# Density and habitat of three deep-sea corals in the lower Hawaiian chain

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**Abstract**

Subphotic contours were surveyed between 350 and 500 m at six deep-sea coral beds in Hawaii. The density and mean height for the deep-sea corals *Corallium secundum* Dana, 1846, *Corallium lauuense* Bayer, 1956, and *Gerardia* sp. at each bed were recorded relative to temperature, substrate, and bottom relief. Species composition and density at the six sites varied; however, the mean size of the coral colonies did not vary except at sites where there was a history of coral harvesting. The *Corallium* species had the highest densities and, at some sites, were found in mono-specific patches. The three coral taxa overlapped in their depth range. Water temperature varied as much as 3–4 °C across the six stations. Multi-year monitoring at two of the sites indicated that temperature differences persisted year-round and exhibited monthly and seasonal fluctuations. All three coral taxa colonized both carbonate and basalt/manganese substrates. The largest patches of *C. secundum* were found on flat exposed bottom, whereas *C. lauuense* encrusted uneven rocky bottom. *Corallium lauuense* was often intermixed with *Gerardia* sp., which colonized cliffs, pinnacles, and the tops of walls. Of the habitat variables, bottom relief best explained the distribution of the three coral taxa. It is hypothesized that the corals favor areas where bottom relief enhances or modifies flow characteristics perhaps improving the colony's feeding success.

Deep-sea coral research in the central Pacific has been focused on describing the geographic range (Grigg, 1974), taxonomic diversity (Grigg and Bayer, 1976), or genetic diversity (Baco and Shank, 2005) of deep-sea or cold-water corals. Few ecological studies have been conducted because of the difficulty of working at greater depths where the corals grow (Genin et al., 1992). Recent analyses of coral distributions and environmental variables at a continental shelf scale indicate there are notable habitat differences between different coral taxa (Gass and Willison, 2005; Leverette and Metaxas, 2005; Watling and Auster, 2005). In the central Pacific, most of what has been learned about deep-sea corals was achieved in conjunction with the Hawaiian precious coral fishery, which uses deep-sea corals as raw materials for the jewelry trade. Three coral species emerged as the basis of this unique small-scale fishery: the short crustose gorgonian fans (Bayer, 1956), *Corallium secundum* Dana, 1846 and *Corallium lauuense* (formally called *Corallium regale*) Bayer, 1956, and the tall flexible hexacoral, *Gerardia* sp. These are commonly referred to as pink, red, and gold coral, respectively. The activity and scale of the fishery is well documented by Grigg (1993, 2002). Coral harvesters initially relied on crude dredges and in 1972 moved to harvesting with small submersibles. For over 30 yrs, harvesting has been sporadic, operationally small, and limited to the coastal coral beds of Makapuu, Oahu, and Keahole, Hawaii.

In recent years, upgrades in research submersibles and support vessels have provided researchers in Hawaii the opportunity to extend surveys to more remote coral beds.

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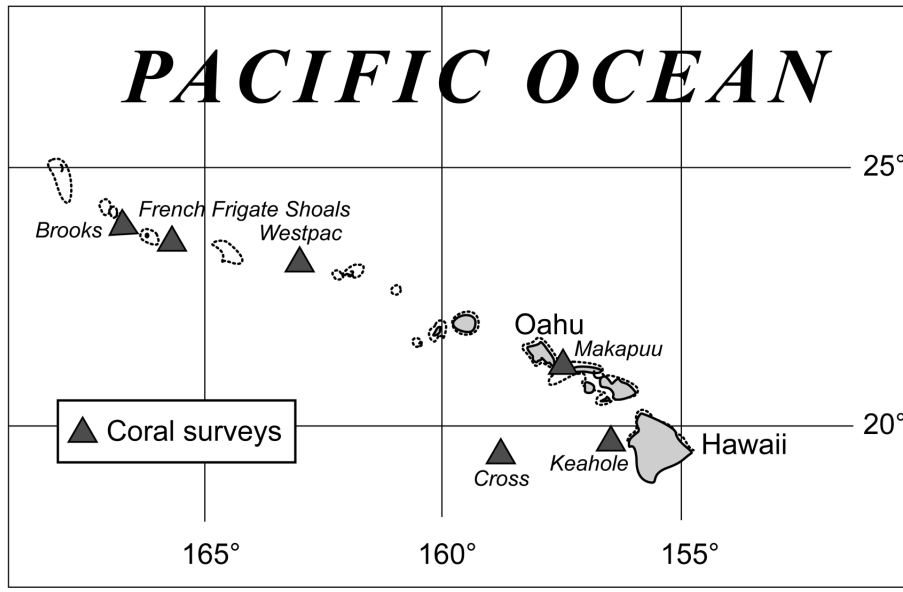


Figure 1. Map of the southern Hawaiian Archipelago with the six coral stations labeled.

Here I report the results of visual surveys at the commercially harvested Makapuu and Keahole coral beds and at four remote coral beds identified in prior studies (Grigg, 1974, Parrish et al., 2002). These surveys systematically assessed density and sizes of *C. secundum, C. lauuense,* and *Gerardia* sp. in relation to depth, water temperature, substrate, and relief types at each of the six sites.

## Methods

All data were collected in a multi-year (1998, 2000, and 2001) series of submersible surveys using the Pisces V, Pisces IV, and Rcv-150 at depths ranging from 350 to 500 m. Dive sites included Makapuu, Keahole, Cross Seamount, Brooks Bank, French Frigate Shoals (FFS), and Westpac Bank (Fig. 1). The sites varied widely in their submarine topography. Cross, Westpac, and FFS were located on the summits of oceanic seamounts. The Cross bed was on a peak, the FFS bed on encrusted pinnacles along a ridge, and the Westpac bed was along the crest of the seamount's summit. The Brooks bed is on the slopes of a bank that rises to within 80 m of the surface. The Makapuu and Keahole beds are on the flanks of the large islands of Oahu and Hawaii. Makapuu is a gradual slope and Keahole is a ledge that runs along the top of a seacliff. The sampling at each site was divided into transects loosely focused along the 350 m, 400 m, 450 m, and 500 m contours. As these beds were previously identified, the transects were laid out such that roughly half of the sampling occurred in the bed and half on areas outside of the bed. This maximized the comparability of the geomorphology for areas inside and outside the bed. The sites of Brooks, Westpac, Makapuu, and Keahole had reasonably comparable bottom morphology in and outside of the bed. At Cross Seamount and FFS, the corals grew on bottom peaks and pinnacles that were less prominent (smaller and fewer) outside the coral bed.

The submersibles are three-person vehicles with the pilot located in the center and observers on either side. Each person can view 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 directed forward and down was operated continuously during the dive. The Rcv-150 is a remote-operated vehicle which surveys a 45 $m^2$ illuminated area.

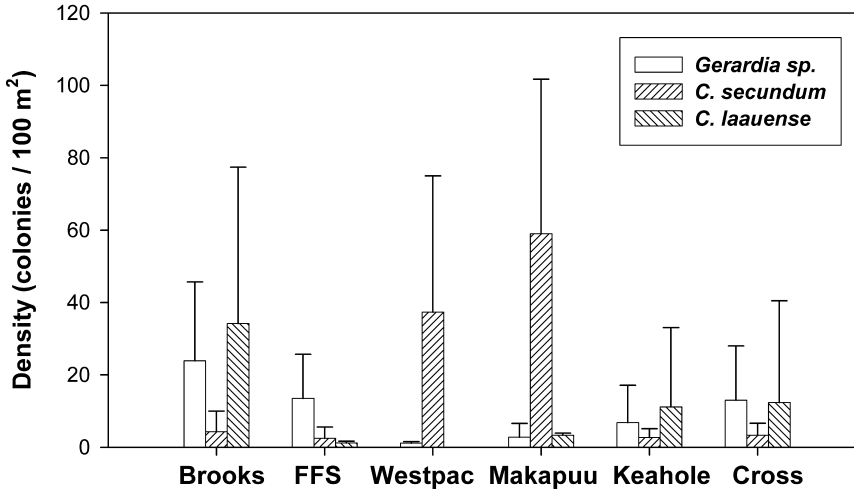


Figure 2. Mean density of three coral types for all pseudo-replicates with coral at the six surveyed coral beds.

Counts and sizes of corals were recorded cumulatively for 5-min segments or "pseudo-replicates" to obtain numerical density and size structure information. The recorded count of the corals was capped at 100 for pseudo-replicates where the density of coral colonies exceeded what observers could count. The coral counts were then normalized by the viewing area of the survey vehicle. This pseudo-replication technique is common in ecological sampling (Oksanen, 2001) and has been used effectively in surveys by the PISCES submersibles (Moffitt and Parrish, 1992; Parrish et al., 2006). A laser reference scale was projected on the bottom within view of the submersible video cameras to assist the observers in estimating coral size.

Surveys were conducted during the fall of each year (September–November). Temperature profiles of water column were recorded at each of the stations and thermographs were deployed at the most northern and southern stations for 2 yrs (2001 and 2002). For each segment, observers logged the primary 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 termed "hardpan" (< 15 cm relief); uneven bottom "outcrops" (15–90 cm); and steep surfaces such as "pinnacles" or cliffs (> 90 cm) (Fig. 2). Pseudo-replicates with multiple substrate and relief type were coded by whichever substrate and relief type was most abundant during the segment.

The coral count and size data were not normally distributed, and analyses of these data relied on nonparametric techniques. Coral occurrence by substrate type and relief class were assessed using Mann-Whitney (M-W) and Kruskal-Wallis (K-W) tests, respectively. Samples sizes for all analyses were adequate to detect differences at large-effect sizes with alpha at 0.01 and a power of 0.80.

## Results

**Coral surveys.—**Surface tracks of the submersible indicate an average 3.5 km distance covered on the visual surveys. The surveys generated a median of 150 pseudo-replicates for each station. Roughly half of the survey effort at each station focused on areas with corals (in the bed) and the other half on areas immediately adjacent, without corals (Table 1). Coral composition varied among stations. Some stations were primarily *C. secundum* or *Gerardia* sp., and the rest were a mixture of *C. lauuense* and *Gerardia* sp. (Fig. 2).

Table 1. Latitude, morphology, linear survey distance, and number of pseudo-replicates conducted, with the percent with coral in brackets, and the decimal fraction of the substrate and relief categories at each of the six sites.

| | | | | Psuedo-replicates* | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Substrate | | | Relief | | |
| Station (latitude) | Morphology | Dist. (km) | Mean SD | Total (%WC) | snd | carb | bas | hard | out | pin |
| Brooks (23°58.6′) | Bank slope | 3 | 1.2 | 114 (84) | 0.03 | 0.97 | 0.00 | 0.69 | 0.24 | 0.07 |
| FFS (23°55′) | Seamount | 2.5 | 1.07 | 283 (17) | 0.04 | 0.49 | 0.47 | 0.45 | 0.37 | 0.18 |
| Westpac (23°14.2′) | Seamount | 2.8 | 1.13 | 103 (51) | 0.00 | 1.00 | 0.00 | 0.85 | 0.15 | 0.00 |
| Makapuu (21°17.5′) | Island slope | 2.8 | 1.39 | 113 (69) | 0.07 | 0.93 | 0.00 | 0.98 | 0.02 | 0.00 |
| Keahole (19°47.7′) | Island slope | 7.3 | 2.6 | 69 (55) | 0.19 | 0.78 | 0.03 | 0.55 | 0.24 | 0.21 |
| Cross (18°43.3′) | Seamount | 3.2 | 0.73 | 150 (36) | 0.38 | 0.15 | 0.47 | 0.13 | 0.66 | 0.21 |

* %WC = pseudo-replicates with coral, snd = sand substrate, carb = carbonate substrate, bas = basalt/manganese substrate, hard = hardpan relief, out = outcrop relief, pin = pinnacle relief.

The coral beds were generally most dense at the center of the patch with colonies diminishing precipitously around the edges. Coral tallies often captured individual corals on the edge and the high density of the patch center in a single pseudo-replicate, making presence-absence type analyses viable. Of the pseudo-replicates with corals, *C. secundum* had the highest density (56 ± 65 colonies 100 $m^{-2}$) and were found predominantly at Makapuu and Westpac. *Corallium lauuense* exhibited the next highest density (33 ± 63 colonies 100 $m^{-2}$) and then *Gerardia* sp. (13 ± 17 colonies 100 $m^{-2}$). The concave "dish" of the coral colonies in a patch generally oriented in the same direction, presumably perpendicular to the prevailing flow pattern in the area to improve feeding opportunities. Consistency in the orientation of the colonies was most apparent for *C. secundum*, less for *C. lauuense*, and not obvious for *Gerardia* sp. The mean size of *C. secundum* colonies at Makapuu was significantly greater than the mean colony size at Westpac (Table 2). There was no apparent difference for *C. lauuense* coral among Brooks, Keahole, and Cross sites. However, *Gerardia* sp. colonies at Keahole were significantly smaller than at Cross and FFS but did not differ from Brooks (Table 2).

**Habitat variables.—**Overlap occurred in the depth range of the three corals. Plotting coral density by depth showed a tendency for *C. secundum* to be shallower and *C. lauuense* and *Gerardia* sp. to extend deeper. This pattern may not be depth-related; but instead, be an artifact of differing physiography among stations. Corals at Brooks Bank ranged from 350 to 550 m whereas the FFS and Keahole corals clustered over a tighter depth range, encrusting discrete bottom features such as a pinnacle or the top edge of a wall (Fig. 3). Temperature-depth profiles at the six stations showing greater depths did not necessarily signify colder temperatures. The thermograph records indicate temperature varied as

Table 2. Comparison of mean heights of coral colonies among sites.

| Coral taxa | Height (cm)/ mean (SD) | Nonparametric test | df | P | A posterior comparisons (0.05 threshold) |
|---|---|---|---|---|---|
| *Corallium secundum* | 17.9 (4.5) | Mann Whitney: $Z = -2.0$ | 1 | 0.05 | Westpac < Makapuu |
| *Corallium laauense* | 20.3 (6.4) | Kruskal Wallis: $\chi^2 = 1.05$ | 2 | 0.589 | Brooks, Keahole, Cross; no diff |
| *Gerardia* sp. | 66.5 (30.7) | Kruskal Wallis: $\chi^2 = 22.6$ | 3 | 0.000 | Keahole < FFS, Cross; Brooks no diff |

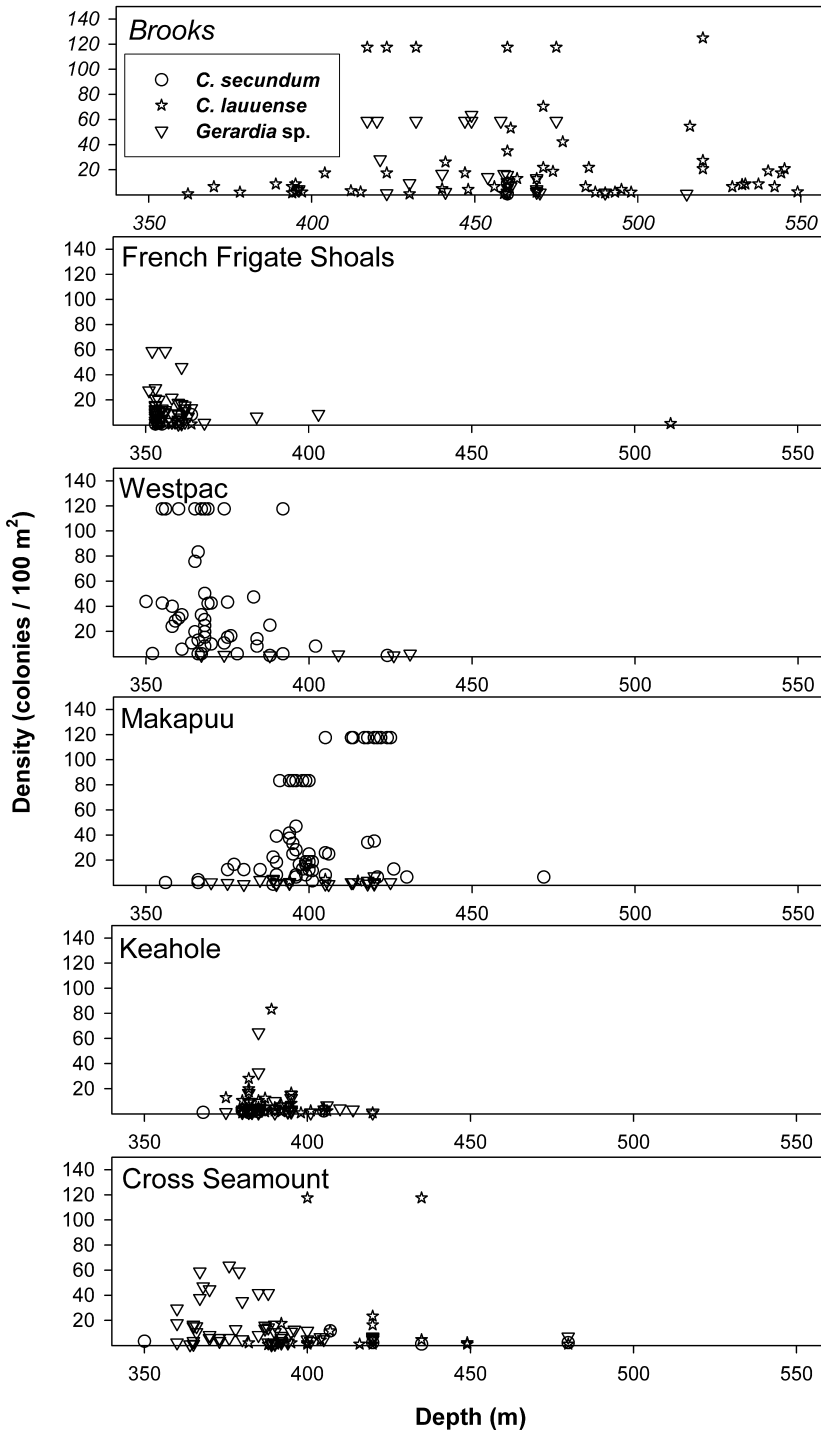


Figure 3. Coral density of pseudo-replicates with coral plotted by depth for each of the three taxa at the six sites.

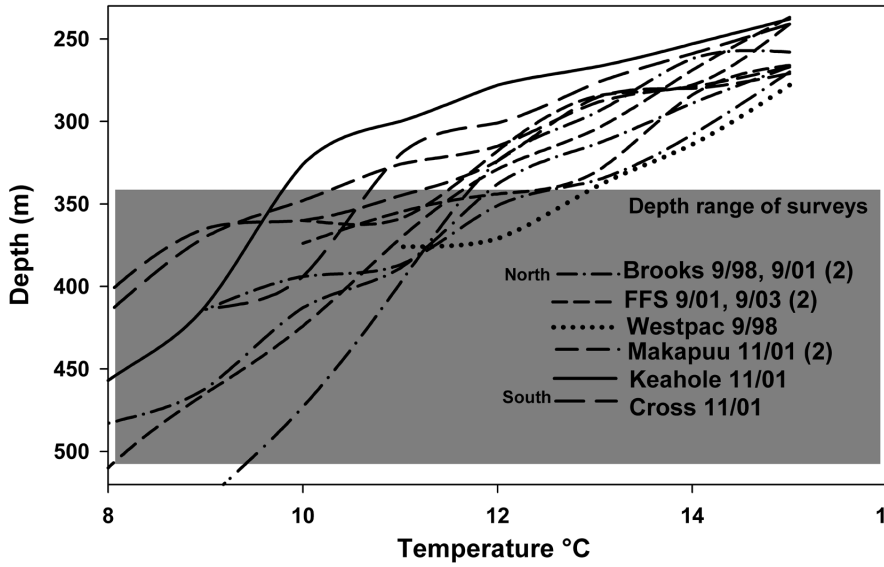


Figure 4. Temperature profiles of the water column measured during the submersible dives at the six coral beds. The number 2 in parentheses following the month/year for each site indicates two dives were made.

much as 4 °C between the latitudinal extremes of the study sites (Fig. 4). These differences persist year-round with monthly, seasonal, and inter-annual variability (Fig. 5).

It was not possible to equally distribute sampling across the three substrate and three relief types for all stations, but all types were well represented in the data (Table 1). The substrate and relief at the six sites ranged from a continuum of one type, such as carbonate hardpan at Makapuu, to a combination of all types at a single site forming a complex matrix, such as the FFS Platform. Sand was the dominant substrate in 11% of pseudo-replicates and, as expected, few corals were found in these segments and the colonies were usually on an isolated rock or high point above the sand scour. Since sand was clearly marginal substrate, pseudo-replicates dominated by sand were eliminated from further analysis. The two *Corallium* species were found in significantly greater density (Mann-Whitney: *C. secundum* $Z = -8.3$, $P < 0.001$; *C. lauuense* $Z = -1.9$, $P < 0.04$) on carbonate substrate. In contrast, *Gerardia* sp. was found more on manganese/basalt substrate (Mann-Whitney: $Z = -6.18$, $P < 0.01$). The patterns seen in the substrate may have been a function of differing scales of bottom relief. *Gerardia* sp. density differed by relief scale (Kruskal-Wallis: $\chi^2 = 238$, df = 2, $P < 0.001$) and was found encrusting pinnacles and cliff faces more than the hardpan or outcrop relief types. These pinnacles and walls were often of manganese/basalt substrate, suggesting a possible cross correlation between substrate and relief types. Despite the similar morphology of the two *Corallium* species, they exhibited different affinities by relief type. *Corallium secundum* (Kruskal-Wallis: $\chi^2 = 132$, df = 2, $P < 0.001$) was found in high densities on flat, hardpan bottom (most often carbonate substrate) whereas *C. lauuense* (Kruskal-Wallis: $\chi^2 = 12.4$, df = 2, $P = 0.002$) was found on outcrops and ledges (usually carbonate but sometimes basalt/manganese substrate).

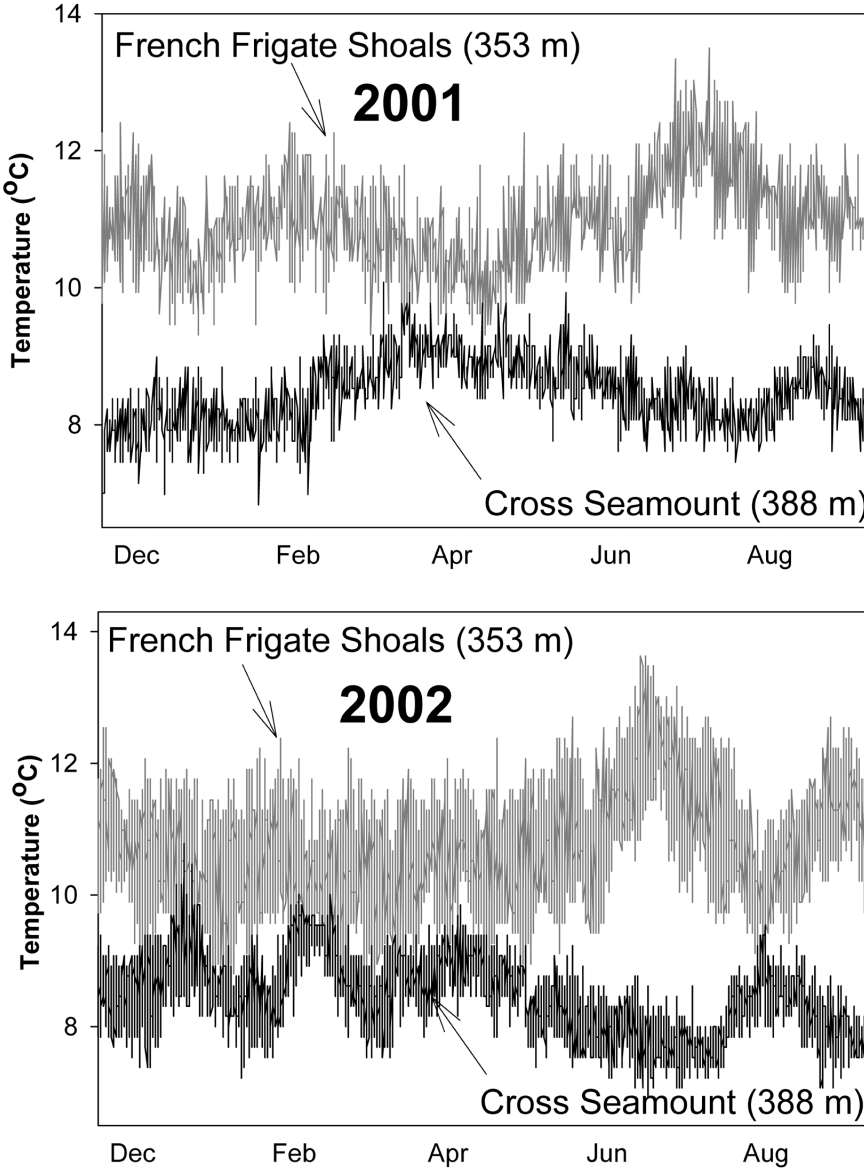


Figure 5. Two years of water temperature data from the most northern and southern coral beds of the six survey sites.

## Discussion

**Coral beds.—**The bed's composition of coral species varied among sites but exhibited surprising within-site homogeneity. The dominance of *C. secundum* at Makapuu and Westpac was the most striking. Colonies of *Gerardia* sp. and *C. lauuense* were seen at these sites, but they were few in number and generally small in size. Makapuu had the highest colony density despite the longest history of coral harvesting (Grigg, 1993). The most recent harvesting activity occurred in 1998–2001. Some areas were encountered where harvesting appeared to have occurred, probably during the most recent phase of the fishery. The bed's large perimeter (Grigg, 2002) and high coral density exceed those of the other coral beds and suggests that habitat and environmental conditions at Makapuu are exceptional for *C. secundum*. Westpac is similar to Makapuu but much more remote and it has never been subject to harvesting. In comparing the size structure of coral colonies between the two sites, it is surprising to see Makapuu having significantly larger mean coral colonies despite a history of coral harvesting. A truncated size structure was expected as a result of earlier harvesting activities, but it is possible recruitment and regrowth (Grigg, 1988) over the intervening decades restored the mean size of coral colonies at the bed (Grigg, 2002). Another explanation would be that the survey dives missed the portions of the coral bed that had been impacted by earlier harvest. Assuming the survey track overlaps with areas where the fishery historically operated, the large mean colony size at Makapuu again would suggest the area has exceptional habitat and environmental conditions for *C. secundum* growth.

*Gerardia* sp. and *C. lauuense* colonies were found mixed to varying degrees across the stations. The FFS site was almost exclusively *Gerardia* sp. whereas Brooks, Keahole, and Cross beds were of somewhat equal proportions of *Gerardia* sp. and *C. lauuense*. *Corallium lauuense* has the stature and morphology of *C. secundum* but colonizes uneven outcrops, including terrain where *Gerardia* sp. occurs in numbers. *Corallium secundum* and *Gerardia* sp. were not seen to coexist in abundance, at any of the stations. Comparing the size structure of colonies at stations where *Gerardia* sp. was found in abundance (Brooks, FFS, Keahole, and Cross) revealed a smaller mean colony size of *Gerardia* sp. at Keahole. It is possible the smaller size is a result of a history of coral harvesters collecting *Gerardia* sp. from the bed. Certainly, recent harvesting (1998–2001) could be the reason, but there could also be lingering effects from earlier harvesting. The high uncertainty of growth rate estimates for *Gerardia* sp. (Grigg, 2002; Roark et al., 2006) could mean recovery to pre-exploitation levels is unlikely even over several decades.

**Temperature.—**Given the overlapping depth range among stations and the fact there was not a single station with a balanced mix of all three coral taxa suggests that depth is not the determining factor for coral distribution within the 350–500 m depth range. Generally, temperatures are cooler with increasing depth. However, the thermal profiles of the water column varied 3–4 °C among the six stations, suggesting bottom topography effects disrupt the water column stratification. Temperature may be an important environmental variable in defining the depth range for these three species to colonize but no obvious patterns emerged within the 350–500 m depth range. The 2-yr data from the thermographs indicate that the southern-most station of Cross Seamount is 3–4 °C colder than the northern-most station of FFS. Some of this difference could be a result

of the greater depth (+ 35 m) at the Cross Seamount station. However, a 3–4 °C change was not observed over a 35-m depth change in any of the thermal profiles across the six stations. Based on these limited observations, temperature did not explain occurrence patterns of the deep-sea corals.

**Substrate and relief.—**Obvious differences were seen among substrate, relief, and coral taxa at each of the stations. The detected differences in the substrate type colonized by the different corals appear to be artifacts of bottom relief which was the dominant influence. "Hardpan" relief was mostly carbonate substrate, "outcrops" were a mixture of carbonate ledges and basalt rocks, and "pinnacles" were basalt columns and carbonate cliffs. Using the crude relief scale, 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 *C. secundum*. The basalt pinnacles on the summits of Cross Seamount and the FFS Platform were similar, and were encrusted with *Gerardia* sp. Brooks and Keahole were a mix of basalt and carbonate outcrops, and both supported *Gerardia* sp. and *C. lauuense*. Although the correspondence of coral types to relief types was good, it is possible that relief serves as a proxy or modifier for near-bottom water flow conditions. Flow and particulate load were variables not considered in this study, but have been identified as important in other studies (Leverette and Metaxas, 2005). Future work should assess the effect of the relief variables on flow characteristics and suspended particles as they pertain to deep corals. Different taxa of corals may thrive in different flow conditions and bottom relief can influence flow directionality, intensity, and character (e.g., laminar, turbulent). Finally, this appraisal of corals and their habitat is subject to considerable uncertainty about coral life history. *Gerardia* sp. is a particularly good example in that it often settles on and grows over other corals that have colonized an area, suggesting that *Gerardia* sp. could be host-limited. The localized structural and environmental conditions found around *Gerardia* sp. may be more critical for the initial colonization of the host coral than to the *Gerardia* sp. itself. Future work is planned to address threshold flow values and particle suspension of the environment around deep corals. Increased insight into the habitat and environmental needs of deep-sea corals will improve our ability to locate these isolated patches for management and protection.

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