage

Avoidance of the submersible and its projected light field varied among fish species. Most of the fish were slow-moving and appeared oblivious to the submersible until nearly struck by the vehicle. Infrequent, large transient fish such as snappers and mackerel moved out of the light field, but these were a small fraction of the fish assemblage, and many were too large to be considered seal prey. These fish surveys were appropriate to address two types of fish assemblages — coral-sheltering assemblages and aggregated assemblages. Surveying fish that use coral colonies as shelter is straightforward. Fish seen in the trees were considered to be sheltering. However, determining when fish were aggregated was often difficult. At shallower depths, aggregating effects have been documented in both benthic systems (Anderson et al., 1989) and pelagic systems (Gooding and Magnuson, 1967). The degree to which fish are concentrated around a source of shelter varies by taxa, so counting the fish around corals is as important as counting fish in the coral branches. The 5-min psuedo replicate survey effectively encompasses the coral and the immediate surroundings. Of the top 20 fish taxa, none appeared exclusively associated with either of the coral types examined. The high densities of *Symphysanodon maunaloae* at the FFS station and *Polymixia* at the WestPac station were atypical of the other stations surveyed. The occurrence of other taxa was comparable across all stations. Of the top 20 taxa, only *Polymixia* and eels

(Congridea, Ophicthidae) were documented as prey from prior scat analyses (Goodman-Lowe, 1998). However, a large number of eel fragments (mostly vertebra) in the scats were classified as "unidentified eels," and many of the eels and eel-like fish in the top 20 taxa could be some of these unidentified eels.

Corals and Fish Assemblages

Generally, fish are attracted to habitats for food or shelter. This work only tested whether fish were in higher concentrations in and around the corals and did not address the reasons. We expected gold coral would be more of a fish attractant than pink coral due to its large size and flexible nature. However, gold coral also has polyps that illuminate when brushed. Thus, a fish moving through the branches of the tree might cause it to glow, attracting attention and bringing other conspecifics or predators.

Based on the fish counts alone, greater fish numerical density occurred in areas with gold coral. However, when the known effects of bottom relief (Friedlander and Parrish, 1998) and depth (Thresher and Colin, 1986; Chave and Mundy, 1994) are accounted for, the relationship with gold coral loses statistical significance. This makes it hard to attribute any increase in fish density to the presence of gold coral. Areas with high relief (e.g., pinnacles, walls) constrict water movement and increase flow speed, and both corals and fish benefit by feeding on the increased delivery of drifting particulates (detritus and zooplankton). There is no clear evidence that the coral colonies aggregate a fish community. All that can be said is that corals and fish exploit the same type of high relief and high flow habitats.

Pink corals were less associated with bottom relief features, and there was no identified co-occurrence with fish as there was with the gold corals. The lack of shelter afforded by the smaller pink corals and the flat pavement bottom they colonize could explain the lack of fish. Another possibility is that gold and pink coral exploit significantly different flow regimes, and fish do better in the gold coral flow regime. However, understanding this situation will require a separate investigation. Tall coral trees, most often gold coral, were used as shelter by some fish. Other coral genera fish used as shelter included the taller trees of *Callogorgia*, *Calyptrophora*, and *Leiopathes*.

Evaluation of fish data using seal prey-evasion guilds showed significantly more bottom hiders around gold coral. No other guilds were associated with gold or pink coral. Bottom hiders typically maintain position and shelter around a source of relief and opportunistically feed on the passing drift. Hence, these fish have evolved to make use of relief and high-flow sites irrespective of the presence of corals. Fish co-occur with corals, but obligate interdependency is not supported by the data.

Few studies have been done on fish associations with deep-water corals. In the Atlantic, Husebo et al. (2002) compared fish catches from longlines and gillnets deployed at areas with coral beds (*Lophelia pertusa*) and at areas without coral. They reported significantly more *Sebastes marinus* (a bottom hider) in area with corals and that they were at least similar to numbers of two other species. They attributed the greater numbers of *S. marinus* to the fish's use of the corals' physical relief as shelter. Their results are consistent with the increased number of bottom hiders observed in

Hawaiian coral beds. However the Husebo et al. (2002) study was only able to account for habitat effects in a general sense. *Lophelia pertusa* grows on exposed rock outcrops and pinnacles and not in the mud flats that the authors reported as the habitat surrounding the bed, making it difficult to isolate the effects of the coral. Syms and Jones (2001) tested the importance of soft corals in the fish community by conducting baseline surveys of some test reefs, then removing the corals, and then resurveying the fish community for a period of 2 years. The baseline surveys on the test reefs revealed that higher fish abundance is correlated with density of soft corals. However, the experimental removal of soft corals resulted in no change to the fish assemblage over a 2-year period of monitoring. This may be a shallow-water example of corals and fish co-occurring in optimal conditions (e.g., high flow). Recent surveys by Boland and Parrish (2005) of fish assemblages in relation to shallow-water black coral trees (*Antipathes dichtoma*) found that the fish assemblage uses the trees generally as shelter much as they used other comparable abiotic relief. Few taxa were documented to rely exclusively on the coral colonies. Based on the available literature, corals and fish appear to co-occur in high densities at areas of relief and high flow. Subphotic fish in Hawaiian waters appear to use deep-water corals interchangeably with abiotic relief sources with no significant difference. However, it is important to remember that all the present surveys were conducted during the day and at the same time of year, so any nocturnal or seasonal differences in fish association with corals were undetected.

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