

Abstract—There is increasing interest in the potential impacts that fishing activities have on megafaunal benthic invertebrates occurring in continental shelf and slope ecosystems. We examined how the structure, size, and high-density aggregations of invertebrates provided structural relief for fishes in continental shelf and slope ecosystems off southern California. We made 112 dives in a submersible at 32–320 m water depth, surveying a variety of habitats from high-relief rock to flat sand and mud. Using quantitative video transect methods, we made 12,360 observations of 15 structure-forming invertebrate taxa and 521,898 individuals. We estimated size and incidence of epizoid animals on 9105 sponges, black corals, and gorgonians. Size variation among structure-forming invertebrates was significant and 90% of the individuals were <0.5 m high. Less than 1% of the observations of organisms actually sheltering in or located on invertebrates involved fishes. From the analysis of spatial associations between fishes and large invertebrates, six of 108 fish species were found more often adjacent to invertebrate colonies than the number of fish predicted by the fish-density data from transects. This finding indicates that there may be spatial associations that do not necessarily include physical contact with the sponges and corals. However, the median distances between these six fish species and the invertebrates were not particularly small (1.0–5.5 m). Thus, it is likely that these fishes and invertebrates are present together in the same habitats but that there is not necessarily a functional relationship between these groups of organisms. Regardless of their associations with fishes, these invertebrates provide structure and diversity for continental shelf ecosystems off southern California and certainly deserve the attention of scientists undertaking future conservation efforts.

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Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral

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Science and conservation communities are increasingly interested in the potential impacts that fishing activities have on megafaunal benthic invertebrates found in continental shelf and slope ecosystems (Dayton et al., 2002; NRC, 2002; Malakoff, 2004; Roberts and Hirshfield, 2004; Rogers, 2004). Megafaunal invertebrates (>5 cm in height) contribute significantly to biodiversity, play important functional ecological roles, and can be indicators of long-term environmental conditions (e.g., Riedl, 1971; Palumbi, 1986; Brusca and Brusca, 1990). Moreover, because large invertebrates, such as sponges and corals, enhance the

diversity and structural component of fish habitat and are vulnerable to impacts by at least some fisheries, they also may signify habitat areas of particular concern (HAPC) and as such would be protected under the Magnuson-Stevens Fishery Conservation and Management Act (Freese, 2001; Etnoyer and Morgan¹).

¹ Etnoyer, P., and L. Morgan. 2003. Occurrences of habitat-forming deep sea corals in the Northeast Pacific Ocean. Technical Report, NOAA Office of Habitat Conservation, 31 p. Marine Biology Conservation Institute, 15806 NE 47th Ct., Redmond, WA 98052.

Deep-sea corals, such as gorgonians (sea fans), antipatharians (black corals), scleractinians (stony corals), and hydrocorals, are of particular interest because they are often long-lived and slow-growing (Andrews et al., 2002; Heifetz, 2002), poorly studied (Etnoyer and Morgan¹), and in certain situations vulnerable to human activities (e.g., mobile fishing gear) (Watling and Norse 1998; Freese et al., 1999; Krieger, 2001; Dayton et al., 2002; Fossa et al., 2002; NRC, 2002;). Other megafaunal invertebrates, such as crinoids, basket stars, and sponges also may enhance the structural components of fish habitat (Puniwai, 2002) and may be disturbed or destroyed by some fishing activities (Freese, 2001; Krieger, 2001).

The potential for invertebrates to add functional structure to benthic communities has centered largely around their size and complex morphology. A size threshold of 1 m has often been used as an indicator of structure-forming species because marked changes in benthic community structure have been observed in areas where rocky substrata exceed 1 m (Lissner and Benech, 1993). The complex structure of deep-sea corals also has been discussed as an important factor that contributes to microhabitat diversity (Krieger and Wing, 2002; Etnoyer and Morgan¹). In this article, besides forming complex structure and large size, we also believe that megafaunal invertebrates form structure if they aggregate in high numbers, especially in areas of low relief. For example, aggregations of sea urchins and sea pens may provide significant structural relief for fishes in mud- and sand-dominated habitats (Brodeur, 2001).

An important question is the extent to which structure-forming invertebrates are ecologically important to fishes, especially those of economical value. Most studies have focused on "associations" between structure-forming invertebrates and fishes as a measure of ecological importance at several spatial scales. Fishes have been considered to be associated with invertebrates if they are found in the same trawl sample (Heifetz, 2002), if fishing is higher in areas with corals than without corals (Husebo et al., 2002), if they are found together within similar habitats observed from a submersible (Hixon et al.²), or if they are observed "among or within 1 m" from corals (Krieger and Wing, 2002). In this article we investigated association at three different levels: 1) fishes that are physically touching large invertebrates; 2) fishes that are found statistically more frequently near large invertebrates in relation to their overall abundance patterns; and 3) fishes that are found as nearest neighbors to large invertebrates.

The goal of this study was to describe patterns in the density, distribution, and size of structure-forming megafaunal invertebrates on deep rocky banks and

outcrops off southern California. Given the recent interest in these organisms as potentially important habitat for groundfishes, and thus targets for protection from fishing activities, these organisms deserve a critical examination of their potential to contribute structure to continental shelf and slope ecosystems and an examination of their associations with fishes and other marine organisms. Accordingly, our specific objectives were the following:

- Identify structure-forming invertebrates based on criteria of size, morphological complexity, and density;
- Quantify the density and size distributions of these invertebrates according to depth and substratum types;
- Quantify associations between large, structure-forming invertebrates and other organisms, particularly fishes; and
- Assess the health of these organisms in terms of obvious physical damage.

Materials and methods

Underwater surveys were conducted off southern California by using nonextractive video-transect methods and direct observations from an occupied research submersible (*Delta*) from 8 October to 6 November 2002. These surveys were conducted as part of a larger investigation into the abundance, size, and distribution of cowcod (*Sebastes levis*) and associated benthic fishes and habitats inside and around the newly established Cowcod Conservation Areas (CCAs) off southern California (Fig. 1). The CCAs, which encompass 14,750 km² and are closed to groundfish harvest in water depth >37 m, were established in 2001 to assist in rebuilding the depleted cowcod population off southern California.

Digital, georeferenced maps of seafloor substratum types, interpreted from side-scan sonar, multibeam bathymetry, seismic reflection, and other past geophysical surveys, were used to identify and select sites of rocky habitats (Greene et al.³). We attempted to restrict the substratum types to mixed sediment and rock and to 30–330 m depth (i.e., likely cowcod habitat).

The *Delta* submersible was tracked by using an ORE Trackpoint II plus (ORE Offshore, West Wareham, MA) USBL system and WINFROG (vers. 3.1, FUGRO, San Diego, CA) software. We linked the tracking system to our ArcView[®] GIS (vers. 3.2, ESRI Corp., Redlands, CA) seafloor mapping project and tracked the submersible real-time in relationship to depth and seafloor habitat maps.

² Hixon, M. A., B. N. Tissot, and W. G. Pearcy. 1991. Fish assemblages of rocky banks of the Pacific northwest, Heceta, Coquille, and Daisy Banks. OCS Study MMS 91-0052, 410 p. U.S.D.I. Minerals Management Service 770 Paseo Camarillo, 2nd Floor, Camarillo, CA 93010.

³ Greene, H. G., J. J. Bizzarro, D. M. Erdey, H. Lopez, L. Murai, S. Watt, and J. Tilden. 2003. Essential fish habitat characterization and mapping of California continental margin. Moss Landing Marine Laboratories Technical Publication Series No. 2003-01, 29 p., 2 CDs. Moss Landing Marine Laboratories, 8272 Moss Landing Rd., Moss Landing, CA 95039.

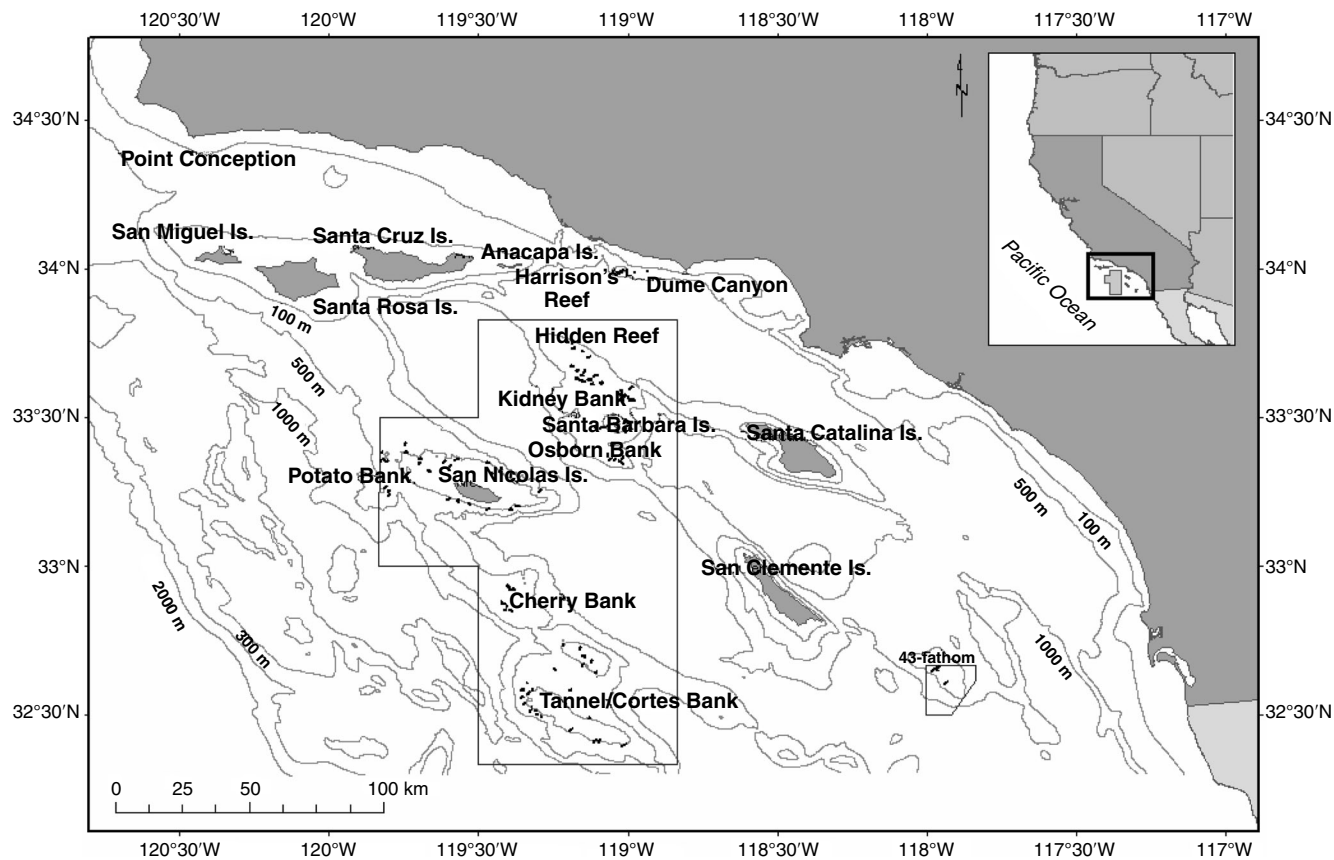


Figure 1

Locations of survey sites and dives (black dots) conducted inside and outside the cowcod conservation areas (delineated by outlined boxes) off southern California in 2002 to ascertain patterns in the density, distribution, and size of habitat-forming invertebrates.

We documented dives continuously during daytime hours with an externally mounted high-8 video camera positioned above the middle viewing-porthole on the starboard side of the submersible. The observer verbally annotated all tapes with observations on fishes, invertebrates, and physical habitats. Two parallel lasers were installed 20 cm apart on either side of the external video camera for estimating fish and invertebrate sizes and delineating a 2 m-wide belt transect for counting fishes and invertebrates. We used personal dive sonar from inside the submersible to verify the width of swath for the belt transects. Digital still and video cameras were used inside the submersible to help document fishes, invertebrates, and habitats.

We defined “habitat” using a combination of nine different categories of substratum and standard geological definitions (see Stein et al., 1992; Yoklavich et al., 2000). In order of increasing particle size or relief, these substrata were the following: mud (code M), sand (S), gravel (G), pebble (P), cobble (C), boulder (B), continuous flat rock (F), rock ridge (R), and pinnacles (T). A two-character code was assigned each time a distinct change in substratum type was noted along the transect, thus delineating habitat patches of uniform type. The first character in the code represented the substratum

that accounted for at least 50% of the patch, and the second character represented the substratum accounting for at least 20% of the patch (e.g., “BC” represented a patch with at least 50% cover by boulders and at least 20% cover by cobble). Each habitat patch also was assigned a code based on the degree of its three-dimensional structure as defined by the vertical relief of the physical substrata from the seafloor. Habitats were coded as 1=low (<1 m), 2=moderate (1–5 m), or 3=high relief (>5 m). Patches less than 10 seconds in duration were not recorded. The area of each habitat patch was determined by calculating the distance between the beginning and end of habitat patches with ArcGIS® and multiplying by the width of the transect (2 m).

A total of 58 different types of habitat patches were observed across all dives. These data were analyzed by a cluster analysis (Euclidean distance, group average method) by using the abundances of the 20 most common invertebrate species, and the resulting dendrogram was used to pool the number of codes into the 17 most distinct habitat types exhibiting a similarity of >50%.

Direct counts of megafaunal invertebrates were made from videotapes within each habitat patch; patch areas varied from 12–1472 m². Densities of invertebrates were estimated by dividing the total number of individuals

Table 1

Number of submersible dives and habitat patches surveyed for structure-forming invertebrates on rocky outcrops inside and outside the cowcod conservation areas in the southern California borderland.

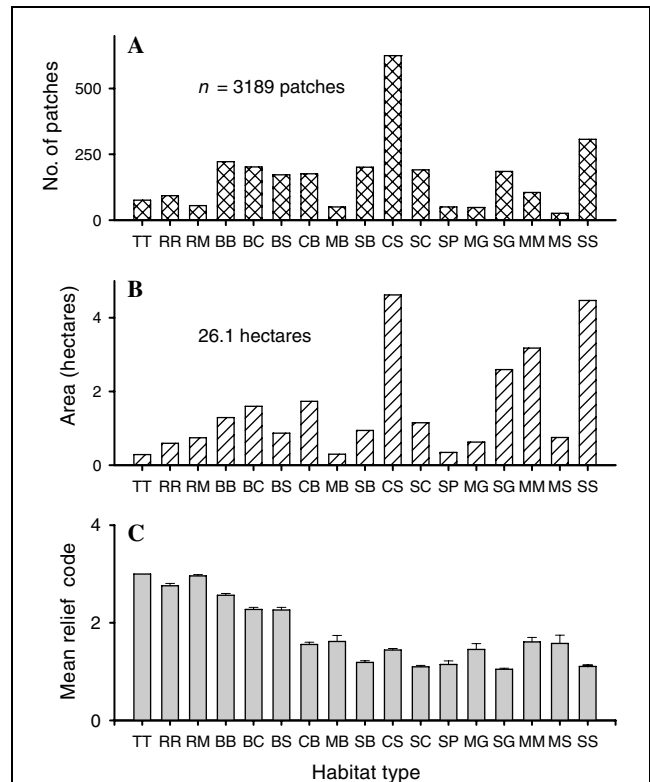
Study site	No. of dives	No. of habitat patches
Inside the cowcod conservation areas		
43-fathom	4	142
Cherry Bank	8	266
Hidden Reef	5	156
Kidney Bank	21	474
Osborn Bank	5	199
Potato Bank	4	113
San Nicolas Island	23	785
Santa Barbara Island	9	203
Tanner and Cortes banks	21	587
Outside cowcod conservation areas		
Harrison's Reef	9	198
Dume Canyon	3	66
Total	112	3189

in each group, identified to the lowest taxonomic level, by the area of their associated habitat patches. For the larger invertebrates we recorded the geographic position and estimated maximum height of each solitary sponge, gorgonian, and black coral. We also noted the color of black corals. We made observations on the occurrence of animals (i.e., epizoids) found directly on sponges, gorgonians, and black corals, and also noted any damaged or dead individuals. Voucher specimens were collected to assist in taxonomic identification.

To quantify fish-invertebrate associations we used ArcGIS® to estimate the distance between each sponge, gorgonian, and black coral invertebrate and the nearest fish. These data were compared to the total number of fishes counted in habitats that contained sponges, gorgonians, and black corals by using a chi-square test to look for significant differences in the frequency of fish observed near corals in relation to overall fish abundance.

Results

We completed 112 dives and surveyed 3189 habitat patches (Table 1), covering 26.1 hectares at 32–320 m depths (median depth of 110 m). The distributions of number of patches and of surface area of habitats were similar except for sand (SS), sand-gravel (SG), and mud (MM) habitats, all of which had greater surface areas in relation to number of patches (Fig. 2, A and B). Overall, cobble-sand (CS), sand, mud, and sand-gravel

**Figure 2**

Characteristics of habitat patches surveyed on southern California rocky banks. (A) Number of patches in each substratum type. (B) Total area of each substratum type. (C) Mean relief (± 1 standard error). See text for description of method and habitat codes. See page 169 for definitions for the substrate abbreviations along the x axis.

constituted the largest habitat areas, but cobble-sand and sand were the most frequent habitat types. Vertical physical structure varied among habitat types; the highest structure was found in high-relief rock areas (TT to BS) and lower structure was found in low-relief mixed rock (CB to SP) and mixed sediment areas (MG to SS; Fig. 2C). The frequency of patches of each substratum type varied by depth (Fig. 3). The incidence of most high-relief rock categories (TT, RR, BB, and BS) decreased with depth, and the occurrence of mud-dominated habitat patches (MB, MG, MS, MM) increased with depth.

Overall, 12,360 observations were made on 521,898 individuals from 15 taxa of megafaunal, structure-forming invertebrates; during these observations, estimates of size and incidence of epizoic animals on 9105 sponges, black corals, and gorgonians were made (Table 2). The most common structure-forming invertebrates (98% of total) included the crinoid *Florometra serratissima* (40%), the brittle star (*Ophiacantha* spp. [33%]), brachiopods (order Terebratulida [11%]), the white sea urchin (*Lytechinus anamesus* [9%]), the fragile sea urchin

(*Alloccentrotus fragilis* [4%]), and sea pens (suborder Subselliflorae; [2%]; Fig. 4).

The density of common structure-forming invertebrates was variable across habitat types; some species were found over a wide range of habitats. Crinoids and basket stars were found on all 17 habitat types but were most dense on either high-relief rock or low-relief mixed rock (Fig. 5). In contrast, brittle stars and brachiopods were dense in low-relief mixed rock but rare or absent in low-relief mixed sediment. White sea urchins were most dense in habitats with sand, whereas fragile sea urchins were most dense in habitats with mud. White-plumed anemones were most dense in mud-gravel habitats, and sea pens were most dense in low-relief mixed-sediments (Fig. 5).

Deep sea corals and sponges were the largest structure-forming invertebrates but were relatively uncommon (2% of total) (Table 2). Gorgonians were difficult to distinguish and were categorized into one group (order Gorgonacea). The black coral is a new species that recently has been described and named the Christmas tree coral (*Antipathes dendrochristos*) (Opresko, 2005). Sponges were categorized into five groups based on their structure and shape: flat, barrel, shelf, vase, and foliose sponges (Fig. 6).

Gorgonians and black corals were most dense on low-relief mixed rock areas (Fig. 7). However, gorgonians were found in only four habitat types at 144–163 m depth, whereas black corals were found on 12 habitat types at 100–225 m depth, including pinnacle, boulder, and sand areas. These differences may be due to the unequal number of observations (i.e., 27 gorgonian vs. 135 black coral colonies).

The five morphological groups of sponges displayed broad distributions across habitat types but were especially dense on high-relief rock and low-relief mixed rock (Fig. 7). Flat, barrel, vase, and foliose sponges were found in all habitats; shelf sponges were found in all habitats except MM, MS, and SS. Foliose sponges were found at significantly deeper depths (mean=191 m; SE=53; $n=1259$) than were other sponge groups (pooled mean=152 m; SE=0.6; $n=7545$), which were not significantly different from each other (Kruskal-Wallis $H=594$; $df=4$; $P<0.01$). Generally sponge size increased with increasing depth, although the correlation was low ($r=0.07$; $P<0.001$; $n=6551$). Although sponges were found throughout the study area, gorgonians and black corals were restricted in their distribution to a small number of sites (Fig. 8).

Structure-forming invertebrates displayed wide variation in size; maximum height ranged from 4 cm for brachiopods to 2.5 m for black corals (Table 2). There was no significant correlation between size of the invertebrate taxa and structural relief of the substratum types ($r=0.28$, $P=0.30$, $n=15$).

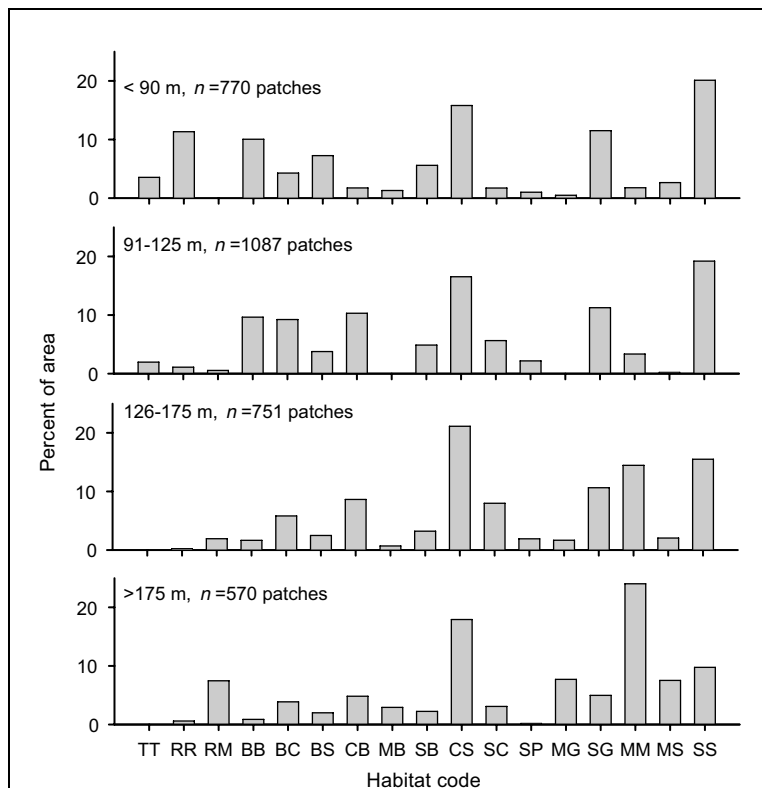


Figure 3

The frequency of habitat patches of each substratum type, stratified by depth. See page 169 for definitions for the substrate abbreviations along the x axis.

Gorgonians and black corals had different size distributions (Fig. 9). Black corals ranged from 10–250 cm in height (mean=33.6; SE=1.9; $n=195$) and most individuals were in the 10–50 cm size category. Individuals were found in three color forms: gray-to-white (50%), rusty-brown-to-red (47%), and gold (3%). Gorgonians ranged in size from 10 to 40 cm (mean=21.7; SE=1.2; $n=27$) and were found in multiple morphological forms from elongate to fan-like (Fig. 6).

Sponges displayed similar size distributions to those of gorgonian corals, but had different mean and maximum sizes (Fig. 9). Mean sizes of flat, barrel, and foliose sponges were not significantly different from each other (pooled mean=19.8 cm; SE=0.1; $n=7373$) but were significantly smaller than vase and shelf sponges (pooled mean=20.9 cm; SE=0.2; $n=1289$), which were not different from each other (one-way ANOVA; $F=4.52$; $df=4,8657$; $P=0.001$). The maximum observed height was 50 cm for shelf sponges, 60 cm for foliose sponges, and 100 cm for barrel, flat, and vase sponges (Fig. 9).

Most (98.2% by number) sponges, gorgonians, and black corals by number did not have any other organisms living on them (Table 3). Overall, crinoids (1.4%) were most commonly associated with these large invertebrates, followed by sponges (0.1%), and nine other

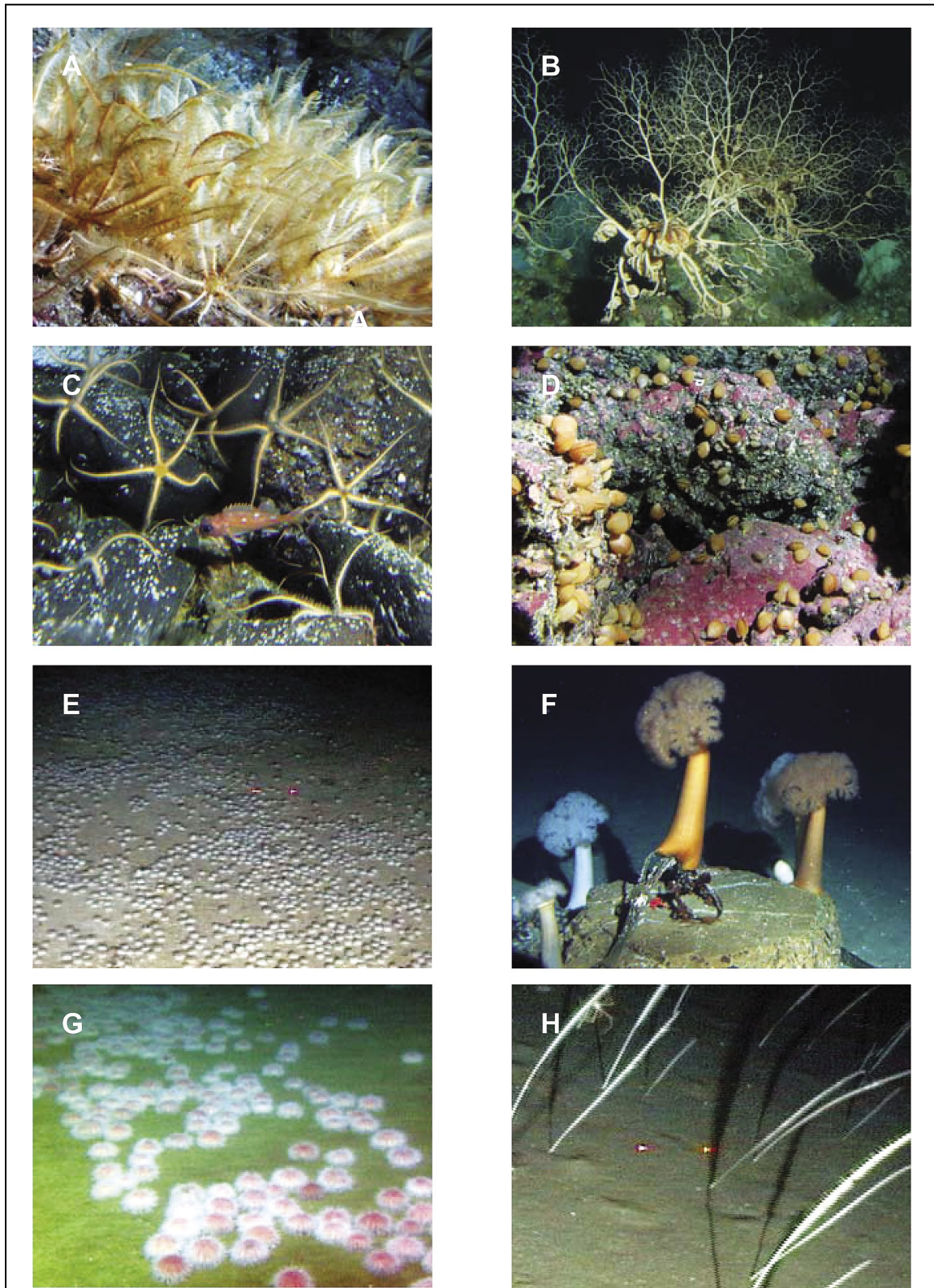


Figure 4

Some major structure-forming invertebrates on southern California rocky banks: (A) crinoids (*Florometra serratissima*), (B) basket stars (*Gorgonocephalus eucnemis*), (C) brittle stars (*Ophiacantha* spp.), (D) brachiopods (Terebratulida), (E) white sea urchins (*Lytechinus anamesus*), (F) white-plumed anemones (*Metridium farcimen*), (G) fragile sea urchins (*Allocentrotus fragilis*), and (H) sea pens (Subselliflorae).

taxa (all <0.1%). Black corals had the largest incidence of associated animals (15.3% of individuals), followed by vase (3.9%), barrel (2%), foliose (1%), shelf (0.7%), and flat (0.5%) sponges. Fish were most commonly observed on black corals (1.3%) but were also observed on vase sponges, including an attached egg case. No organisms were observed living on gorgonians.

The frequency of fish species near sponges, gorgonians, and black corals was significantly different from the frequency of those same species found elsewhere along transects (chi-square, all $P < 0.01$; Table 4). Of the 108 species adjacent to these large invertebrates, six species were found at significantly higher frequencies than predicted by their density along transects: cowcod, bank rockfish (*Sebastes rufus*), swordspine rockfish (*Sebastes ensifer*), shortbelly rockfish (*Sebastes jordani*), pinkrose rockfish (*Sebastes simulator*), and members of the rockfish subgenus *Sebastomus* (Table 4).

The distribution of mean nearest-neighbor distances between fishes and large invertebrates varied from 0.1 to 9.9 m (Fig. 10). Overall median distances varied from 0.9 m (shelf sponges) to 1.8 m (black corals). However, there were no statistical differences between the median distances for each group (Kruskal-Wallis, $H=10.4$; $df=6$; $P=0.11$). For the six fishes that were found more frequently near large invertebrates than on transects, the overall median distances to the invertebrates were 5.5 m (cowcod), 1.0 m (bank rockfish), 1.3 m (swordspine rockfish), 1.5 m (shortbelly rockfish), 1.7 m (pinkrose rockfish), and 1.4 m (*Sebastomus*).

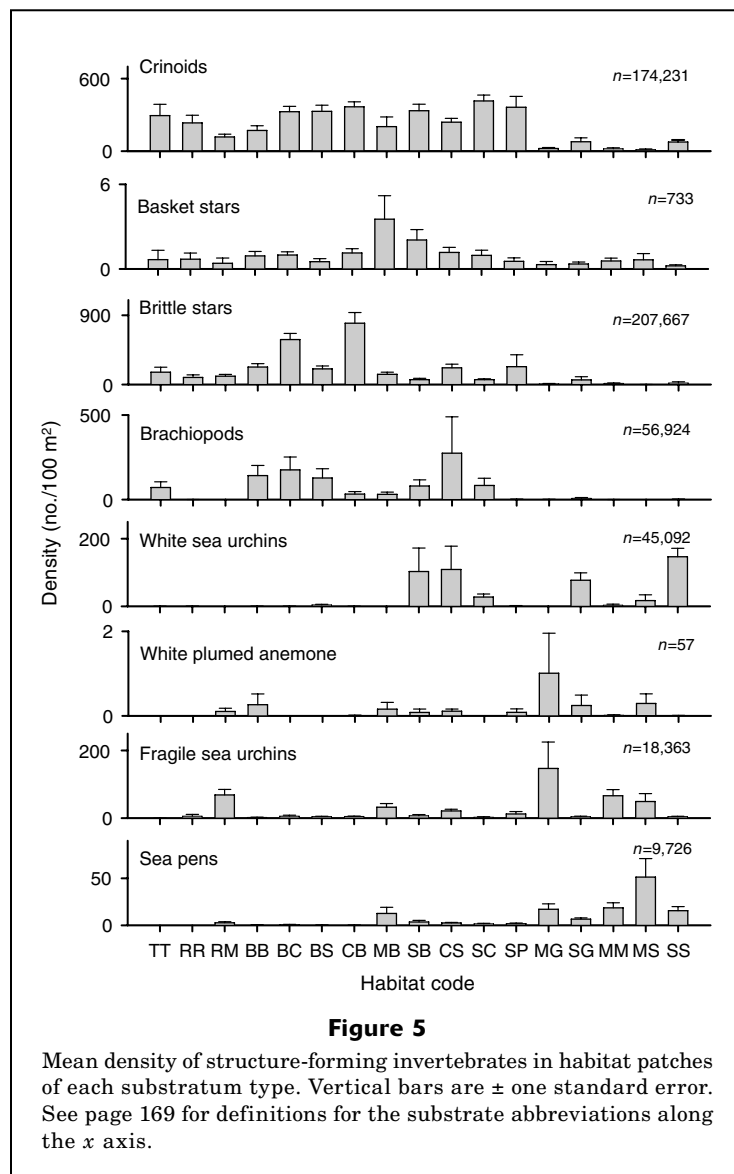
The overall incidence of damaged and dead sponges, gorgonians, and black corals was low (0.3% of total number observed). Black corals were more commonly damaged (1.7%) or dead (1.1%), followed by vase sponges (0.6% and 0.1%, respectively), barrel sponges (0.5% and 0%), and foliose sponges (0% and 0.1%). No dead or damaged flat or shelf sponges or gorgonians were observed. Damage in black corals included portions of the colony that appeared discolored; dead black corals lacked polyps and were discolored. Among sponges, the most common damage was individuals that had broken from the substratum and were lying on their side or broken colonies.

Discussion

Several groups of invertebrates were distinguished by their large size, such as black corals, sponges, crinoids, basket stars, anemones, and sea pens. Organism size is an important aspect of structural habitat because it contributes to vertical relief and increases the availability of microhabitats. For example, yelloweye (*Sebastes ruberrimus*) rockfish may use the large gorgonian coral *Primnoa* as a vantage point to prey upon small fishes (Krieger and Wing, 2002). Size variation among structure-forming invertebrates was significant. Individual black corals, sea pens, and sponges greater than 1 m in height represented only 0.1% of all organisms, and 90% of the individuals were <0.5 m high.

Similarly, the complex structures of crinoids, gorgonians, black corals, and basket stars may increase the availability of microhabitats and create a high surface area for settlement or retention of other organisms. Fish egg cases have been observed attached to both gorgonians (Etnoyer and Morgan¹) and vase sponges (present study, Table 3).

High-density aggregations have not been used as a criterion for defining structure-forming invertebrates, but there are several examples that illustrate the potential importance of these aggregations. High density "forests" of crinoids provide refuge and substrata for a wide variety of small fishes and invertebrates in rocky areas (Lissner and Benech, 1993; Puniwai, 2002).



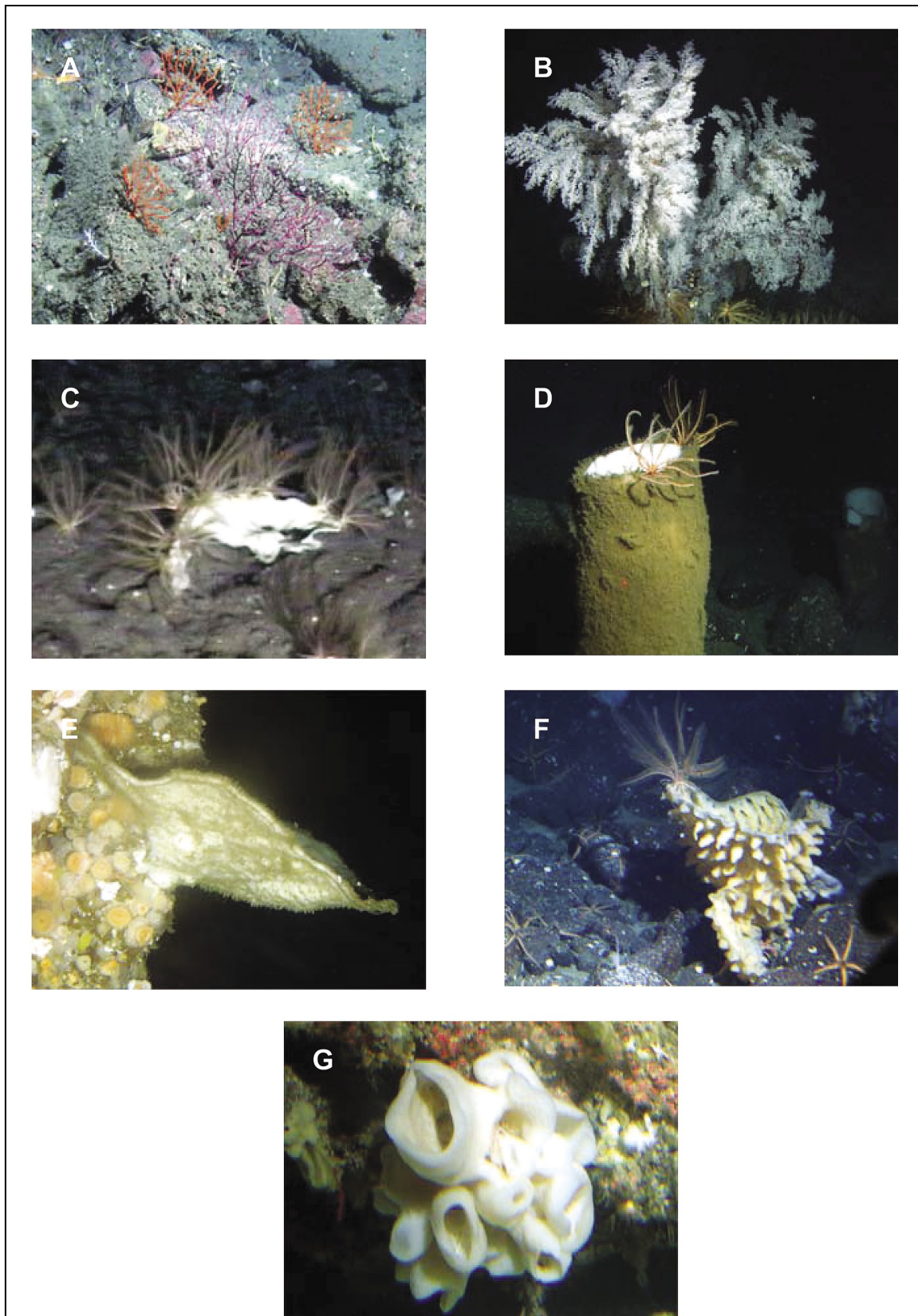


Figure 6

Structure-forming invertebrates: (A) gorgonians (Gorgonacea), (B) black coral (*Antipathes dendrochristos*), (C) flat, (D) barrel, (E) shelf, (F) vase, and (G) foliose sponges on southern California rocky banks.

Similarly, high-density aggregations of brittle stars and brachiopods in boulder-cobble areas and fields of sea pens and sea urchins in sand and mud habitats also may provide space and structure for other organisms (e.g., Brodeur, 2001).

With the exception of black corals and sea pens, the largest structure-forming invertebrates, such as sponges, *Metridium* spp., and crinoids, were most common on high- to moderate-relief rocky habitats. These long-lived organisms are likely to be favored in stable habitats that are more insulated from sediment transport and high particle loads than low-relief, mud-dominated areas (Lissner and Benesh, 1993). Large invertebrates add structure and micro-scale complexity to these rocky habitats that already contain high-to-moderate amounts of relief. Sponges, with their broad distributions, may also provide structure for flatfishes in low-relief mud habitats (Ryer et al., 2004)

Black corals and gorgonians, in contrast, are more commonly found in current-swept areas near drop-offs and under ledges (Grigg, 1974; Parrish, 2004). In our study, these invertebrates were found in low-relief mixed cobble-boulder-sand habitats at 100–225 m depths, providing significant vertical structure for potential use by a wide variety of organisms.

Aggregations of sea pens and sea urchins may provide important structure in low-relief sand and mud habitats where there is little physical habitat complexity. In addition, these organisms may provide refuge for small planktonic and benthic invertebrates, which in turn may be preyed upon by fishes. They also may alter water current flow, thereby retaining nutrients and entraining plankton near the sediment. Urchins rapidly respond to patches of drift kelp (Harrold and Reed, 1985), which provide organic material to deep sea habitats (Harrold et al., 1998).

One of the central issues currently relevant to structure-forming invertebrates is the degree to which these species contribute to the spawning, breeding, feeding, or growth-to-maturity of economically important fishes. Although there are several studies that report fish-invertebrate associations within common habitats (Hixon et al.²), or make anecdotal or general observations on fish-invertebrate associations (e.g., Krieger and Wing, 2002), few studies have systematically quantified these relationships. In our study, for 9105 observations on the larger invertebrates found on southern California rocky banks only 1.8% of individuals had other organisms lying on or attached to them. Moreover, the vast majority of these organisms were other invertebrates, including crinoids, sponges, crabs, basket stars, brittle stars, seastars, anemones and salps. Less than 1% of the observations of organisms actually sheltering in or located on invertebrates involved fishes (a total of five individuals and one egg case), and most were observed on large black corals (Table 3). This result implies that fishes are not strong-

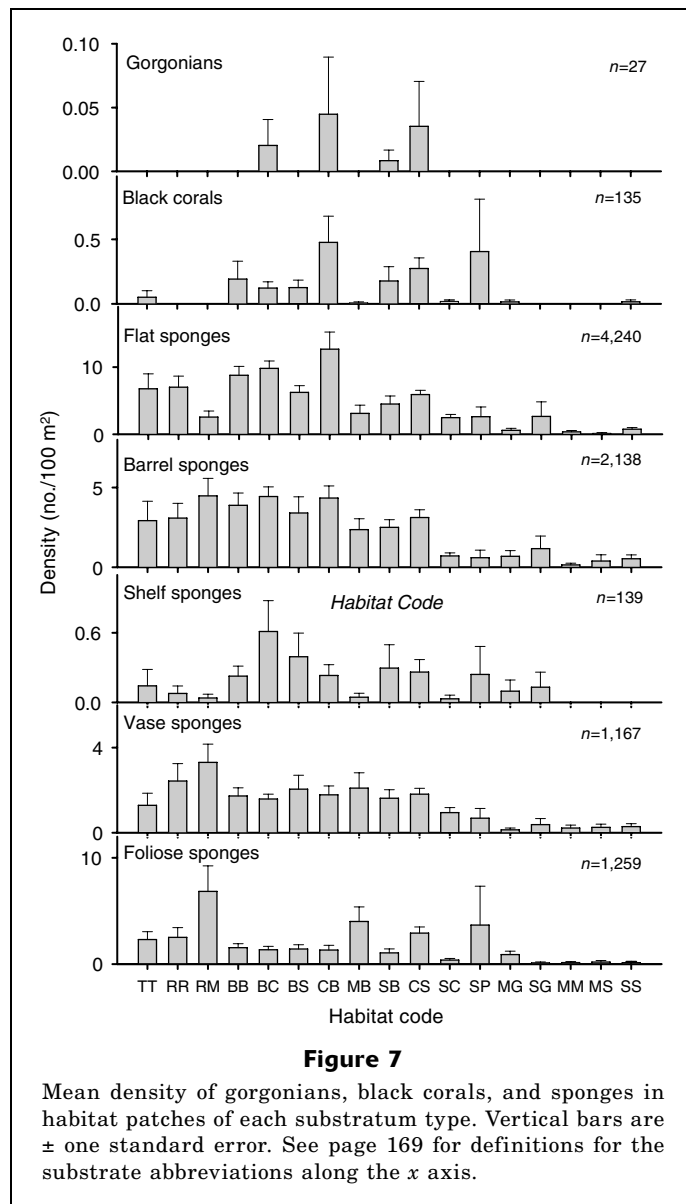


Figure 7

Mean density of gorgonians, black corals, and sponges in habitat patches of each substratum type. Vertical bars are \pm one standard error. See page 169 for definitions for the substrate abbreviations along the x axis.

ly associated with structure-forming invertebrates in the areas we surveyed off southern California.

However, we should note that our observations were limited to daylight hours and that the viewing angle from the submersible generally precluded seeing inside some of the sponges (especially vase and barrel types). Moreover, our analyses focused on associations between fishes and individual solitary invertebrates, most of which were <0.5 m in height. We did not examine associations between all structure-forming invertebrates, nor did we examine associations between invertebrates and assemblages of fishes at the level of discrete habitat patches (100–1000 m scale) (e.g., Tissot et al.⁴)

⁴ Tissot, B. N., M. A. Hixon, D. L. Stein. Unpubl. manuscript. Habitat-base submersible assessment of groundfish assemblages at Heceta Bank, Oregon from 1988–1990.

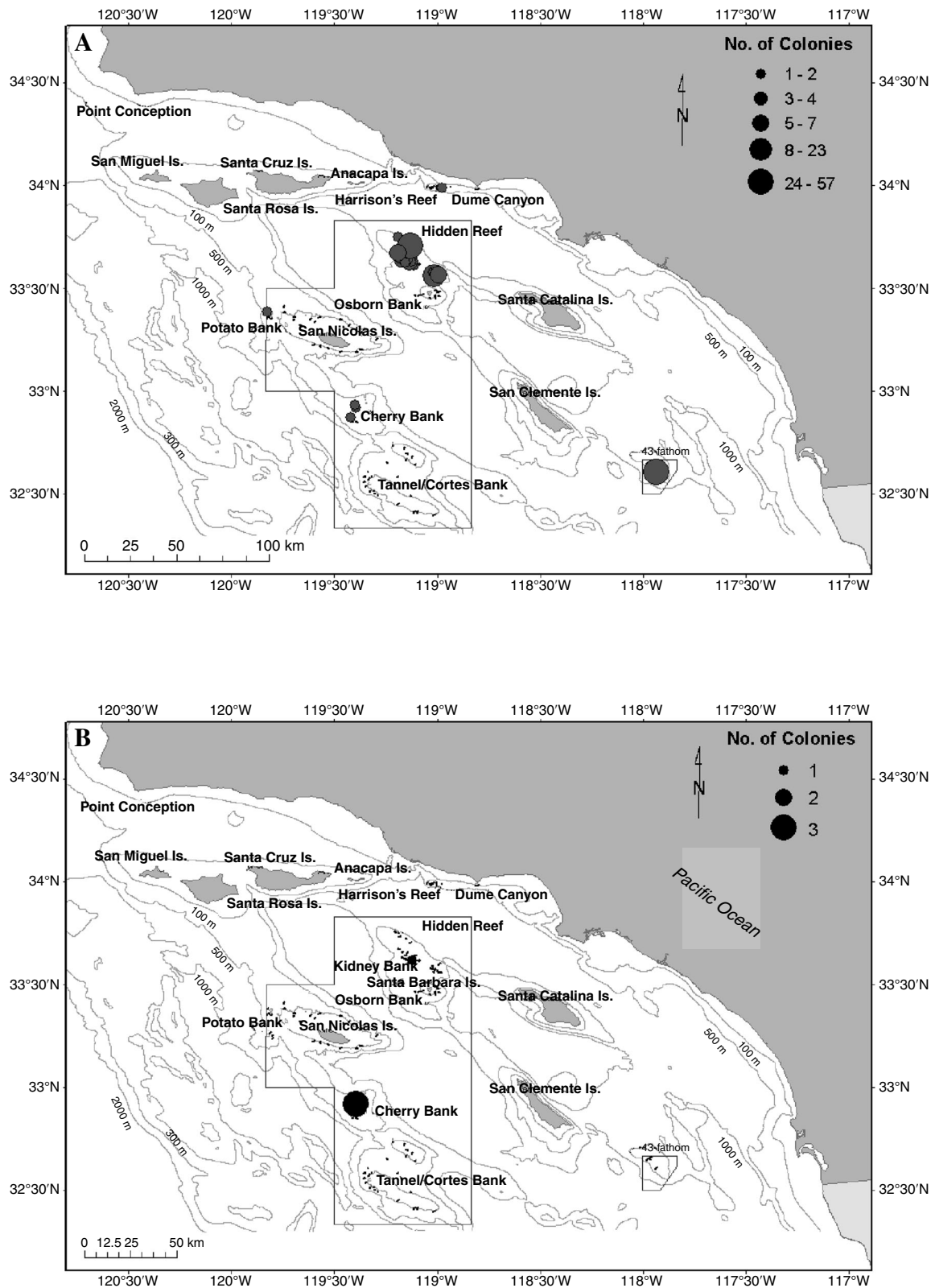


Figure 8

Distribution and number of (A) black coral and (B) gorgonian colonies inside and outside the cowcod conservation areas (delineated as outlined boxes) of southern California in 2002. Dive sites are indicated by black dots.

From the analysis of spatial associations between fishes and large, individual structure-forming invertebrates, six of 108 species were found more often adjacent to colonies than predicted by their abundance along transects. This result indicates that there may be spatial associations that do not necessarily include physical contact with the sponges and corals. However, the median distances between these six fish species and large invertebrates (1.0–5.5 m) were not particularly small. Thus, it is likely that these fishes and invertebrates are present in the same types of habitats and that there is not necessarily a functional relationship between these two groups of organisms.

Parrish (2004) reached similar conclusions on studies of black coral in Hawaii. Although fish densities were higher in areas that included corals, when bottom relief and depth were accounted for these densities were not higher than those for surrounding areas without corals. Thus, there was no clear evidence that corals served to aggregate fish. Rather, fishes and corals co-occurred in areas with similar physical relief and unique flow regime (Parrish, 2004). Auster (2005) also reached similar conclusions by finding no significant difference in the density of a common rockfish species (*Sebastes fasicatus*) between areas of rock and boulders with dense coral cover and similar areas having dense epifaunal cover (i.e., without coral). Auster concluded that although dense coral and dense epifaunal habitats were functionally equivalent, the epifaunal habitat was more widespread in his study area, making that habitat perhaps more important to the greater rockfish population. Finally, Syms and Jones (2001) demonstrated that removal of high densities of soft corals caused no significant changes in the associated fish communities and that the heterogeneity of habitat generated by soft corals was indistinguishable from equivalent habitat formed by rock alone. Thus, fish-invertebrate associations, by themselves, do not necessarily demonstrate the functional importance of invertebrates as habitat to benthic fish populations.

One possible conclusion from our study is that observed fish-invertebrate associations, like those reported for many cold-water corals, can be overstated. In the absence of quantitative information, observers may remember the few positive associations between fishes and structure-forming invertebrates but ignore (or forget) the more numerous observations of large invertebrates with no associated fishes. Indeed, the general impression of the authors after making submersible observations was that there were higher numbers of fishes associated with large invertebrates when in reality only five fishes were observed lying directly on a large invertebrate in the video transects. A more likely conclusion, however, is that the continental shelf communities of southern California are unique and that large black corals do not have the high number of commensals as seen, for example, on *Primnoa* in Alaska. An additional consideration is the relatively low number and size of individual sponges, gorgonians, and black corals observed in this study. *Primnoa* in Alaska can form massive stands 3 m

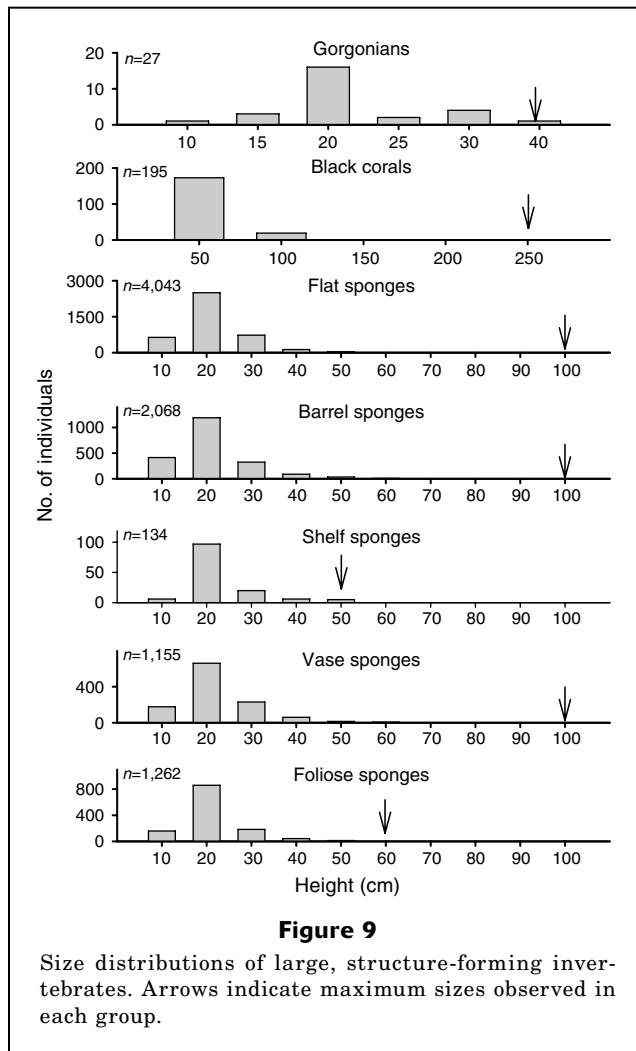


Figure 9

Size distributions of large, structure-forming invertebrates. Arrows indicate maximum sizes observed in each group.

tall and 7 m wide in some areas (Krieger and Wing, 2002). Moreover, the majority of fishes were observed on the largest individuals in their study (>15 m³ in volume). Most of the corals in our study were <0.5 m in height. Given the importance of this issue, we argue for more rigorous quantitative studies on fish-invertebrate associations that would include densities of fishes and sizes of both fishes and invertebrates.

Regardless of their associations with fishes, the structure-forming invertebrates described in this study are very likely to be ecologically important on continental shelf ecosystems and are certainly significant in their own right. Observation on the health of the larger invertebrates indicates few damaged (0.1%) or dead (0.2%) individuals and a low incidence of fishing gear in the areas surveyed (Tissot et al., unpubl. data). These observations are consistent with the absence of a significant commercial bottom trawling fishery in our survey area, which has been associated with negative impacts on large invertebrates in other locations (Watling and Norse, 1998; Freese et al. 1999; Krieger, 2001). Thus, this study affords a unique view of what appears to be

Table 4

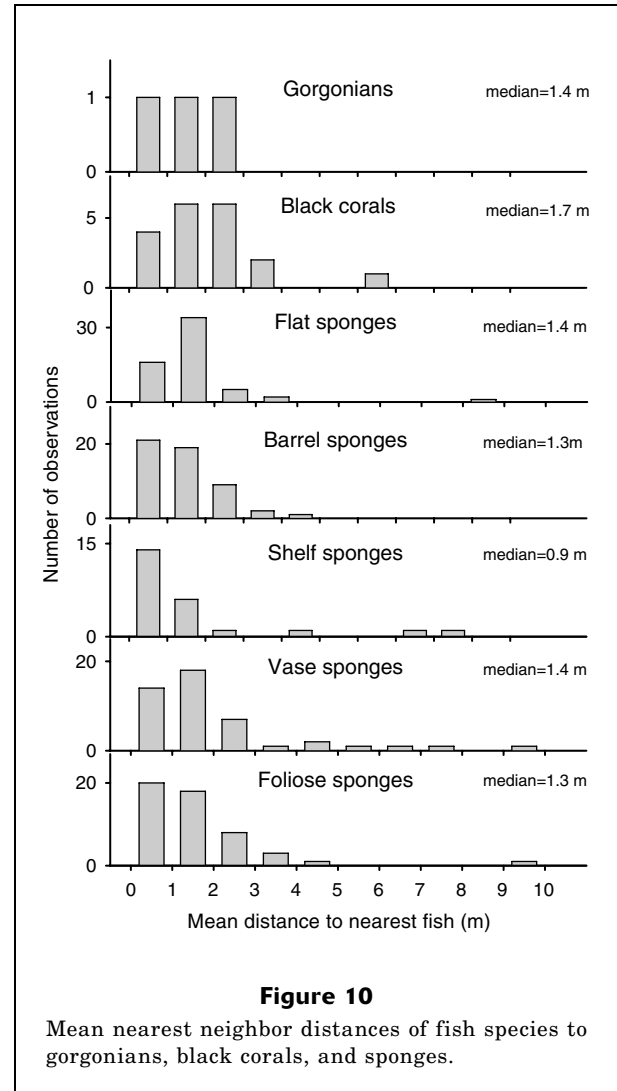
Percentage of fish species near sponges, gorgonians, and black coral in relation to fishes counted along transects. Species that are less than 1% of the overall total number along all dives are not included. Species that were found more often near these invertebrates than expected by chance are indicated with an *.

Taxa	Common sponges				Shelf sponges			Gorgonians			Black coral	
	Total near tarrel sponges	Total near flat sponges	Total near vase sponges	Total on transect	Total near shelf sponges	Total on transect	Total near gorgonians	Total on transect	Total near black corals	Total on transect	Total on transect	
Unknown <i>Sebastomus</i>	19*	17*	16*	6	18*	6	0	7	38*	13		
Swordspine rockfish <i>Sebastes ensifer</i>	16*	14*	24*	6	16*	6	92*	31	23*	13		
Pygmy rockfish <i>Sebastes wilsoni</i>	9	12	8	16	7	14	0	7	4	16		
Pinkrose rockfish <i>Sebastes simulador</i>	6	5	2	1	8	1	0	1	3	1		
Squarespot rockfish <i>Sebastes hopkinsi</i>	6	9	4	24	4	24	0	30	4	17		
Shortspine combfish <i>Zaniolepis frenata</i>	5	4	5	2	6	2	4	1	8	5		
Bank rockfish <i>Sebastes rufus</i>	4*	3	13*	1	5*	1	0	2	4	2		
Halfbanded rockfish <i>Sebastes semicinctus</i>	2	5	0	3	5	3	0	<1	4	4		
Unknown rockfishes <i>Sebastes</i> spp	4	4	1	2	3	2	0	2	4	2		
Juvenile rockfish <i>Sebastes</i> spp	3	3	3	18	1	22	0	10	1	12		
Shortbelly rockfish <i>Sebastes jordani</i>	2	2	1	1	3	1	0	1	1	2		
Unidentified combfishes <i>Zaniolepis</i> spp	2	2	2	1	3	1	0	1	1	2		
Cowcod <i>Sebastes levis</i>	2	2	9*	<1	2*	<1	0	<1	2*	<1		
Starry rockfish <i>Sebastes constellatus</i>	2	2	2	1	2	1	0	1	0	1		
Greenstriped rockfish <i>Sebastes elongatus</i>	2	1	3	1	2	1	0	1	0	1		
Rosy rockfish <i>Sebastes rosaceus</i>	2	2	1	1	2	1	0	0	0	<1		

continued

Table 4 (continued)

Taxa	Common sponges				Shelf sponges			Gorgonians		Black coral	
	Total near tarrel sponges	Total near flat sponges	Total near foliose sponges	Total near vase sponges	Total on transect	Total near shelf sponges	Total on transect	Total near gorgonians	Total on transect	Total near black corals	Total on transect
Dwarf-red rockfish <i>Sebastes rufinanus</i>	1	2	<1	2	3	1	3	0	<1	0	<1
Greenspotted rockfish <i>Sebastes chlorostictus</i>	1	1	<1	1	1	1	<1	0	<1	1	<1
Blackeye goby <i>Rhinogobiops nicholsii</i>	1	2	<1	0	4	<1	3	4	1	0	<1
Lingcod <i>Ophiodon elongatus</i>	2	1	1	0	<1	1	<1	0	<1	0	<1
Bocaccio <i>Sebastes paucispinis</i>	1	1	1	2	1	1	1	0	1	0	<1



relatively undisturbed megafaunal invertebrate communities in the southern California Borderlands, and supports the continued protection of these animals within the Cowcod Conservation Areas.

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Literature cited

- Andrews, A. H., E. E. Cordes, M. M. Mahoney, K. Munk, K. H. Coal, G. M. Calliet, and J. Heifetz.
2002. Age, growth, and radiometric age validation of a deep-sea, habitat-forming gorgonia (*Primnoa resedaeformis*) from the Gulf of Alaska. *Hydrobiologia* 471:101–110.
- Auster, P. J.
2005. Are deep water corals important habitat for fishes? Cold-water corals and ecosystems (A. Freiwald and J. M. Roberts (eds.), 1244 p. Springer, New York, NY.
- Brodeur, R. D.
2001. Habitat-specific distribution of Pacific ocean perch (*Sebastes alutus*) in Pribilof Canyon, Bering Sea. *Cont. Shelf Res.* 21:207–224.
- Brusca, R. C., and G. J. Brusca.
1990. Invertebrates, 922 p. Sinauer Associates, Inc., Sunderland, MA.
- Dayton, P. K., S. Thrush, and F. C. Coleman.
2002. Ecological effects of fishing in marine ecosystems of the United States, 52 p. Pew Oceans Commission, Arlington, VA.
- Fossa, J. H., P. B. Mortensen, and D. M. Furevik.
2002. The deep-sea coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia* 471:1–12.
- Freese, J. L.
2001. Trawl-induced damage to sponges observed from a research submersible. *Mar. Fish. Rev.* 63(3):7–13.
- Freese, J. L., P. J. Auster, J. Heifetz, and B. L. Wing.
1999. Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. *Marine Ecol. Prog. Ser.* 182:119–126.
- Grigg, R. W.
1974. Distribution and abundance of precious corals in Hawaii. *In Proc. second international coral reef symposium* (A. M. Cameron et al., eds.), p. 235–340. Great Barrier Reef Committee, Brisbane, Queensland, Australia.
- Harrold, C., and D. Reed.
1985. Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* 66:1160–1169.
- Harrold, C., K. Light, and S. Lisin.
1998. Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forests. *Limnol. Oceanogr.* 43:669–678.
- Heifetz, J.
2002. Coral in Alaska: distribution, abundance, and species associations. *Hydrobiologia* 471:19–28.
- Husebo, A. L. Nottestad, J. H. Fossa, D. M. Furevik, and S. B. Jorgensen.
2002. Distribution and abundance of fish in deep-sea coral habitats. *Hydrobiologia* 471: 91–99.
- Krieger, K. J.
2001. Coral (*Primnoa*) impacted by fishing gear in the Gulf of Alaska. *In Proceedings of the first international symposium on deep-sea corals* (Willison et al., eds.), 106–116. Ecology Action Centre, Halifax, Canada.
- Krieger, K. J., and B. L. Wing.
2002. Megafaunal associations with deepwater corals (*Primnoa* sp.) in the Gulf of Alaska. *Hydrobiologia* 471:83–90.
- Lissner, A., and S. Benech.
1993. Benthic hard-substrate community ecology of the Santa Maria basin and western Santa Barbara channel. *In Taxonomic atlas of the benthic fauna of the Santa Maria Basin and western Santa Barbara Channel* (J. A. Blake and A. L. Lissner, eds.), p. 33–45. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- Malakoff, D.
2004. U.S. asked to act immediately to protect deep-sea corals. *Science* 304(5667):31.
- NRC (National Research Council).
2002. Effects of trawling and dredging on seafloor habitat. Committee on Ecosystem Effects of Fishing: Phase 1—effects of bottom trawling on seafloor habitats, 136 p. National Research Council, National Academy Press, Washington, D.C.
- Opreko, D. M.
2005. A new species of antipatharian coral (Cnidaria: Anthozoa: Antipatharia) from the southern California Bight. *Zootaxa* 852:1–10.
- Palumbi, S. R.
1986. How body plans limit acclimation: responses of a demosponge to wave force. *Ecology* 67(1):208–214.
- Parrish, F. A.
2004. Foraging landscape of the Hawaiian monk seal. Ph.D. diss., 146 p. Univ. Hawaii, Manoa.
- Puniwai, N. P. F.
2002. Spatial and temporal distribution of the crinoid *Florometra serratissima* on the Oregon continental shelf. M.S. thesis, 34 p. Washington State Univ., Vancouver, WA.
- Roberts, S., and M. Hirshfield.
2004. Deep-sea corals: out of sight, but no longer out of mind. *Front. Ecol. Environ.* 2(3):123–130.
- Rogers, A.
2004. The biology, ecology and vulnerability of deep-sea coral reefs. IUCN publication:1–13.
- Riedl, R.
1971. Water movement: animals. *Marine ecology: a comprehensive, integrated treatise on life in oceans and coastal waters* (O. Kinne, ed.), 1(2):1123–1156. Wiley-Interscience, London.
- Ryer, C. H. A. W. Stoner and R. H. Titgen.
2004. Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. *Mar. Ecol. Prog. Ser.* 268:231–243.
- Stein, D. L., B. N. Tissot, M. A. Hixon and W. Barss.
1992. Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. *Fish. Bull.* 90:540–551.
- Syms, C., and G. P. Jones.
2001. Soft corals exert no direct effects on coral reef assemblages. *Oecologia* 127:560–571.
- Watling, L., and E. A. Norse.
1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Cons. Biol.* 12(6):1180–1197.
- Yoklavich, M. M., H. G. Greene, G. M. Cailliet, D. E. Sullivan, R. N. Lea, and M. S. Love.
2000. Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. *Fish. Bull.* 98:625–641.