HABITAT-BASED ASSESSMENT OF STRUCTURE-FORMING MEGAFAUNAL INVERTEBRATES AND FISHES ON CORDELL BANK, CALIFORNIA

By

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the thesis of JODI L. PIRTLE find it satisfactory and recommend that it be accepted.

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Chair

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HABITAT-BASED ASSESSMENT OF STRUCTURE-FORMING

MEGAFAUNAL INVERTEBRATES AND FISHES

ON CORDELL BANK, CALIFORNIA

Abstract

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Cordell Bank is a submerged rocky island at the edge of the continental shelf 40 km west of Point Reyes California and is recognized for supporting populations of commercially important groundfish and a unique assemblage of benthic invertebrates. To determine the distribution and structure of physical habitats and communities of megafaunal invertebrates and fish communities, a total of 27 quantitative dives were conducted in 2002 with the submersible *Delta* between 55 – 250 m depth across the area of Cordell Bank.

From these dives, megafaunal invertebrate and fish distribution was distinguished by four general communities in association with distinct physical habitats at Cordell Bank. Certain megafaunal invertebrates, such as sponges, gorgonian corals, crinoids, and large anemones, were identified as structure-forming based on large size, complex

morphology, or the ability to form high density aggregations. Structure-forming invertebrates were observed with several species of fish in close proximity more than expected by chance occurrence within physical habitats. Within these statistically significant, non-random associations, close associations were distinguished behaviorally and were observed to be especially important to certain species of fish in habitats lacking large structural relief or complexity, or to smaller fish in open and exposed habitats. In conclusion, the physical habitats of Cordell Bank are the most probable factor, in addition to the lifestyle requirements of individual species and their life-stages, that determine community distribution and structure. However it is likely that megafaunal invertebrates with the morphological ability to provide structure affect the close association of certain fishes with these invertebrates that in turn influence the community structure of the Cordell Bank ecosystem as an ecologically important component of living habitat.

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Introduction

An ecosystem-based approach to fisheries management requires that habitats supporting populations be well defined (Rosenberg et al., 2000; and Pikitch et al., 2004). Habitat requirements of groundfish populations in deep marine ecosystems have been investigated by focusing on the physical structure and geology of submerged rocky banks and submarine canyons (Hixon et al. 1991; Stein et al., 1992; Auster et al., 1995; Yoklavich et al. 2000; Nasby-Lucus et al., 2002; Greene et al., 2003; Tissot et al., in review a). Several studies have used occupied and remotely operated vehicles to directly observe species in association with the physical habitat and have reported human induced disturbance and damage to the habitat and associated megafaunal benthic invertebrates including upright sponges, deep cold-water corals, and sea pens (Brodeur, 2001; Freese, 2001; Krieger, 2001). Concern over damage to these species and their ecosystems has led to recent studies of megafaunal invertebrates as living components of habitat and their ecological relationships with groundfish (Hiefetz, 2002; Puniwai, 2002; Tissot et al., 2004; Auster, 2005; Tissot et al., in review b). These studies have identified megafaunal invertebrates as unique components of biodiversity in deep marine ecosystems; however their specific habitat requirements and functional role as living habitat for groundfish and other species are not well understood. Accordingly, there is a need to more clearly identify important habitats supporting megafaunal invertebrates and to clarify their ecological relationships with groundfish populations on Cordell Bank, California.

Approximately 95% of marine fishery catch comes from continental shelf regions (Roberts and Hawkins, 1999). This high level of activity in areas where many megafaunal invertebrates occur makes them vulnerable to destruction from bottom contacting fisheries. Destructive fishing methods can alter and destroy megafaunal invertebrate communities through direct damage and removal of individuals, and by decreasing habitat heterogeneity and community biodiversity (Engel and Kvitek, 1998; Freese et al., 1999; Bianchi et al., 2000; Freese, 2001; Fossa et al., 2002). These effects may be prolonged due to life-history characteristics common to many megafaunal invertebrates such as longevity and slow growth (Andrews et al., 2002; and Miller et al., 2004). In addition, adverse impacts to megafaunal invertebrate communities may exacerbate the decline of structure-oriented groundfish if they are dependent upon megafaunal invertebrates as components of habitat and community structure to maintain healthy populations in deep marine ecosystems. Thus, there is a need to identify habitat requirements of megafaunal invertebrates and understand their ecological relationships with groundfish populations to implement appropriate conservation policies to protect these species and their ecosystems from further degradation.

Megafaunal invertebrates are operationally defined as epibenthic species larger than 5 cm. Representative taxa include crinoids, upright sponges, anemones, deep cold-water corals, and sea pens. These species may function as a living component of habitat in deep marine ecosystems due to their morphological ability to add structure and complexity to the physical habitat. This added structure and complexity has the potential to create additional space for fish and invertebrates to utilize for shelter and other needs. An enhanced level of structure and complexity has been demonstrated to be of particular importance during times of reproduction, and for juvenile life-stages (Auster, 2005), or at night for daytime active species (Brodeur, 2001). It is further argued that deep cold-water corals with complex morphological structure provide foraging opportunities for perching species (Krieger and Wing, 2002). Tissot et al. (in review b) identified structure-forming megafaunal invertebrates on deep rocky banks in southern California on the basis of having large size (> 30 cm), complex morphology, and the ability to form high density aggregations. There is a need to take a similar approach in other ecosystems to identify structure-forming megafaunal invertebrates and to further investigate their potential ecological role as habitat and components of community structure to more fully determine their ecological associations with groundfish.

The degree to which groundfish and other species interact with structure-forming megafaunal invertebrates is unclear and must be addressed to effectively determine the functional importance of species with the potential to provide habitat in deep marine ecosystems. Efforts to identify and describe associations between structure-forming invertebrates and groundfish have been approached at multiple levels, including co-occurrence in similar habitats and examination of close associations.

The general co-occurrence of structure-forming invertebrates with groundfish in similar habitats has been described by Hixon et al. (1991) for three deep rocky banks off the coast of Oregon. In this study species distribution and abundance varied by location based on differences in habitat availability between locations; for example, juvenile rockfish (*Sebastes spp.*) were most abundant in rock ridge and boulder habitat at the location with the greatest amount of this habitat, where sponges and the basket stars (*Gorgonocephalus eucnemis*) were the most common megafaunal invertebrates with preference for this habitat. A subsequent study by Puniwai (2002) examined the distribution of the crinoid *Florometra serratissima* on the Oregon continental shelf and identified juvenile rockfish as a taxonomic group commonly observed with dense crinoid aggregations on rock ridges. This co-occurrence may have been due to mutual preference for this physical habitat, however juvenile rockfish were often observed amongst the arms of the crinoids indicating a potential close association based on shelter or foraging opportunities. It is clear from these two studies that physical habitat is important in determining the distribution of fishes and megafaunal invertebrates and may influence their general co-occurrence. What is unclear is whether or not fish and invertebrate distribution on rocky bank ecosystems is solely mediated by the presence of physical habitat, or if other factors have a significant influence on distribution including the presence of species with the potential to provide structural relief and complexity to the physical habitat.

This uncertainty was addressed by Auster (2005) with a focus on deep cold-water corals on the northeastern continental shelf, where habitats with a high abundance of corals were determined to be functionally equivalent to other habitats important to groundfish. The presence of corals however did not determine the demography of fishes across the survey area, which indicated that the presence of large invertebrates like corals may provide structure but may only affect the distribution of fishes due to their ability to provide structural relief that may be available in other habitats without large invertebrates. Tissot et al. (in review b) used a different approach to determine if the presence of large invertebrates influenced the distribution of fishes on deep rocky banks off southern California. This study identified that certain species of groundfish occurred in close association with structure-forming invertebrates more often than expected by chance association. These species were most commonly small unidentifies rockfish of the subgenus *Sebastomus*, swordspine rockfish (*Sebastes ensifer*), and bank rockfish

(*Sebastes rufus*), associated with sponges of varied morphology, black corals (*Antipathes dendrochristos*), and gorgonians.

Other studies have identified and described close associations between fishes and megafaunal invertebrates, including the facultative association between the temperate fish, *Oxylebius pictus* and anemones of the genus *Urticina,* which were observed to provide physical structure and protection from predators, as described by Elliot (1992). Juvenile flatfish were demonstrated by Ryer et al. (2004) to associate with sponges in low-relief mud habitats and were less abundant in similar habitats without emergent structure provided by sponges, pebbles, and shells. Pacific ocean perch (*Sebastes alutus*) were observed associated with dense beds of the sea whip (*Halipteris willemoesi*) in deep low-relief mud-dominated habitat at Pribilof Canyon in Alaska during evening hours when this species was inactive (Brodeur, 2001). Areas of mud habitat where sea whips were less dense or absent did not support diurnally associated aggregations of this rockfish. Epifaunal invertebrates including crustaceans, anthozoans, sponges, and echinoderms were identified as common associates with deep cold-water corals of the genus *Priminoa* in the Gulf of Alaska (Krieger and Wing, 2002), and there has been further support that this genus and other corals in Alaska are important structural components of habitat for adult and juvenile groundfish and juvenile golden king crab (*Lithodes aequispina*) (Stone, in review). Several studies have described general co-occurrence or specific close interactions between megafaunal invertebrates and groundfish; however most have not described community structure created by close associations existing within the general co-occurrence of species with the physical habitats of deep rocky bank ecosystems. This type of information will benefit ecosystem-based fisheries management that intends to incorporate knowledge of habitat requirements for different life-stages of commercially valuable species and the structure of the communities to which they belong (Rosenberg et al., 2000; and Pikitch et al., 2004).

The overall goal of this study is to accomplish a community-level habitat-based assessment of the megafauna of Cordell Bank: a submerged deep-water rocky bank on the U.S. west coast continental shelf. The objectives of this study were 1) to determine the taxonomic composition and assess the abundance and distribution of megafaunal invertebrates and fishes at Cordell Bank; 2) to identify communities of invertebrates and fishes in association with the physical habitat; 3) to identify invertebrates with the potential to add structure and complexity to the physical habitat; and 4) to investigate the associations of fish with structure-forming invertebrates as a biological component of habitat and community structure.

Methods and Materials

Study Site

Studies were conducted at Cordell Bank (ca. 38^{o}1’42”N, 123^{o}26’41”W), a submerged granitic island at the edge of the continental shelf 40 km west of Point Reyes, California (Figure 1). Cordell Bank ascends from 200 m depth at the western flank to 50 m at the central area of the bank and shallow pinnacles. Cordell Bank is the main feature within the Cordell Bank National Marine Sanctuary, established in 1986 in recognition of the unique marine ecosystems of the area. This study focused on Cordell Bank but efforts were also directed at surveying the adjacent continental shelf and slope to cover an area of about 120 km^2, between 52 – 365 m depth.

Submersible Surveys

The occupied submersible *Delta* was used to conduct non-extractive surveys of the physical habitats and associated invertebrates and fishes at the Cordell Bank study area from September 23 – 29, 2002. To maximize spatial coverage, dive sites were uniformly selected at an approximate distance of 2.7 km apart using a sampling grid of ninety-nine 1.9 km by 1.4 km blocks distributed across a bathymetric map of the study site (Figure 2).

Quantitative dives were conducted during daylight hours using survey methods similar to Stein et al. (1992) and Yoklavich et al. (2000). Each dive consisted of two or three 30-min starboard-looking transects conducted at a height of 1 m off the bottom traveling at a speed of approximately 1 kn. A 5-min interval was taken between transects in which the submersible continued to travel a linear path to the start location of the succeeding transect. Submersible observations were documented with a Hi-8 color video camera externally mounted above the starboard viewing porthole looking down at an angle 27^{o} below the horizontal. Transect width was maintained approximately constant at 2 m and measured using hand-held sonar from inside the submersible. Transect width was also determined using a set of parallel lasers mounted 20 cm apart on either side of the external starboard camera and aligned within the central field of view. These lasers were additionally used to determine the size of objects encountered along the transect (i.e. habitat features, fish, and large invertebrates). Lights were used at all times during transects and a digital flash equipped still camera was used from inside the submersible to assist in identification of invertebrates, fishes, and habitats. Observers (D. Howard, D.A. Roberts, T. Anderson, J. Baltan, R.N. Lea, L. Snook, and M.M. Yoklavich) verbally annotated fish species identification, abundance, and size estimates for all fish within the transect. Video observations and audio tracks were recorded with paired Sony miniDV decks on 80-min digital tapes. The underwater location of *Delta* was tracked every 10-sec by the support vessel *R.V. Velero* using an ultra short baseline (USBL) acoustic tracking system. Trackpoint II data was integrated with the ship's differential GPS position and gyro heading data using Winfrog navigational software (GeoPacific Solutions).

Video Analysis

Dive videotapes were later used to quantify fish, habitat, and invertebrates. Fish observations were assigned individual times along the transect and verified for identification, abundance, and maximum size by J. Baltan and L. Snook. The abundance of schooling species and young-of-year rockfish were estimated when they was too numerous to count individuals.

Habitat was characterized using eight different categories of geological substrate similar to the studies of Stein et al. (1992) and Greene et al. (1999). Substrate categories in order of decreasing particle size and vertical relief were: rock ridge (R, high to low relief), boulder (B, high to low relief, diameter $\geq$ 25.5 cm), cobble (C, low relief, diameter $\geq$ 6.5 and < 25.5 cm), pebble (P, low relief, diameter $\geq$ 2 and < 6.5 cm), gravel (G, low relief, diameter $\geq$ 4 mm and < 2 cm), flat rock (F, continuous, low relief), sand (S, grains distinguishable), and mud (M, noticeable organic particles). Habitat data were quantified by subdividing transects into unique segments using the two-code system of

Stein et al. (1992). This method assigns two habitat codes to each distinct change in habitat along the transect creating habitat patches as sampling units of uniform bottom type. The primary code represents the substrate type accounting for > 50% and ≤ 80% of the patch, and the secondary code accounts for ≥ 20% and < 50% of the patch (e.g., RS represented at least 50% cover by rock ridge with at least 20% cover by sand). Habitat patches less than 10-seconds duration were not recorded as unique patches. The area of each habitat patch was determined by multiplying the transect width (2 m) by the length of the habitat patch as determined from the geographic position at the start and end of the patch. Of the 64 habitat combinations possible, the observed habitats were analyzed by Cluster Analysis (group average linkage method) using Bray-Curtis Similarity to determine the dominant habitat types based on the log transformed ($\log_{10}$ +1) abundance of 23 taxa of fishes. Species selected for this analysis had total abundances greater than 0.1% of the total abundance of all observed fish species.

Vertical relief was quantified for each habitat patch using a two-coded system similar to the methods described above. Numerical categories in order of increasing vertical relief were: flat (0, no vertical relief), low (1, vertical relief < 0.5 m), moderate (2, vertical relief ≥ 0.5 m and < 2 m), and high (3, vertical relief ≥ 2 m). The overall vertical relief for each habitat patch was estimated as the mean of the two codes.

Invertebrates (for example, aggregating anemones, encrusting sponges, and tubiculous polychaetes) that were too small to be counted, or did not occur as solitary individuals, in addition to algae, were grouped into the category of encrusting organisms. The extent of these organisms was determined by estimating percent cover within habitat patches using one of four numerical codes. These codes in order of increasing cover were: none (0), light (1, 20-50% cover), moderate (2, > 50-75% cover), and heavy (3, > 75% cover). A two-code system was used to describe the primary and secondary type of encrusting organisms covering the habitat for patches where 20% or more of the substrate was covered by encrusting algae and (or) invertebrates. Using proportions identical to those used for physical habitat, the encrusting organism codes were: algae (A), colony-forming coral (C), colonial ascidian (D), hydroid (H), aggregating anemone (N), tubiculous polychaetes (P), sponge (S), and zooanthid (Z).

Megaufaunal invertebrates (height $\geq$ 5 cm) were identified to the lowest taxonomic level and counted directly from videotapes within habitat patches. Sponges were distinguished by general morphological structure (i.e., foliose, shelf, and barrel sponges). Cupcorals (*Balanophylia elegans*), marine snails, and hermit crabs were < 5 cm but were distinguishable as solitary individuals and were therefore counted as separate from the encrusting organisms and included with counts of megafaunal invertebrates. Densities of megafaunal invertebrates (and fishes) were estimated by standardizing species abundance (or lowest taxonomic group) to the area of their associated habitat patch.

Data Analysis

Detrended Correspondence Analysis (DCA) was used to determine patterns of community-level associations between fishes, megafaunal invertebrates, and physical habitats. This multivariate technique (see Pimentel, 1979) provides an ordination of species and space, in this case habitat patches, in terms of the best fit of one to the other. Ordination is arranged along two ecological gradients (multivariate dimensions) and maximum associations are often ecologically meaningful. Species with abundance greater than 0.1% of the total abundance of all fishes or megafaunal invertebrates were selected for this analysis. Multivariate scores were used to interpolate the combined spatial pattern of physical habitats and species distribution described by the first multivariate dimension across Cordell Bank. This was accomplished with Ordinary Krigging Analysis using the exponential model (root mean square, 0.92) provided by the Geostatistical Analyst program in ArcGIS®. Krigging creates weights from spatially adjacent measured values and predicts continuous values at all unmeasured locations (Johnston et al., 2001). Based on the spatial pattern of the physical habitat and species associations with specific physical habitats, the most likely distribution of megafaunal invertebrate and fish communities at Cordell Bank was predicted.

For some megafaunal invertebrates, designated as potential structure-forming invertebrates on the basis of large size ($\geq$ 20 cm), complex morphology, and the ability to form high-density aggregations (Tissot et al., in review b), observation time, geographic location, and estimated maximum height to the nearest 5 cm were recorded. A Nearest Neighbor Analysis was conducted using ArcGIS® to quantify the occurrence of fishes near certain structure-forming invertebrates relative to all observations of these organisms along dive transects using methods similar to Tissot et al. (in review b). These data were compared using a Chi-square test to identify significant differences in fish distribution near structure-forming invertebrates compared to overall abundance, and for individual species abundance near structure-forming invertebrates relative to the overall abundance for that species. With this analysis the focus was on fishes occurring more adjacent to structure-forming invertebrates, as opposed to less often than expected by chance occurrence. Also derived from Nearest Neighbor Analysis were distance estimates between individual structure-forming invertebrates and the nearest fish. These data were used in conjunction with video observations to quantify close associations between structure-forming invertebrates and fishes to further describe the level of association between species with the potential to provide structure and fishes at Cordell Bank. Close associations were defined as either direct physical contact or activity (i.e., swimming by, hovering above, or resting on the substrate) within a distance of ≤ 1 m or one fish body length, and were categorized by activity codes similar to Stone (in review). In order of increasing association the codes were: no close association (0); in the water column or at rest at a distance ≤ 1 m (1); in the water column at a distance ≤ 1 fish body length (2); at rest at a distance ≤ 1 fish body length (3); and physical contact (4).

Results

Physical Habitats

A total of 27 quantitative dives were completed at 27 stations distributed across Cordell Bank (Figure 2). Dives were conducted between 55 – 250 m depth and ranged in distance from 0.61 – 1.92 km covering a total area equal to 5.84 h (Table 1). Thirty-one unique combinations of physical substrate were observed from a total of 1,378 habitat patches. These habitats were pooled into 17 habitats based on ≥ 70% similarity using Cluster Analysis.

Diversity within habitats was greatest for rock ridges that varied from smooth granite spires to jagged uplifted slabs (Figure 3). Habitat diversity among dives ranged from one unique habitat per transect, an expanse of mud at the eastern slope of Cordell Bank (Dive 5746), to as many as 106 habitat patches, composed of 18 unique habitats at the southern edge of Cordell Bank (Dive 5741) (Table 1). Overall, dives located at the western and eastern extent of Cordell Bank had the least number of individual patches with little habitat diversity, and dives located at the southern, northern, and central areas of Cordell Bank had the greatest number of patches and habitat diversity (Table 1). Half of the observed habitat patches were combinations of high to moderate-relief habitats composed of rock ridge and boulders (Figure 4, and Figure 5, A – C); however, the majority of the total area surveyed was composed of moderate/low to low-relief habitats with almost half of the total area composed of sand and mud habitats with little to no vertical relief (Figure 4, and Figure 5, D – H).

Among physical habitats, percent cover of the encrusting organisms was greatest for hard-substrate habitats of greater structural relief, with the greatest cover at the shallow peaks of rock ridges (50 – 80 m) (Figure 6, A). Taxonomic composition at the shallow crests of rock ridges and pinnacles was dominated by cnidarians including the aggregating corallimorpharian *Corynactus californica*, the branching hydrocoral *Stylaster californica*, hydroids, and the yellow zooanthid *Epizoanthus scotinus,* in addition to bryozoans, sponges, and coralline algae, often covering 100% of the substrate (Figure 6, B). Different encrusting organisms with less cover were observed in hard and mixed-substrate habitats at the flanks of rock ridges, and included encrusting sponges and small tubiculous polychaetes with algae (Figure 6, C).

Overall, the combined spatial pattern of the physical habitats at Cordell Bank was depicted by the first dimension of the Detrended Correspondence Analysis as gradient from hard substrates to soft substrates (Figure 7). Habitats composed of hard substrates with the greatest vertical structure and encrusting cover (RR, RB, BR, BB) were concentrated in shallower depths (mean depth 77 m) at the northern, central, and southeast areas of Cordell Bank. A transition of mixed habitats (BC, CB, RS, SR, BS, SB, CS, RM, MR, BM, MB) of moderate/low to low vertical relief were found at the edges of hard-substrate habitats (mean depth 98 m) and extended to soft-sediment habitats (SS, MM) of little to no vertical structure or encrusting cover, located at greater depths (mean depth 115 m) along the extent of Cordell Bank. These transitions in habitat are further illustrated in Figure 8 for Dives 5741 and 5742 at South and North Cordell Bank.

Species Associations with Physical Habitats

Megafaunal invertebrate observations at Cordell Bank totaled 52,667 individuals from 57 taxa representing 7 phyla. The most common megafaunal invertebrates (81% of total individual invertebrate abundance) included the crinoid *Florometra serratissima* (34%), brittle stars (Ophiacanthidae) (12%), and the sea star *Mediaster aequalis* (2%) (Table 2). Cupcorals were not considered megafaunal invertebrates, but were the most abundant invertebrate counted and comprised 41% of the total abundance of individual invertebrates (Table 2). A total of 73 taxa from 21 families of fishes were observed from 87,291 individual observations. The most common fishes observed (90% of total abundance) were juvenile rockfish (*Sebastes spp.*) (61%), pygmy rockfish (*Sebastes wilsoni*) (27%), and unknown adult rockfish (*Sebastes spp.*) (2%) (Table 3).

A total of nineteen megafaunal invertebrates were identified as providing structural relief and complexity to the physical habitats of Cordell Bank (Table 4). These taxa were identified on the basis of having one, or a combination of the following qualities, including large size ($\geq$ 20 – 120 cm, the maximum size observed) (barrel sponges and *Metridium*), complex morphology (gorgonian corals and foliose sponges), or the ability to form high density aggregations in association with the physical substrate (brittle stars and crinoids) (Figure 9).

Structure-forming invertebrate density varied in distribution across depths (Table 4) and habitat types with fishes (Figure 10 and 11, Appendix A and B). Foliose sponges, shelf sponges, and crinoids; in addition to other invertebrates, including cupcorals, sea cucumbers of the genus *Parastichopus*, and *Ceramaster* sea stars, were more common in high to moderate-relief rock and boulder habitats at the shallower areas of Cordell Bank with greater encrusting cover. These taxa were also present in moderate/low to low-relief mixed habitats located at transitions from high-relief rock and boulder-dominated habitats to sand dominated habitats, but were less common or avoided habitats of mud. Fishes that occurred at high densities with structure-forming invertebrates in high to moderate-relief habitats included yellowtail rockfish (*Sebastes flavidus*), widow rockfish (*Sebastes entomelas*), squarespot rockfish (*Sebastes hopkinsi*), and painted greenling (*Oxylebius pictus*) (Figure 11 and Appendix B). Also having high densities in high to moderate-relief habitats but abundant in mixed habitats were lingcod (*Ophiodon elongatus*), pygmy rockfish, rosy rockfish (*Sebastes rosaceus*), and juvenile rockfish (Figure 11 and Appendix B).

In contrast, structure-forming invertebrates common in mud-dominated habitats with low or no vertical relief and encrusting taxa were sea pens of the genus *Ptilosarcus* and the suborder Subsellaflorae; high densities of sea pens were also observed in low-relief rock ridge habitat with mud (RM) (Figure 10). Other megafaunal invertebrates abundant in mud habitats included snails (subclass Prosobranchia), box crabs

(*Lopholithodes foraminatus*), and urchins (*Allocentrotus fragilis*) (Appendix A). Fishes commonly observed in low-relief mud-dominated habitats were Dover sole (*Microstomus pacificus*) and other unknown flatfish, poachers (Agonidae), combfish (*Zaniolepis spp.*), and spotted ratfish (*Hydrolagus colliei*) (Figure 11 and Appendix B). Deeper mud habitats at the western slope of Cordell Bank had similar species of megafaunal invertebrates and fishes to other mud habitats, but included taxa specific to this area such as galatheid crabs (*Munida quadrispina*), and spot prawns (*Pandalus platyceros*). These taxa were observed with hagfish (*Eptatretus stoutii*), and deep-water rockfishes including splitnose (*Sebastes diploproa*), stripetail (*Sebastes saxicola*), sharpchin (*Sebastes zacentrus*), and greenstriped rockfish (*Sebastes elongatus*) (Figure 11 and Appendix B). Low-relief habitats dominated by sand were less diverse than mud-dominated habitats for both megafaunal invertebrates and fishes. The sea star *Luidia foliolata* and sandabs (*Citharichthys spp.*) were the only species specific to sand-dominated habitats (Appendix A and B). *Ptilosarcus* sea pens were the only megafaunal invertebrate observed in open sand habitats with the potential to provide structural relief to fishes. Sand-dwelling brittle stars occurred frequently at interfaces between flat sand and rock habitats in high density aggregations oriented with arms protruding upwards out of the substrate (Figure 9).

Structure-forming invertebrates with densities greatest in mixed-substrate habitats of moderate to low vertical relief in transition between high-relief rock and boulder habitats and sand and mud habitats, were gorgonian corals, serpulid polychaetes, hard-substrate associated brittle stars, and *Urticina picivora* that occurred with other large anemones, and the sea star *Mediaster* having a near ubiquitous distribution among habitats (Figure 10 and Appendix A). Fishes with high densities in these habitats in comparison to other habitats were black-eyed goby (*Coryphopterus nicholsii*), unknown adult rockfish, unknown rockfish of the subgenus *Sebastomus*, and unknown sculpin (Cottidae) (Appendix B). Fishes found at interfaces between high-relief hard and mixed substrate moderate to low-relief habitats included canary rockfish (*Sebastes pinniger*), and greenspotted rockfish (*Sebastes chlorostictus*) (Figure 11 and Appendix B).

The first and second dimensions from DCA provided a quantitative synthesis of the associations between megafaunal invertebrates, fishes, and physical habitats at Cordell Bank (Figure 12). The first dimension depicted a gradient of hard (RR, BB) to soft (SS, MM) substrates and their associated invertebrate and fish species. Depth distribution of the habitats of Cordell Bank was also reflected on this dimension, as sand habitats are composed of fine grained unconsolidated sediments but occurred shallower than mud habitats. Negative multivariate scores at one extreme of this dimension were hard-substrate habitats (RR, RB, BR, BB) and species in association with these habitats; including rock ridge with boulders (RB), pygmy, yellowtail, and widow rockfish, black-eyed goby, foliose, shelf, and barrel sponges, crinoids, and *Ceramaster* sea stars. The habitats and associated megafauna at the negative end of this dimension were depicted as lighter shaded areas in Figure 7 in the shallow north, central, and southeast areas of Cordell Bank. Conversely, deeper soft sediment habitats (MM, MS) and associated species with high positive scores had ordination at the other extreme of this gradient; including expanses of mud (MM), poachers, Dover sole and other flatfish, greenstriped and stripetail rockfish, sea pens, urchins, and box crabs. These habitats and associated megafauna were depicted as darker shaded areas in Figure 7 at deeper depths descending from the main structure of Cordell Bank and at the extent of the study area. Distinct from the positive and negative extremes of this gradient were sand-dominated habitats and sandabs at values between zero and one (Figure 12). The second DCA dimension reflected a more subtle gradient of habitat complexity and separated the mixed-substrate habitats in transition between high-relief rock and boulder habitats and low-relief mud and sand-dominated habitats. Most noticeable at the positive end of this gradient included mud with boulders (MB), large tubeworms, and greenspotted rockfish, commonly observed at interfaces of mud and hard substrates (Figure 12). These mixed substrate habitats and associated species were depicted as medium shades in Figure 7, located at intermediate depths between the main structure of Cordell Bank and the deeper surrounding areas.

Non-random Co-occurrence of Fishes and Structure-forming Invertebrates

Nearest Neighbor Analysis and Chi square indicated that some fishes on Cordell Bank (with abundances > 0.1 % of total abundance) were observed more often adjacent to structure-forming invertebrates than expected by chance in habitats where these organisms occurred (the majority of significant associations $p \leq 0.001$) (Table 5). Fishes significantly nearer to large sponges with complex morphology (foliose, barrel, and shelf) were fishes with similar affinity to hard-substrate habitats preferred by sponges. These fishes included several rockfish (yellowtail, squarespot, widow, rosy, pygmy, canary, greenspotted, unknown juveniles, and unknown adult *Sebastomus*), black-eyed goby, combfishes, painted greenling, and lingcod (Table 5). Some of the same rockfish (widow, rosy, unknown juveniles, and unknown adult *Sebastomus*), black-eyed goby, and combfishes were also observed nearest to gorgonian corals in the mixed-substrate habitats. Smaller fishes were significantly nearer than expected to the large anemones

Urticina picivora and *Metridium gigantium,* but differed slightly in assemblage between these two species. Rosy rockfish, and unknown adult *Sebastomus*, in addition to yellowtail, juvenile rockfish, and small individuals of unknown adult rockfish, were observed often near *Urticina* in hard and mixed-substrate habitats. *Metridium* were observed over a greater range of habitats with some amount of hard substrate present (Figure 10). These included the shallower rock ridge habitats, and the deeper mud habitats with low-relief rock and boulders. Fishes observed significantly more often adjacent to *Metridium* were sharpchin rockfish, sculpin, combfishes, and flatfishes. Fishes observed in sand and mud-dominated habitats with *Ptilosarcus* sea pens, the only structure-forming invertebrate numerous in these habitats, included flatfishes, poachers, combfishes, and greenspotted rockfish. Although the purpose of this analysis was to examine fishes occurring near structure-forming invertebrates more often than expected by chance; certain fishes were less common near these invertebrates, and these results were also included in Table 5.

Close Associations Between Fishes and Structure-forming Invertebrates

Distances between structure-forming invertebrates and the nearest individual fish, ranged between zero and greater than 10 m with median distances less than 1.5 m for most sponges and gorgonians and less than 1 m for the anemones *Urticina* and *Metridium* (Figure 13). Distances between zero and 1 m, indicative of potential non-random close associations, had the greatest number of individual observations than any other range of distances between fishes and each of these invertebrates (Figure 13). However for some invertebrates one or two fishes made up most of the observations from zero to 1 m, such as *Urticina* with rosy rockfish, and other small unknown adult rockfish of the subgenus *Sebastomus* in mixed-substrate habitats.

Observed close associations at a distance of ≤ 1 m between fishes and structure-forming megafaunal invertebrates included half or greater than half of all observations of *Metridium*, *Urticina*, gorgonians, barrel sponges, shelf sponges, and branching sponges, (Table 6). Most close associations included swimming or hovering in the water column at a distance of ≤ 1 m (code 1) (46.4% of total observations for large structure-forming taxa); however for the large anemones and *Ptilosarcus* sea pens, fishes were also observed within one body length, either in the water column (code 2) (0.4%) or at rest next to these large invertebrates on the bottom (code 3) (0.3%), especially in moderate to low-relief habitats (Table 6). None of the fish were observed in physical contact with these cnidarians, but in rare instances were perched on barrel and shelf sponges (code 4) (0.1%) (Table 6). More frequently observed were pygmy and juvenile rockfish hovering amongst or just above the arms of crinoids in moderate to high-relief rock and boulder habitats and mixed substrate habitats with boulders and moderate to low relief rock. Other interactions involving physical contact were between invertebrates, most commonly crinoids perched at the highest point of a sponge, in particular foliose, barrel, and shelf sponges. Sea stars, brittle stars, and large solitary tunicates were also observed in contact with structure-forming invertebrates.

Discussion

Megafaunal invertebrates and fishes on Cordell Bank co-occurred in four general community types in association with distinct physical habitats. The physical habitats of

Cordell Bank are likely the main factor, in addition to the lifestyle requirements of individual species, that drive community composition; however it is probable that megafaunal invertebrates with the morphological ability to provide structure affect the positive association of fishes with these organisms to form the communities of the Cordell Bank ecosystem.

To document variation in community composition, a range of depths and locations were covered by submersible dives providing a well mixed representation of the physical habitats of Cordell Bank that included all eight categories of substrate and combinations of each. Variation observed within physical habitat types was proportional to the amount of hard substrate present, and was most apparent with observed differences in vertical relief and structural complexity. The degree of physical complexity within habitats likely affected the distribution of species, as complex habitat can offer additional space for shelter and surface area to colonize. Rock ridge habitats exhibited the greatest within-habitat variation and were more diverse by observation, in comparison to Heceta Bank Oregon, where smooth rolling rock ridges are a characteristic feature (Hixon et al., 1991). Boulder habitats also exhibited high variation and were some of the more structurally complex habitats observed at Cordell Bank.

Differences in the amount of unique habitats among dives can be used as a descriptor of the variation in overall habitat complexity between locations. Dives with a greater amount of individual habitat patches located at the northern, central, and southern areas of Cordell Bank, were locations with a greater amount of hard and mixed substrate habitats of greater relief and structural complexity. Conversely, habitat diversity at the edge of Cordell Bank was low and reflected the presence of low complexity habitats with little to no vertical structure, dominated by sand and mud. Overall, Cordell Bank can be described as a rocky bank with characteristic shallow high relief rock ridges and pinnacles surrounded by habitats of rock and boulder that transition into mixed substrate habitats and sand with expanses of mud at the deeper extent and seaward continental slope. The spatial arrangement of physical habitats of varying relief and complexity in conjunction with oceanographic patterns of the area appeared to affect the taxonomic diversity and distribution of invertebrates and fish across the Cordell Bank ecosystem.

A strong southward flowing oceanographic current extending to 25 m depth and an opposing deeper current detectable at 55 m have been demonstrated by Wing et al. (1998) at Cordell Bank within the Northern California Upwelling System. This observation supports the presence of strong current exposure at the shallow rock ridges of Cordell Bank, where the limited distribution of cnidarian-dominated encrusting taxa may be due to flow requirements favorable for feeding and growth that could be facilitated by the presence of strong oceanographic currents at these areas of the bank. Alternatively, the encrusting organisms in hard and mixed substrate habitats of lower relief at the flanks of rock ridges were composed of different organisms (sponges and tubed-polychaetes) that may favor more moderate exposure to oceanographic currents for settlement, growth, and feeding.

The four general communities of megafaunal invertebrates and fishes recognized at Cordell Bank included: 1) species associated with high to moderate-relief rock ridge and boulder habitats; communities in 2) sand-dominated, and 3) mud-dominated habitats; and 4) species associated with mixed-substrate habitats in transition between the two structural extremes.

Habitats composed of rock ridge and boulders varied in relief and complexity across Cordell Bank. Foliose sponges, shelf sponges, and crinoids were the structure-forming invertebrates most numerous in these habitats. However the same taxa and other invertebrates (sea cucumbers, and sea stars) were also abundant in mixed-substrate habitats, indicating their occurrence may have been directed by the amount of available hard substrate. Exposure to currents may have also been an important factor contributing to the distribution and abundance of crinoids (a structure-forming invertebrate) and cupcorals that often occurred in high densities over hard substrate, but with decreasing density near the crests of rock ridges. Puniwai (2002) observed a similar distribution of crinoids at Heceta Bank Oregon, where this perching suspension-feeder tended to avoid areas with potential for exposure to strong oceanographic currents in preference to moderate current exposure. Lifestyle requirements of cupcorals could also affect the ability of this species to colonize hard substrate when strong currents or competition from other sessile invertebrates, such as *Corynactus californica*, are too strong for effective settlement and growth of their planular larvae (Rossi et al., 2001; Miller et al., 2004).

Likewise, the presence of fishes that exhibited patterns of specific association with exposed high-relief habitats may have been related to patterns of water masses moving over Cordell Bank that established favorable feeding conditions. Circulating water masses have been observed over other rocky banks and seamounts, and have been hypothesized to concentrate prey (as reviewed by Genin, 2004). It is also possible that vertically migrating zooplankton become trapped over the summit regions of Cordell Bank at dawn due to currents advecting these aggregations over the bank and blocking their decent. This may have created feeding opportunities for schooling rockfish, as hypothesized by Pereyra (1969) at Astoria Canyon, where large schools of yellowtail rockfish were confirmed (by diet analysis and plankton tows) to be feeding on an aggregation of mesopelagic zooplankton and fish trapped over the down-current flank of the canyon at dawn. Dense schools of yellowtail rockfish and other rockfish, including widow and squarespot, at Cordell Bank may have been present in these habitats due to a consistently available prey source during daylight hours when dives for this study were conducted. Other fishes observed in high numbers in these habitats included pygmy rockfish, juvenile rockfish, rosy rockfish, and lingcod. However, these species were also abundant within the lower relief mixed habitats at the flanks of rock ridges, indicating their distribution may have been determined by a balance between shelter requirements and food availability.

In contrast with high to moderate-relief rock ridge and boulder habitats, different communities of megafaunal invertebrates and fishes were observed in mud and sand-dominated areas of Cordell Bank. The mud community most typically consisted of snails, box crabs, urchins, and sea pens in association with Dover sole and other flatfish, poachers, combfish, and spotted ratfish. The sand community was unique from that of mud-associated taxa, with sandabs and the sea star *Luidia foliolata* as the most specifically associated species. *Ptilosarcus* and Subsellaflorae sea pens were the only structure-forming invertebrates in open sand and mud habitats. Although the egg-cases of spotted ratfish and skates were commonly observed in sand habitat, none were on or next to sea pens, as observed with sponges on deep rocky banks in southern California (Tissot et al., in review b). Lifestyle characteristics that require feeding on top of, or in, soft sediments, or a need to anchor support structures, as required by Pennatulaceans, could have determined the co-occurrence of these invertebrates and fishes in soft sediment habitats.

Within mud habitats, a unique sub-community occurred at the deeper western slope of Cordell Bank between 160 – 250 m, where the substrate was composed of mud with areas of steep consolidated clay with holes created by hagfish or potentially invertebrates. This unique community included galatheid crabs and spot prawn co-occurring with hagfish and rockfishes such as splitnose, stripetail, sharpchin, and greenstriped rockfish. The majority of species observed with this type of habitat were not observed elsewhere; indicating depth and (or) habitat were important factors in their distribution. However feeding requirements may have been another important influence on the structure of this community, as several of these species are zooplanktivorous rockfish (Love et al., 2002) or invertebrates such as galatheid crabs, known to perch and select zooplankton from the water column (Romero et al., 2004). This type of habitat located at the shelf break at the western edge of Cordell Bank, represents an abrupt change in topography known to aggregate migrating zooplankton (as reviewed by Genin, 2004). Dense swarms of euphausiids observed on several dives in this location indicate this area may concentrate prey, which could be an important ecological factor structuring this community of species with diets supported by crustacean zooplankton.

The mixed-substrate habitats in transition between high and moderate-relief rock ridge and boulders, and low-relief sand and mud had a specific community of structure-forming invertebrates and fishes observed in high densities in comparison to other habitats, including brittle stars numerous in the cracks and on top of hard substrate, gorgonian corals, mound and flat sponges, serpulid polychaetes, *Urticina picivora* and other larger anemones, black-eyed goby, small (10 – 20 cm) unknown adult rockfish (in particular the subgenus *Sebastomus*), and sculpin. Crinoids were observed in dense aggregations in these habitats when hard substrate was available in addition to foliose, barrel, and shelf sponges.

Large structure-forming octocorals with complex morphology such as gorgonians were infrequent with a maximum density of 344 individuals/ha (n = 138, SE 13) in mixed mud habitat with boulders. This distribution may be due to the exposed nature of Cordell Bank, and the presence of gorgonians in transition habitats, as observed in Tissot et al. (in press b) may reflect a need for more moderate currents to support settlement, early survival, and feeding. This pattern is similar to the observed decreases in density of crinoids and cupcorals in the more current exposed areas of rock ridge.

There were a greater number of smaller rockfish specific to mixed-substrate habitats in addition to associated species that appear to have general hard substrate requirements, such as pygmy and juvenile rockfish in addition to smaller individuals (< 20 cm) of the subgenus *Sebastomus*. This pattern may have been attributed to space or food limitations in high-relief habitats, or a need to seek shelter from predators on the open faces of ridges with less physical complexity. However, these fishes were confronted with different predators in mixed-substrate transition habitats where the larger picivorous rockfish were most abundant (Love et al., 2002), including yelloweye (*Sebastes ruberrimus*), canary, and greenspotted rockfish, in addition to lingcod, that were abundant across all hard-substrate habitats and may have been distributed largely based on prey availability.

Two of the larger piscivorous rockfish, canary and greenspotted, were commonly found at interfaces between high-relief hard and mixed-substrate moderate to low-relief habitats, but differed in distribution slightly in that canaries were not specific to either sand or mud interfaces, and greenspotted rockfish were most common at interfaces between hard substrate and mud. This distribution could have been influenced by resource partitioning or differences in preferred prey, as observed by York (2005) at Heceta Bank, Oregon for a similar rockfish assemblage. Structure-forming invertebrates that exhibited preference for sand/rock interface habitats were sand-dwelling brittle stars, observed buried with arms exposed and oriented upwards providing structure analogous to patchy grass at the base of a rocky slope. This additional structure in what would otherwise be flat sand could have concentrated particulate matter and affected food availability for other invertebrates and fish, and thus potentially influenced community composition at sand/rock interface habitats.

Megafaunal invertebrates provided additional structure and complexity to the physical habitats of Cordell Bank as observed from frequent, statistically significant, non-random associations at relatively close median distances between fishes and structure-forming invertebrates. Specific close associations were also identified within each of the four general communities. Fishes in association with large morphologically complex sponges in high-relief rock ridge dominated habitats were species with similar affinity for these habitats. Both sessile invertebrates and fish were likely present in these shallow and exposed areas of the bank due to food availability that may have been augmented by oceanographic currents and advective processes. However more than half of large sponge observations in these habitats were in close association with fish ($\leq$ 1 m), indicating that sponges may provide useful structure to mobile fauna that potentially utilized the living structure for shelter, territorial needs, or to decrease the energetic expense of having to keep position on exposed rock walls. Similar levels of close associations were categorically observed by Stone (in review) for corals in Alaska, and were visually documented by Krieger and Wing (2002). Rocky banks in southern California had less close associations between fishes and invertebrates; however the study by Tissot et al. (in review b) only compared associations of physical contact, which were few relative to total observations, as observed at Cordell Bank. Observations between the two locations may have been more similar had close associations been examined by specific categories of association in southern California. *Metridium* and crinoids also provided structure in high relief rock ridge habitats and close associations were common with small juvenile and pygmy rockfish observed hovering just above both invertebrates or amongst the arms of crinoids. The presence of crinoids in dense aggregations atop the physical substrate likely contributed to the high abundances of pygmy and juvenile rockfish in high to moderate-relief hard and mixed-substrate habitats, where the protection offered to these small ($\leq$ 10 cm) fish by the living structure of these invertebrates could have influenced their presence in these exposed habitats. These smaller rockfish were also abundant in mixed-substrate transition habitats that may have been less exposed to oceanographic currents, but were not without predators. Although the presence of crinoids in these habitats did not necessarily determine the presence of these fishes, it is likely their abundances would not have been so great without this additional structure for protection from predators. Moreover, crinoids could have provided foraging opportunities for smaller fishes as suggested by Puniwai (2002) in their morphological potential to trap particulate matter. Dense aggregations of brittle stars in boulder and cobble fields could have had a similar role to crinoids in adding complexity to the habitat as the same smaller rockfish were observed in and amongst the arms of ophiuroids in these habitats. Large structure-forming octocorals such as gorgonians occurred infrequently at Cordell Bank and were smaller (maximum size observed 30 cm) than large corals typically observed in Alaska (Krieger and Wing, 2002; Stone, in review) or in southern California (Tissot et al., in review b). Gorgonians were most dense in mixed-substrate transition habitats at the flanks of rock ridges and high-relief boulder fields, other large invertebrates in these areas were the anemones *Urticina* and *Metridium*. Although these taxa were not in great abundance at Cordell Bank, statistically significant, non-random, close associations with fish were present and unique. A notable interaction occurred between *Urticina* and rosy rockfish, in addition to other small (10 – 20 cm) unidentified adult rockfish of the subgenus *Sebastomus*. Half of the close associations ($\leq$ 1 m) with *Urticina* were with rosy rockfish at a median distance of just over ½ m (about three body lengths relative to the fish), and associations within one body length were observed. The presence of *Urticina* often predicted the presence of rosy rockfish, but rosy rockfish were also present in areas without *Urticina*. A potentially similar facultative association between painted greenling and this large anemone was observed by Elliot (1992), where interactions were similar to those observed with rosy rockfish on Cordell Bank, but differed in that painted greenling were often in physical contact with the anemones and more so during evening and crepuscular hours not surveyed at Cordell Bank. In these associations, the large size and lifestyle of *Urticina* likely provided shelter and protection to these fishes, as most observations at Cordell

Bank and with Elliot's study were in habitats with more solid rock and less boulders or crevasses offering additional spaces and physical complexity for shelter. In low-relief habitats dominated by mud, sharpchin rockfish, combfishes, and flatfishes were closely associated with *Metridium*, often resting on the bottom at a distance of $\leq$ 1 m or within $\leq$ 1 fish body length at the base of this anemone. These same fishes were observed resting next to low-relief rock outcrops and boulders in the same habitats when *Metridium* was absent, thus the distribution of these fishes was not likely predicted by the presence of this anemone; although potentially influenced, as living and physical structure were equally utilized by these fishes, especially sharpchin rockfish. Open sand and mud habitats absent of structural relief had few observations of large structure-forming invertebrates. Sea pens were however present in these habitats and close associations with fishes common to these habitats were observed $\leq$ 1 m and infrequently at closer distances. Although not numerous in areas surveyed in 2001 on Cordell Bank, high densities of tall (up to 1 m) Subsellaflorae sea pens were observed at the eastern side of the bank shoreward in a subsequent survey, where mud-associated fishes were observed resting amongst the Pennatulaceans and in holes during evening hours (pers. obs.). This was documented in greater detail by Brodeur (2001) with Pacific ocean perch in association with dense forests of sea whips at night in Pribilof Canyon, Alaska. It is possible that greater instances of close associations between structure-forming invertebrates and fishes may have been observed at Cordell Bank if dives were conducted during evening hours when certain species seek shelter to rest. Night dives conducted with an ROV at Heceta Bank, Oregon demonstrated that sharpchin, greenstriped, and pygmy rockfish were closely associated and often in physical contact underneath or on top of large sponges in boulder and cobble habitats during evening hours as opposed to daytime dives when these fishes were more active (Hart, 2004).

Based on the high occurrence of non-random close associations observed with fishes, certain structure-forming invertebrates can therefore be considered ecologically important living components of habitat at Cordell Bank. The distribution of physical habitats and lifestyle requirements of individual species were the primary influence structuring the observed communities at Cordell Bank; however it is likely the presence of structure-forming invertebrates in association with specific physical habitats contributed to the observed community structure. This is not to imply that fishes were in dependence upon this living structure for survival, reproduction, or other processes. Rather these large, complexly shaped, or densely aggregated invertebrates augment the structural relief and complexity of the physical habitats and may create more favorable conditions for these structurally oriented fishes. The potential however, for relationships of greater dependency between fishes and structure-providing species should be the focus of future work, in addition to an examination of nocturnal behavior on nighttime dives when fishes are less active and potentially associated more closely with the living and physical structure.

In conclusion, structure-forming megafaunal invertebrates and fishes were associated in four general communities at Cordell Bank, based on the spatial arrangement of the physical habitats. Certain fishes were closely associated with structure-forming invertebrates within these general communities, including commercially important species of groundfish. These statistically significant, non-random close associations suggest that structure-forming invertebrates such as sponges, crinoids, and large anemones, have an ecological role as living components of habitat within invertebrate and fish communities at Cordell Bank. Ecosystem-based fisheries management should consider this relationship in decision-making processes that will affect the removal of species and potentially disturb the habitats of submerged rocky bank ecosystems along the U.S. West Coast continental shelf and slope. Removal or alteration of the habitats of these areas including large invertebrates will undoubtedly have affect on community composition and the long-term health of marine populations including commercially important species of groundfish.

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Table 1. Submersible dives on Cordell Bank by location with total distance (km) and area (h) surveyed, and the number of habitat patches and substrate types observed with mean depth for each dive.

Location on Cordell Bank	**Dive Number**	**Total Distance (km)**	**Total Area (h)**	**No. of Habitat Patches**	**No. of Substrate Types Observed**	**Mean Depth (m)**
Central	5717	0.92	0.18	68	12	72
Central	5720	1.04	0.21	71	11	70
Central	5723	1.06	0.21	62	11	111
Central	5724	1.17	0.23	65	12	72
Central	5725	1.03	0.21	63	12	65
Central	5732	0.81	0.16	50	11	55
Central	5733	0.89	0.18	63	13	69
Central	5734	1.15	0.23	71	10	95
Central	5739	0.97	0.19	77	13	65
East	5718	1.14	0.23	53	9	102
East	5719	1.31	0.26	10	4	107
East	5746	0.83	0.17	2	1	174
Northeast	5745	1.06	0.21	34	8	127
North	5716	0.78	0.16	51	8	92
North	5742	1.38	0.28	76	13	131
North	5743	0.83	0.17	77	12	86
Northwest	5722	1.01	0.20	73	12	116
Northwest	5729	1.32	0.26	45	8	160
West	5728	1.47	0.29	3	1	250
Southwest	5731	0.61	0.12	11	6	115
Southwest	5730	1.22	0.24	5	1	210
Southwest	5737	0.95	0.19	49	12	88
Southwest	5738	1.29	0.26	10	4	192
South	5727	1.21	0.24	93	14	58
South	5736	0.93	0.19	77	13	65
South	5741	1.92	0.38	106	18	75
Southeast	5726	0.89	0.18	13	3	100
TOTAL:	**27**	**29.19**	**5.84**	**1378**	**31**	**108**

Table 2. Number of individual observations and percent of total observations for solitary benthic invertebrates identified at Cordell Bank, California, September 2002.

Phylum	Phylum and Taxon Name	Number of Observations	Percent of Total Observations	Phylum	Phylum and Taxon Name	Number of Observations	Percent of Total Observations
Porifera	round yellow sponge	388	0.44		hermit crab	15	0.02
	foliose sponge	1124	1.27		large hermit crab	5	0.01
	flat sponge	4	<0.01		*Munida quadrispina*	121	0.14
	barrel sponge	145	0.16		*Loxorhynchus crispatus*	1	<0.01
	shelf sponge	295	0.33		unknown decorator crab	1	<0.01
	Vase sponge	5	<0.01		*Pleuroncodes planipes*	5	0.01
	mound sponge	118	0.13		*Murcia guadichaudii*	2	0.02
	branching sponge	11	0.01		*Cancer spp.*	8	0.01
	upright sponge	25	0.03		unknown crab	5	0.01
Cnidaria	*Metridium senile*	43	0.05	**Echinodermata**	*Allocentrotus fragilis*	573	0.65
	Metridium gigantium or farcimen	13	0.02		*Lovenia cordiformis*	1	<0.01
	Urticina piscivora	50	0.06		unknown urchin	41	0.05
	Hormathidae	6	0.01		*Florometra serratissima*	30226	34.1
	unknown sand anemone	771	0.87		*Gorgonocephalus eucnemis*	4	0.01
	unknown anemone	1139	1.28		Ophiacanthidae	10743	12.1
	Balanophyllia elegans	36016	40.6		*Mediaster aequalis*	1679	1.89
	unknown cup coral	4	0.01		*Henricia spp.*	77	0.09
	Ptilosarcus spp.	16	0.02		*Pycnopodia helianthoides*	27	0.03
	Subselliflorae sea pen	486	0.55		*Pteraster militaris*	6	0.01
	Gorgonacea	138	0.16		*Pteraster tesselatus*	1249	1.41
Mollusca	*Octopus dofleini*	6	0.01		*Pteraster spp.*	35	0.04
	Octopus rubescens	1	<0.01		*Luidia foliolata*	41	0.05
	Octopus spp.	9	0.01		*Luidia spp.*	1	<0.01
	Chlamys rubidia	8	0.01		*Pateria (Asterina) miniata*	22	0.01
	Opistobranchia	109	0.12		*Poraniopsis inflata*	1	<0.01
	Pleurobranchea californica	30	0.03		*Orthasterias spp.*	19	0.02
	Prosobranchia	321	0.36		*Ceramaster spp.*	964	1.09
	gastropod shells	40	0.05		unknown sea star	16	0.02
Annelida	Serpulid polychaete	1228	1.39		*Parastichopus spp.*	1	<0.01
Arthropoda	*Lopholithodes foraminatus*	122	0.14	**Chordata**	*Thetys vagina*	15	0.02
	Pandalus platyceros	74	0.08		solitary tunicate	34	0.04

Table 3. Number of individual observations and percent of total observations for fishes identified at Cordell Bank, September 2002.

Family	**Scientific Name**	**Common Name**	**Number of Observations**	**Percent of Total Observations**
Agonidae	Agonidae.	unknown poachers	259	0.30
Anarhichadidae	*Anarrhichthys ocellatus*	wolf-eel	1	<0.01
Anoplopomatidae	*Anoplopoma fimbria*	sablefish	1	<0.01
Argentinidae	*Argentina sialis*	Pacific argentine	1	<0.01
Bothidae	*Citharichthys sordidus*	Pacific sanddab	2	<0.01
	Citharichthys spp.	unknown sanddab	327	0.38
Chimaeridae	*Hydrolagus colliei*	spotted ratfish	162	0.19
Cottidae	*Icelinus filamentosus*	threadfin sculpin	7	0.01
	Icelinus tenuis	spotfin sculpin	5	0.01
	Icelinus spp.	Icelinus sculpins	10	0.01
	Cottidae	unknown sculpin	179	0.21
Embiotocidae	*Hypsurus caryi*	rainbow surfperch	1	<0.01
	Zalembius rosaceus	pink seaperch	1	<0.01
Gadidae	*Gadus macrocephalus*	Pacific cod	1	<0.01
Gobiidae	*Coryphopterus nicholsii*	blackeye goby	245	0.28
Hexagrammidae	*Oxylebius pictus*	painted greenling	45	0.05
	Hexagrammos decagrammus	kelp greenling	29	0.03
	Ophiodon elongatus	lingcod	125	0.14
	Zaniolepis frenata	shortspine combfish	6	0.01
	Zaniolepis latipinnis	longspine combfish	29	0.03
	Zaniolepis spp.	unknown combfishes	233	0.27
Hexanchidae	*Hexanchus griseus*	bluntnose sixgill shark	2	<0.01
Liparididae	*Careproctus melanurus*	blacktail snailfish	1	<0.01
Myxinidae	*Eptatretus stoutii*	Pacific hagfish	1	<0.01
	Eptatretus spp.	unknown hagfish	63	0.07
Pholidae	*Pholidae spp.*	unknown gunnels	4	0.01
Pleuronectidae	*Eopsetta jordani*	petrale sole	7	0.01
	Errex zachirus	rex sole	56	0.06
	Hypsopsetta guttulata	diamond turbot	1	<0.01
	Lyopsetta exilis	slender sole	21	0.02
	Microstomus pacificus	Dover sole	183	0.21
	Platichthys stellatus	starry flounder	1	<0.01
	Pleuronectes vetulus	English sole	9	0.01
Rajidae	*Raja binoculata*	big skate	1	<0.01
	Raja inornata	California skate	6	0.01
	Raja rhina	longnose skate	9	0.01
	Raja spp.	unknown skate	5	0.01
Scorpaenidae	*Sebastes mystinus*	blue rockfish	24	0.03
	Sebastes paucispinis	Bocaccio	31	0.04
	Sebastes pinniger	canary rockfish	43	0.05
	Sebastes rubrivinctus	flag rockfish	2	<0.01
	Sebastes chlorostictus	greenspotted rockfish	183	0.21
	Sebastes elongatus	greenstriped rockfish	126	0.14
	Sebastes helvomaculatus	rosethorn rockfish	4	0.01

Table 3. Continued

Family	**Scientific Name**	**Common Name**	**Number of Observations**	**Percent of Total Observations**
Scorpaenidae	*Sebastes serranoides*	olive rockfish	1	<0.01
	Sebastes ovalis	speckled rockfish	13	0.02
	Sebastes wilsoni	pygmy rockfish	23887	27.4
	Sebastes babcocki	redbanded rockfish	1	<0.01
	Sebastes spp.	unknown rockfishes	1601	1.83
	Sebastes rosenblatti	greenblotched rockfish	2	<0.01
	Sebastes rosaceus	rosy rockfish	995	1.14
	Sebastes jordani	shortbelly rockfish	20	0.02
	Sebastes zacentrus	sharpchin rockfish	112	0.13
	Sebastes diploproa	splitnose rockfish	12	0.01
	Sebastes hopkinsi	squarespot rockfish	186	0.21
	Sebastes constellatus	starry rockfish	28	0.03
	Sebastolobus alascanus	shortspine thornyhead	3	<0.01
	Sebastomus spp.	unknown sebastomus	804	0.92
	Sebastes saxicola	stripetail rockfish	154	0.18
	Sebastes ensifer	swordspine rockfish	14	0.02
	Sebastolobus spp.	unknown thornyheads	16	0.02
	Sebastes nigrocinctus	tiger rockfish	1	<0.01
	Sebastes miniatus	vermilion rockfish	13	0.02
	Sebastes entomelas	widow rockfish	229	0.26
	Sebastes ruberrimus	yelloweye rockfish	33	0.04
	juvenile *Sebastes spp.*	juvenile unknown rockfish	53391	61.2
	Sebastes flavidus	yellowtail rockfish	1370	1.57
Stichaeidae	Stichaeidae	Pricklebacks	60	0.07
Torpedinidae	*Torpedo Californica*	pacific electric ray	1	<0.01
Zoarcidae	Zoarcidae	unknown eelpout	10	0.01
	Lycodes cortezianus	bigfin eelpout	3	<0.01
Unknown	Unknown	unknown flatfishes	621	0.71
	Unknown	unidentified fishes	1258	1.44

Table 4. Criteria and characteristics of structure-forming invertebrates on Cordell Bank, California: total observed (n), density (#/hectare) with standard error, maximum height (cm), mean depth (m) with standard error, and mean vertical relief.

Taxa	N	Criteria			Density (#/hectare)		Maximum height (cm)	Depth (m)		Mean vertical relief
		Size	Morphology	Density	Mean	SE		Mean	SE	
Foliose sponge	1,124	X	X		425	38	120	73	<1	2.5
Shelf sponge	295	X	X		114	14	120	83	2	2.5
White-plumed anemone *(Metridium gigantium)*	82	X			15	7	80	130	10	2
Stalked sea pen (Subselliflorae)	486	X	X		28	7	70	138	7	0
Barrel sponge	145	X	X		60	8	60	90	2	2
Mound sponge	118	X			42	7	50	84	3	2
Upright sponge	25	X			9	3	35	78	5	2
Gorgonians (Gorgonacea)	138	X	X		59	13	30	103	3	1.5
Serpulid Polychaete	1,228	X			505	41	30	107	1	1.5

Table 4. Continued

Branching sponge	11	X			3	2	30	56	11	2
Crinoid *(Florometra serratissima)*	30,226	X	X	X	11,663	942	25	100	1	1.5
Vase sponge	5	X	X		4	2	25	90	2	2
Fish eating anemone *(Urticina piscivora)*	51	X			19	5	20	57	<1	2.5
Plumed sea pen *(Ptilosarcus spp.)*	16	X			6	2	20	110	10	0.5
Solitary tunicate (Urochordata)	34	X			11	2	20	72	2	2
Flat sponge	4	X			1	<1	20	85	6	2
Round sponge	388			X	83	27	10	100	6	2
Brittlestar (Ophiacanthidae)	10,199		X	X	3,742	32	5	101	2	1.5

Table 5. Percentage of fishes (total abundances > 0.1% of total species abundance) near sponges, gorgonians, *Ptilosarcus spp.* sea pens, the anemones *Urticina picivora*, and *Metridium gigantium* relative to fishes counted along transects. Species that occurred statistically more often near these invertebrates are indicated with an * (p = 0.05), and ** (p ≤ 0.001) respectively. Species that were statistically less common near these invertebrates are indicated with a ϕ.

Taxa	Total near Foliose Sponges	Total on Transect	Total near Barrel Sponges	Total on Transect	Total near Shelf Sponges	Total on Transect	Total near Mound Sponges	Total on Transect	Total near Branching Sponges	Total on Transect	Total near Round Sponges	Total on Transect
unknown rockfish	1ϕ	2	1ϕ	2	<1ϕ	2	7**	2	<1	2	5**	2
juvenile unknown rockfish	78**	63	78**	62	50ϕ	62	34ϕ	64	3ϕ	64	69**	59
unknown *Sebastomus*	1**	1	1**	1	2**	1	1**	1	2**	1	2**	1
greenspotted rockfish	<1*	<1	<1**	<1	<1	0	<1**	<1	<1	<1	2	<1
greenstriped rockfish	<1*	<1	<1	<1	<1	0	<1	<1	<1	<1	<1*	<1
widow rockfish	<1	<1	<1	<1	<1*	0	<1**	<1	<1	<1	<1	<1
yellowtail rockfish	1ϕ	2	2**	2	5**	2	3**	2	<1	2	1ϕ	2
sqaurespot rockfish	<1**	<1	<1**	<1	<1	0	<1	<1	<1	<1	<1	<1
canary rockfish	<1**	<1	<1	<1	<1	0	<1	<1	<1	<1	<1	<1
rosy rockfish	2**	1	1**	1	1**	1	2**	1	3*	1	3**	1
stripetail rockfish	<1	<1	<1	<1	<1	0	<1**	<1	<1	<1	<1**	<1
pygmy rockfish	16ϕ	28	16ϕ	28	42**	29	52**	28	93**	26	13ϕ	30
sharpchin rockfish	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1
black-eyed goby	<1**	<1	<1**	<1	<1	<1	1	<1	<1	<1	1**	<1
combfishes	<1	<1	<1	<1	<1**	<1	<1**	<1	<1	<1	<1	<1
unknown sculpin	<1	<1	<1	<1	<1	<1	<1**	<1	<1	<1	<1	<1
unknown poacher	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1
painted greenling	<1**	<1	<1**	<1	<1	<1	<1*	<1	<1	<1	1**	<1
lingcod	<1	<1	<1**	<1	<1**	<1	<1	<1	<1	<1	<1	<1
sandabs	<1	<1	<1	<1	<1	<1	<1	<1	<1	1	<1	<1
unknown flatfishes	<1	<1	<1	<1	<1	<1	<1	<1	<1	1	<1ϕ	1
spotted ratfish	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	1**	<1

Table 5. Continued

Taxa	Total near Gorgonians	Total on Transect	Total near Ptilosarcus	Total on Transect	Total near Urticina	Total on Transect	Total near Metridium	Total on Transect
unknown rockfish	1ϕ	2	7	2	2**	1	1**	1
juvenile unknown rockfish	80**	60	<1ϕ	23	66*	65	85**	59
unknown *Sebastomus*	2**	1	7	2	2*	1	<1	1
greenspotted rockfish	1	<1	7**	1	<1	<1	<1**	<1
greenstriped rockfish	<1	<1	<1	2	<1	<1	<1	<1
widow rockfish	1**	<1	<1	<1	<1	<1	<1	<1
yellowtail rockfish	<1ϕ	2	<1	1	2*	2	7**	2
sqaurespot rockfish	<1	<1	<1	<1	<1	<1	<1	<1
canary rockfish	<1	<1	<1	<1	<1	<1	<1	<1
rosy rockfish	1**	1	<1	1	4**	1	1**	1
stripetail rockfish	<1	<1	<1	2	<1	<1	<1	<1
pygmy rockfish	11ϕ	29	<1	21	23ϕ	28	<1	28
sharpchin rockfish	<1	<1	<1	2	<1	<1	3**	<1
black-eyed goby	1**	<1	<1	<1	<1	<1	1**	<1
combfishes	1*	<1	47**	3	<1	<1	<1	<1
unknown sculpin	<1	<1	<1	2	<1	<1	<1**	<1
unknown poacher	<1	<1	7**	4	<1	<1	<1	<1
painted greenling	<1	<1	<1	<1	<1	<1	<1	<1
lingcod	<1	<1	<1	<1	<1	<1	<1	<1
sandabs	<1	<1	<1	5	<1	<1	<1	1
unknown flatfishes	<1ϕ	1	27**	9	<1	<1	1**	1
spotted ratfish	<1	<1	<1	2	<1	<1	<1	<1

Table 6. Associations of organisms with large structure-forming invertebrates on Cordell Bank, California. Fish associations listed by category: (none); (1) in the water column $\leq$1 m; (2) in the water column $\leq$1 fish body length; (3) at rest next to $\leq$1 fish body length; (4) physical contact.

Taxa	n	Associated Organisms (% of total observations)								
		Fish Association Category					Other Associations			
		None	1	2	3	4	crinoids	sea stars	brittle stars	tunicates
Round sponge	388	56.2	39.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Foliose sponge	1124	51.6	47.5	0.0	0.0	0.0	0.9	0.0	0.2	<0.1
Barrel sponge	145	49.7	49.0	0.0	0.0	0.7	19.0	0.0	0.7	0.0
Shelf sponge	295	46.8	52.5	0.0	0.0	0.7	14.0	0.0	0.0	0.0
Mound sponge	118	60.2	37.3	0.0	0.0	0.0	0.0	2.0	0.0	0.0
Branching sponge	11	9.1	90.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metridium gigantium	82	51.2	39.0	2.4	7.3	0.0	0.0	0.0	0.0	0.0
Urticina piscivora	51	45.1	39.2	11.8	3.9	0.0	0.0	0.0	0.0	0.0
Ptilosarcus spp.	16	62.5	31.3	6.3	0.0	0.0	0.0	0.0	0.0	0.0
Gorgonians	138	47.1	52.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Summary	**2368**	**51.5**	**46.4**	**0.4**	**0.3**	**0.1**	**3.3**	**0.1**	**0.1**	**<0.1**

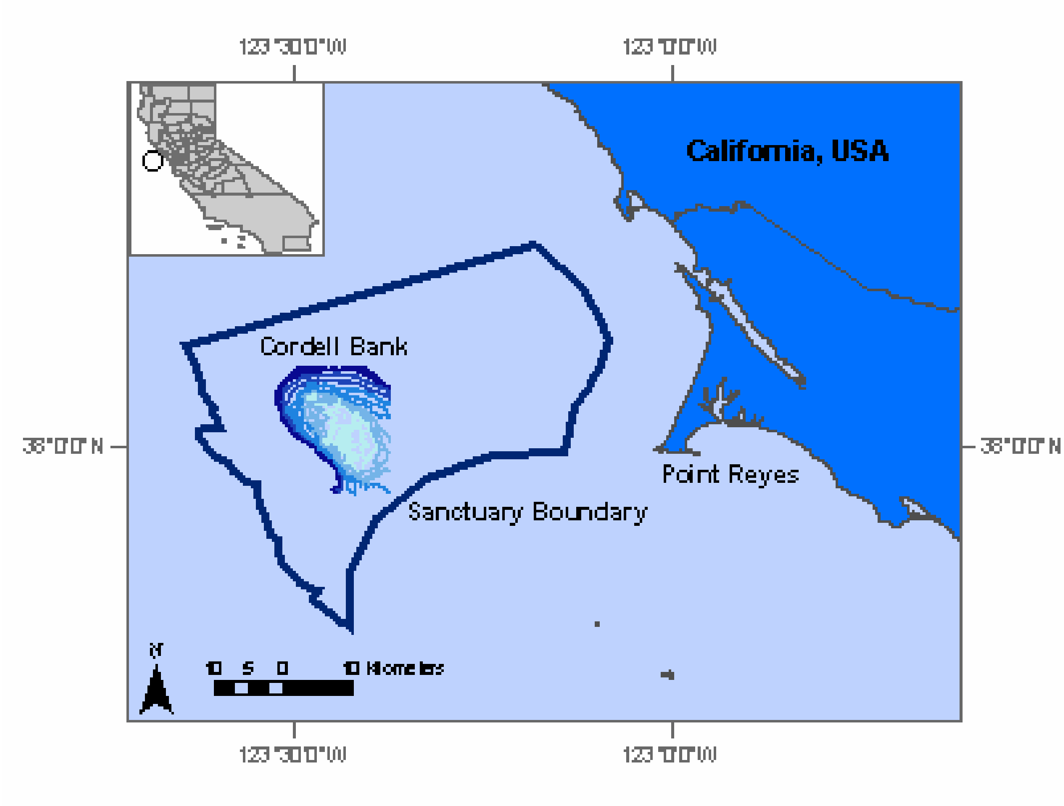


Figure 1. Cordell Bank location within the Cordell National Marine Sanctuary, with reference to Point Reyes, California.

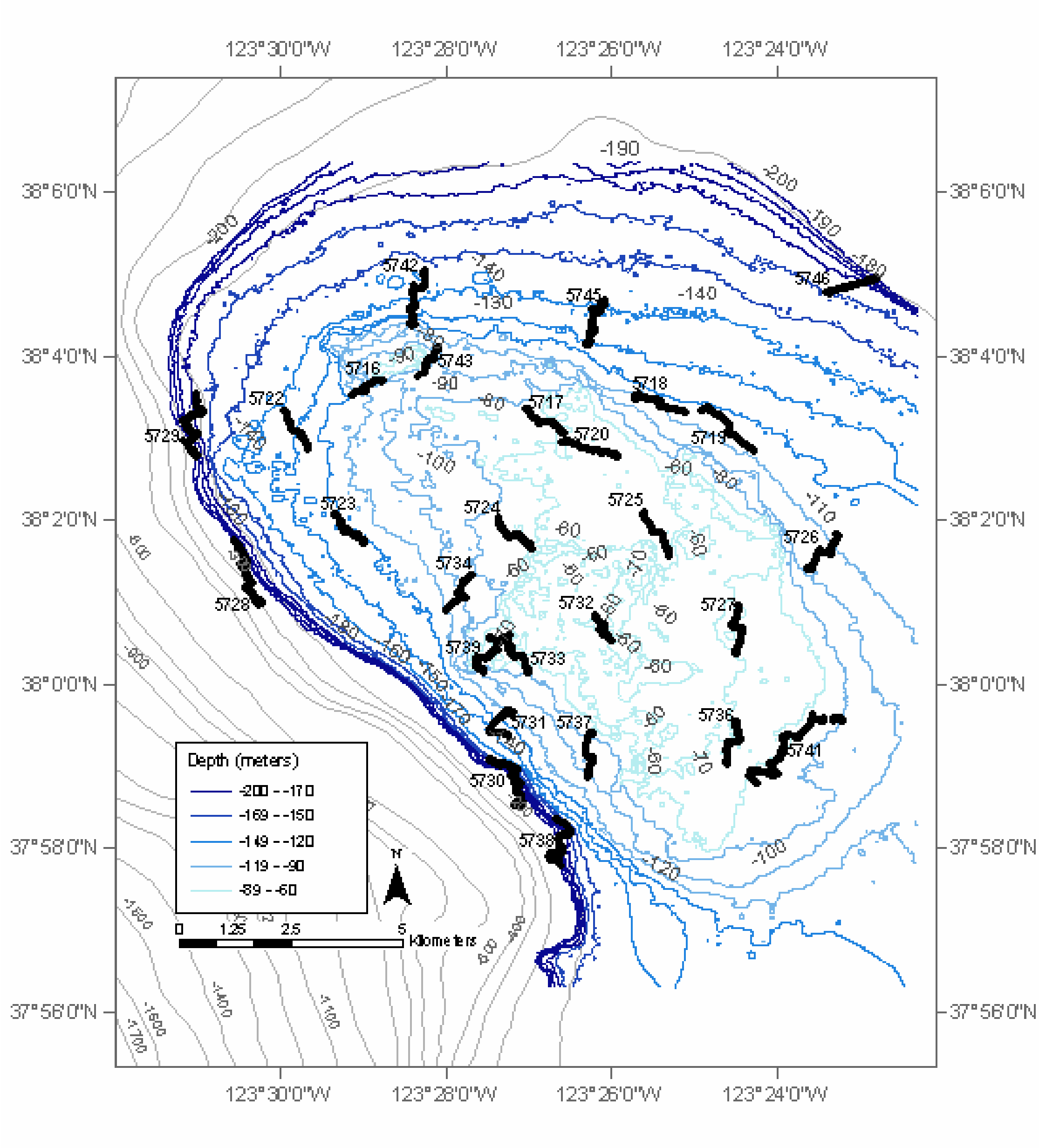


Figure 2. Cordell Bank bathymetry and 2002 *Delta* submersible dive locations.

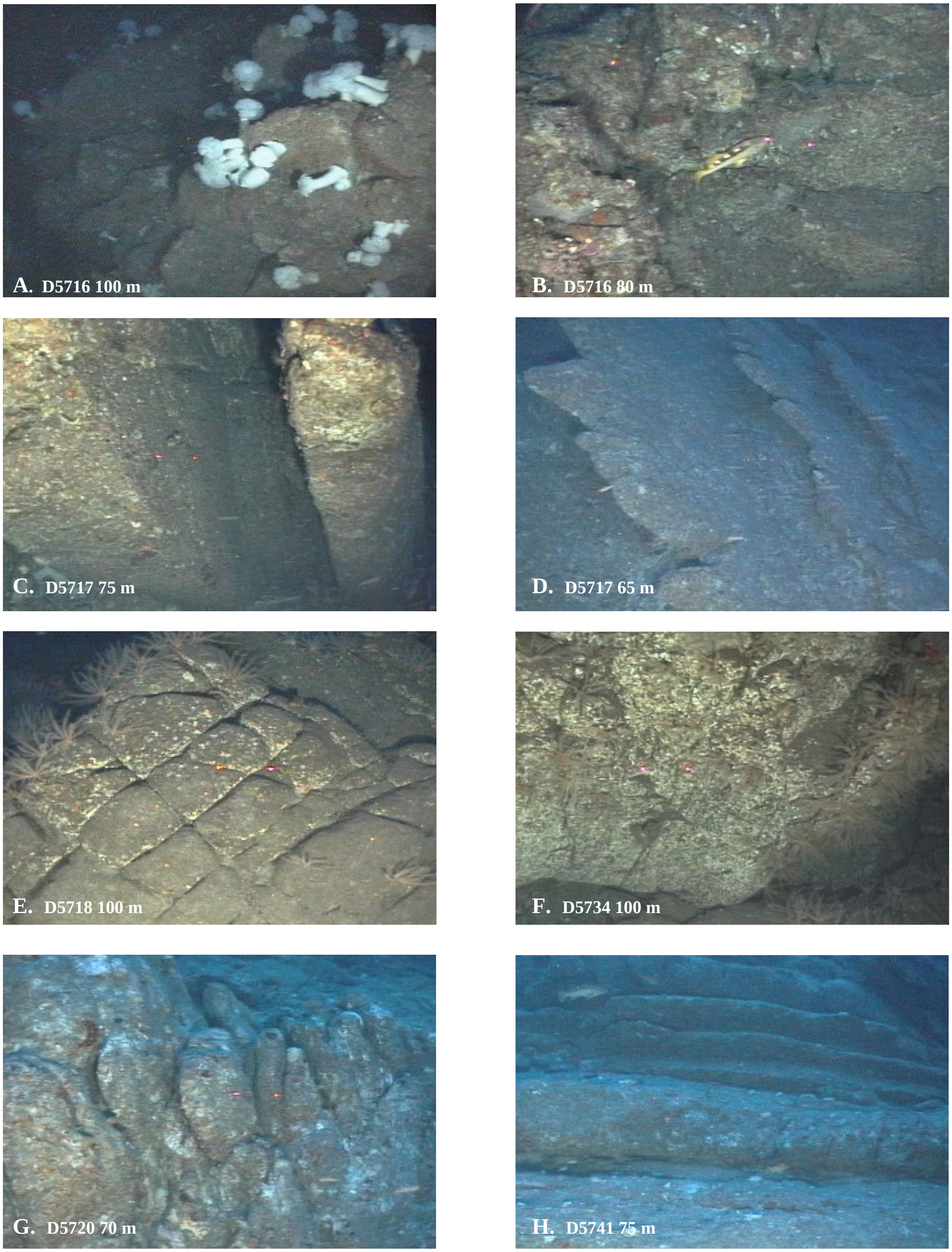


Figure 3. Variation within rock ridge habitats at Cordell Bank by location: North Bank (A,B); Central Bank (C-F); East Bank (G); and South Bank (H). Delta dive number and depth are indicated for each habitat.

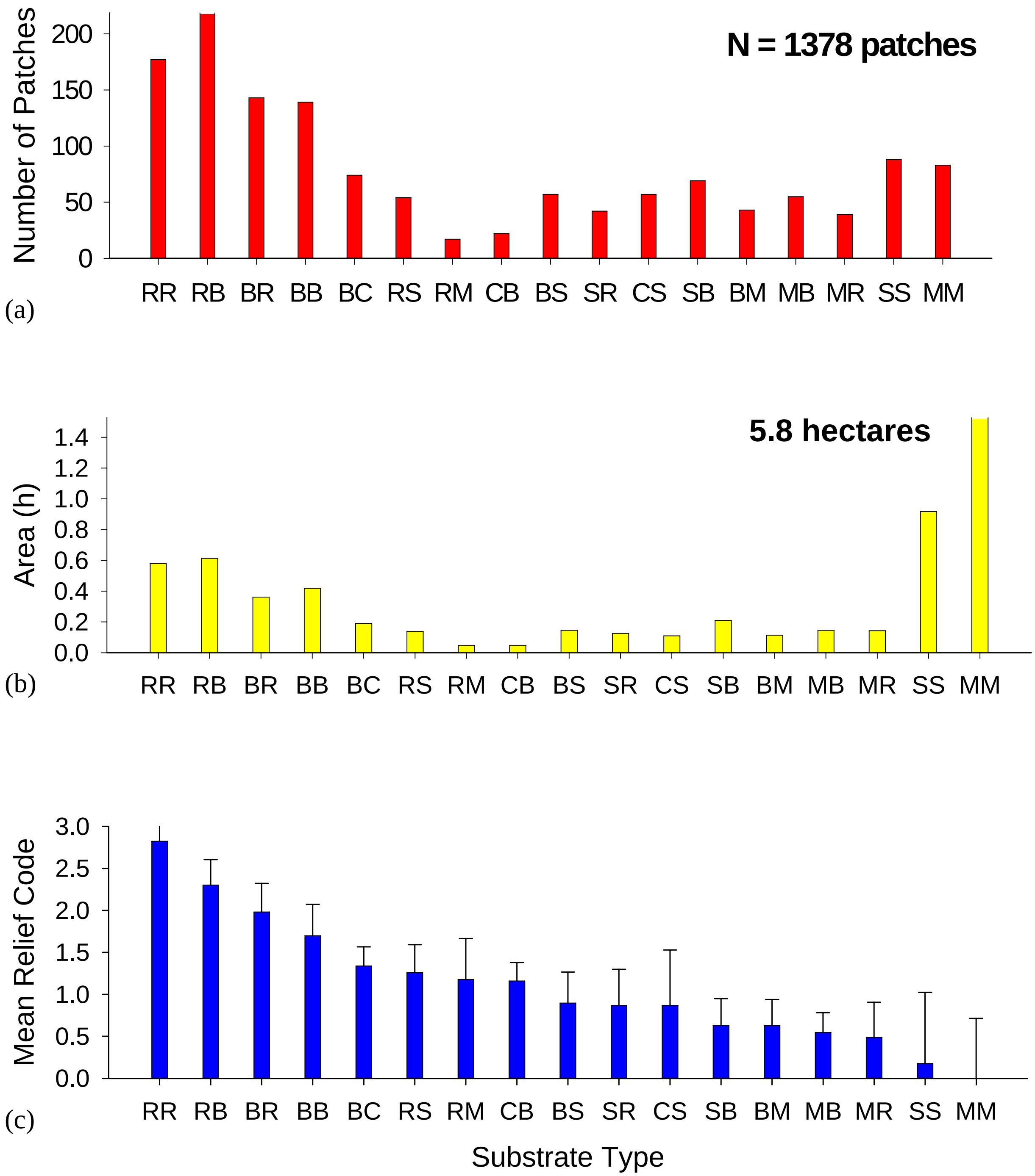


Figure 4. Physical characteristics of Cordell Bank habitats by pooled substrate type; (a) number of habitat patches, (b) total area (h) surveyed, (c) and mean vertical relief with standard error.

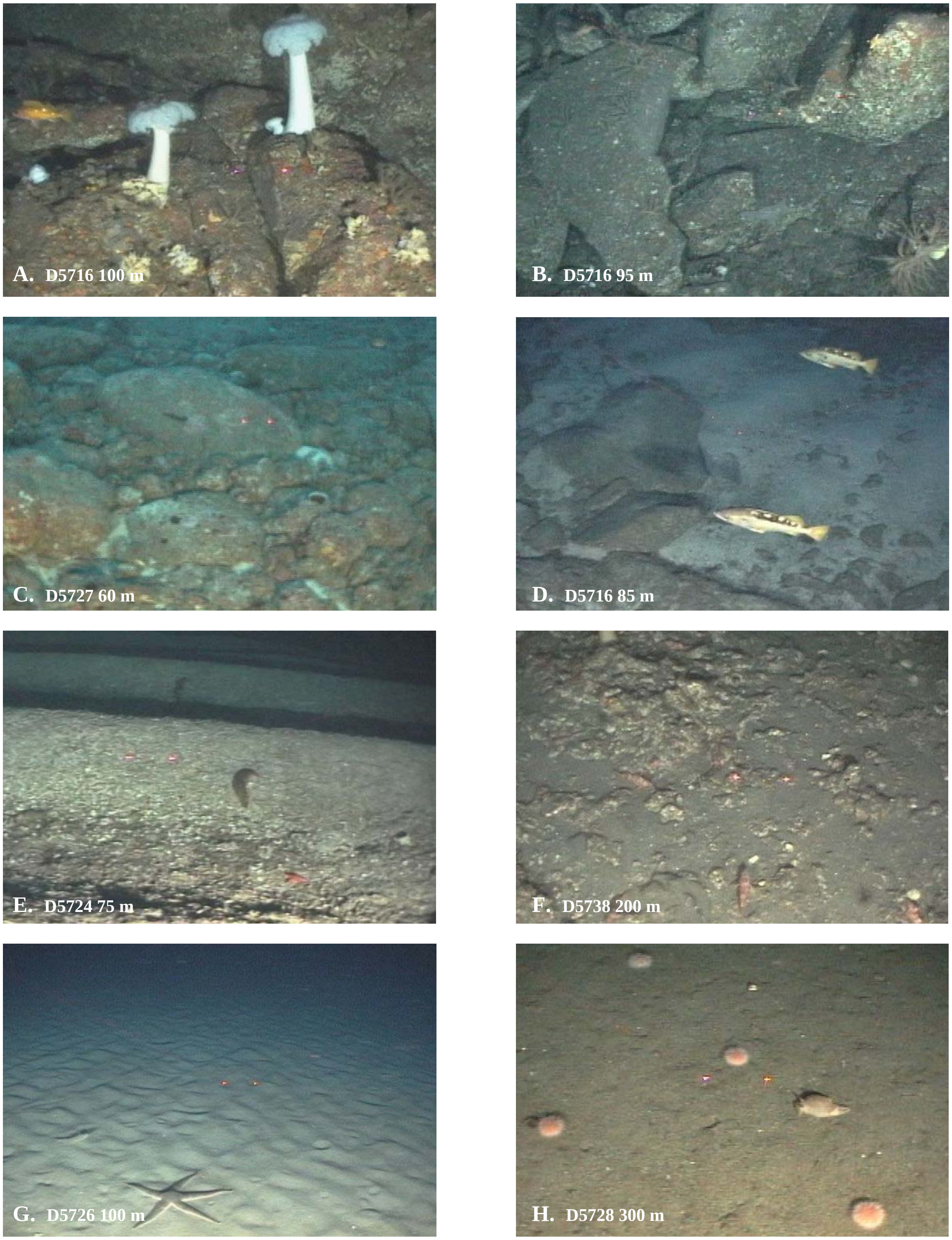
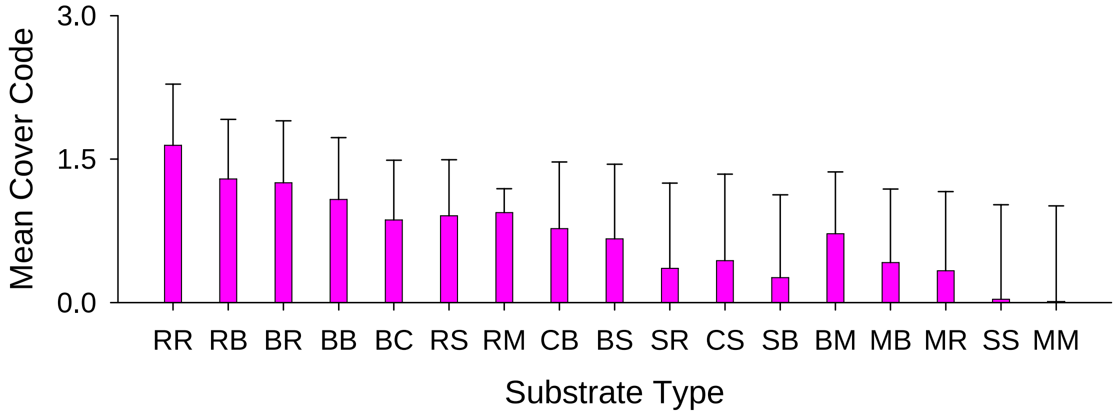
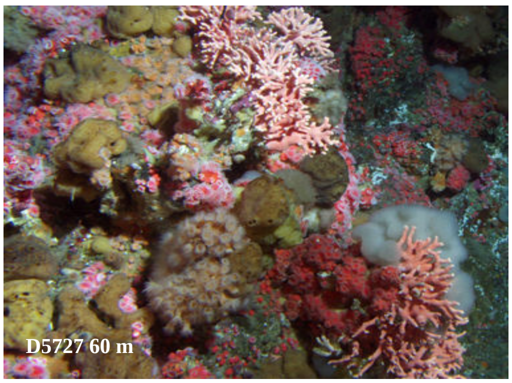


Figure 5. Representative habitats at Cordell Bank by decreasing vertical relief: A, rock ridge; B, rock ridge with boulders; C, boulders; D, sand with boulders; E, sand with gravel; F, mud with rock ridge; G, sand; and H, mud. Delta dive number and depth are indicated for each habitat.



(a)



(b)

(c)

Figure 6. (a) Mean percent cover of encrusting organisms at Cordell Bank by substrate type with standard error. (b,c) Variation in encrusting organisms and cover by habitat type; (b) shallow rock ridge top, and (c) deep boulders with rock ridge, sponge and tubiculous polychaete cover. Delta dive number and depth indicated for each representative photo.

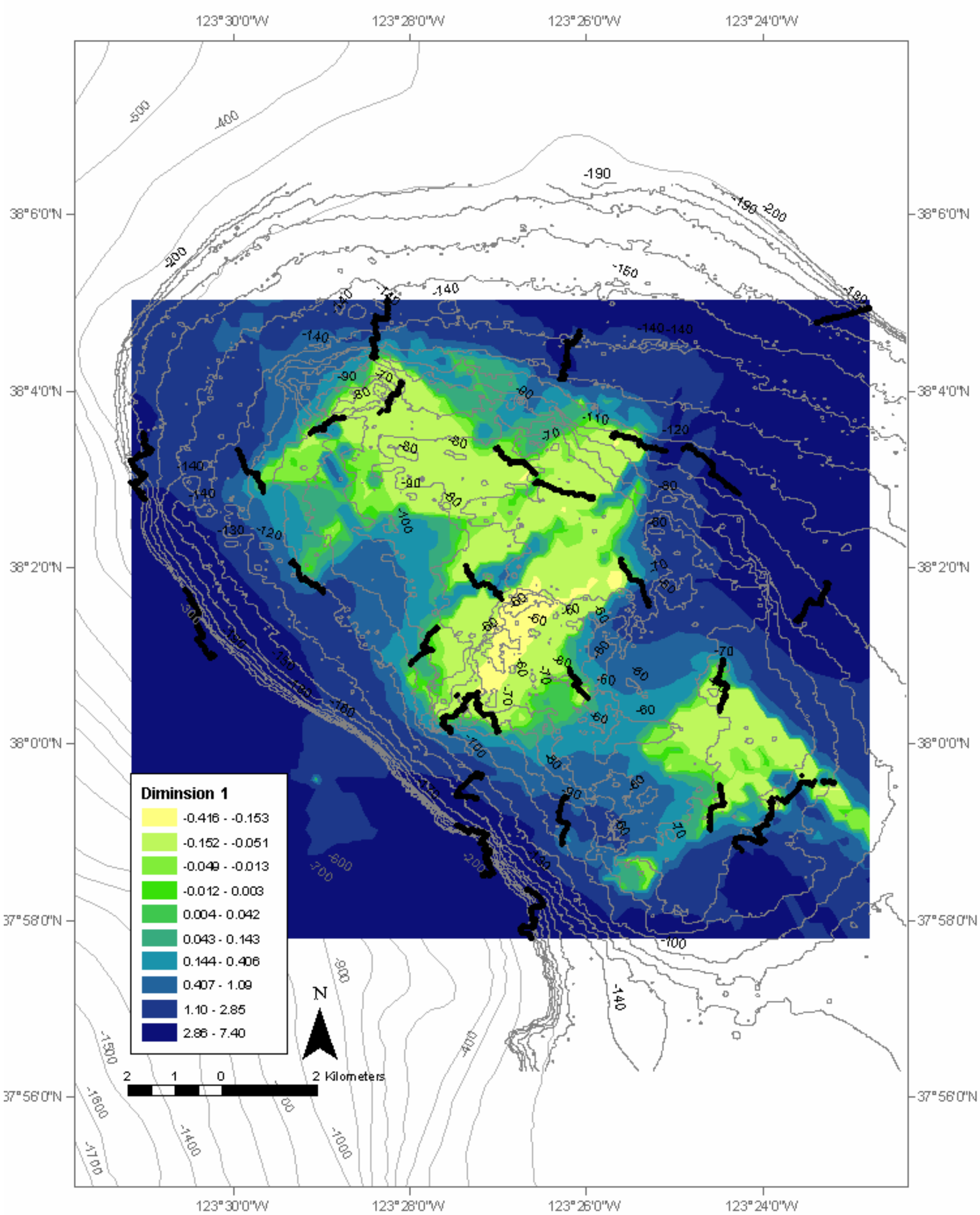


Figure 7. Krigging Analysis prediction map produced using multivariate scores from the first dimension of the Detrended Correspondence Analysis, displaying the spatial pattern of physical habitats and associated invertebrates and fishes, from hard-substrate communities (lighter shades) to soft-substrate communities (darker shades) across Cordell Bank.

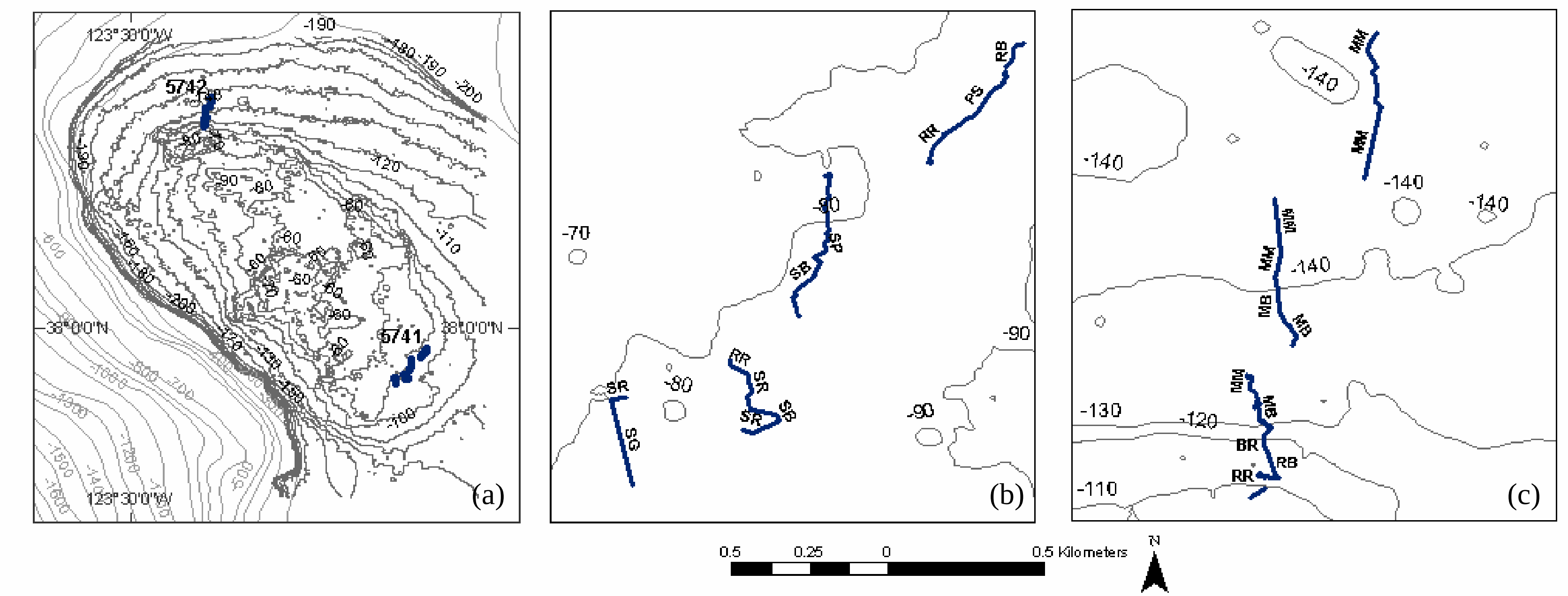


Figure 8. (a) Location of Dives 5741 (South Bank) and 5742 (North Bank) at Cordell Bank. (b) Habitat distribution for Dive 5741 displaying the transitions from high-relief rock and boulder dominated habitats to low-relief sand dominated habitats traveling northeast to southwest. (c) Habitat distribution for Dive 5742 displaying the transition from mud dominated habitats to rock and boulder dominated habitats traveling north to south.

Figure 9. Representative structure-forming invertebrates on Cordell Bank, California: A, crinoids; B, *Urticina picivora*; C, gorgonian; D, barrel sponges; E, foliose sponges; F, brittle stars in sand with arms extended.

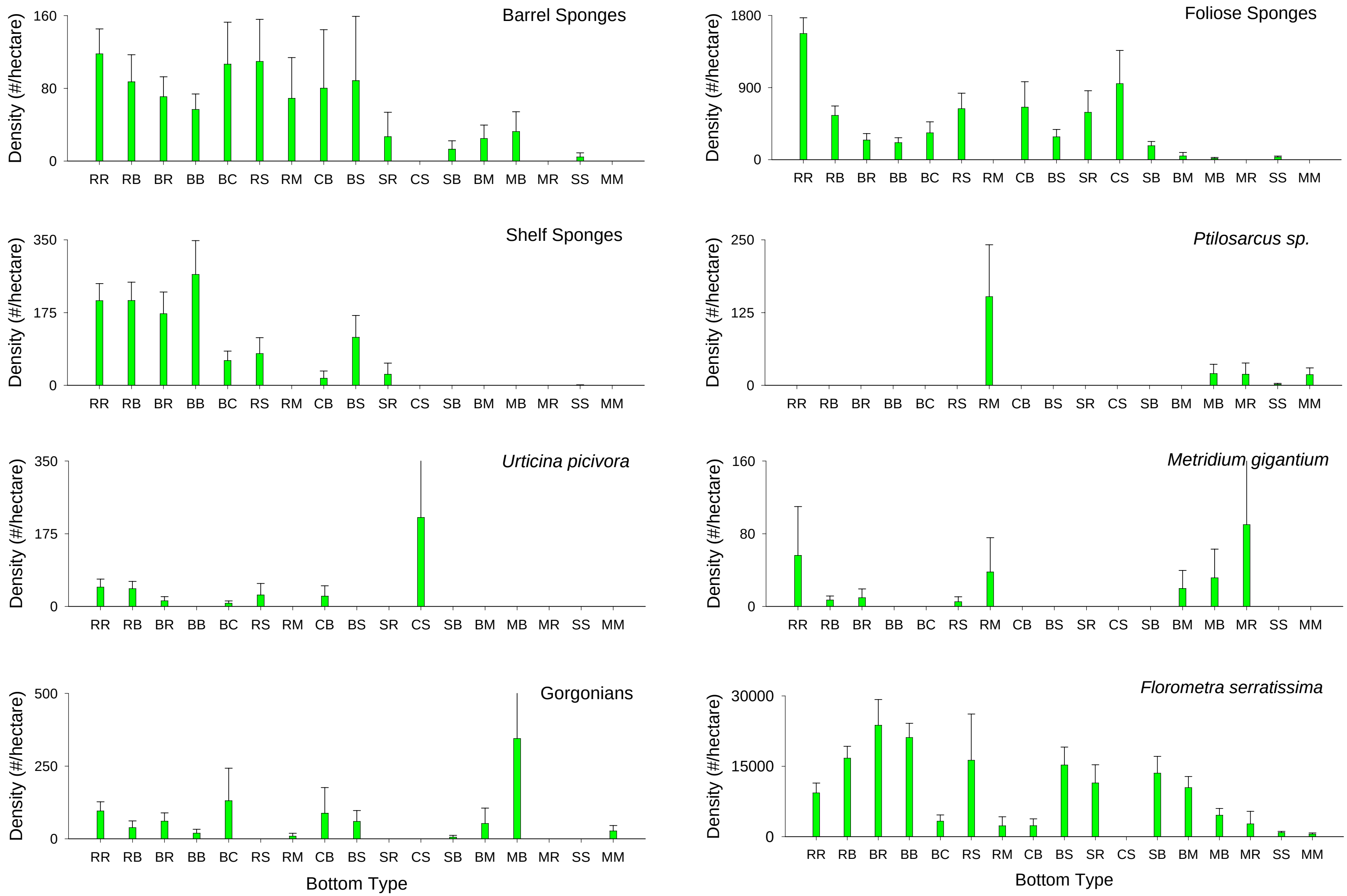


Figure 10. Density (#/h) with standard error by pooled substrate type for structure-forming megafaunal invertebrates at Cordell Bank.

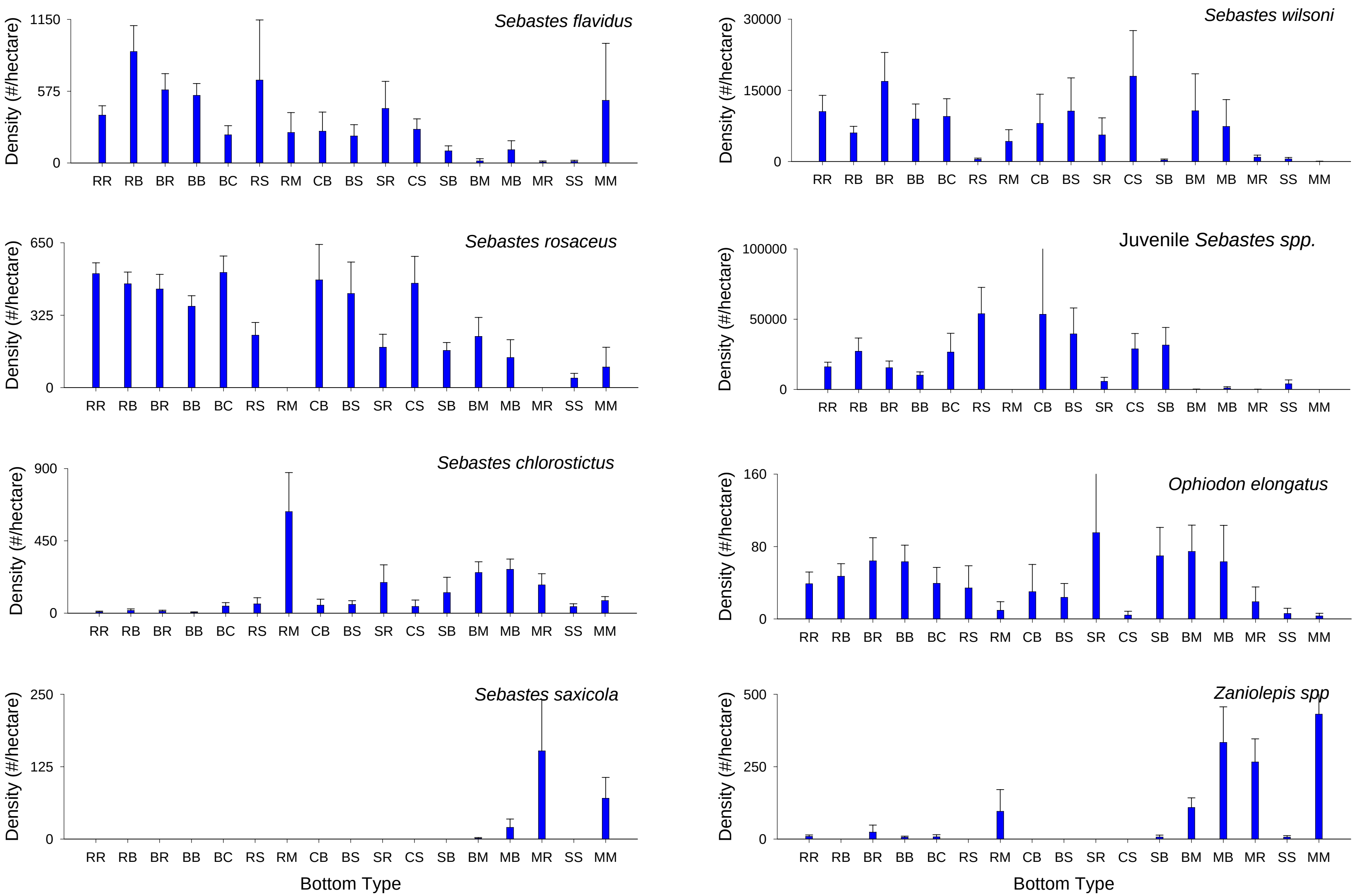
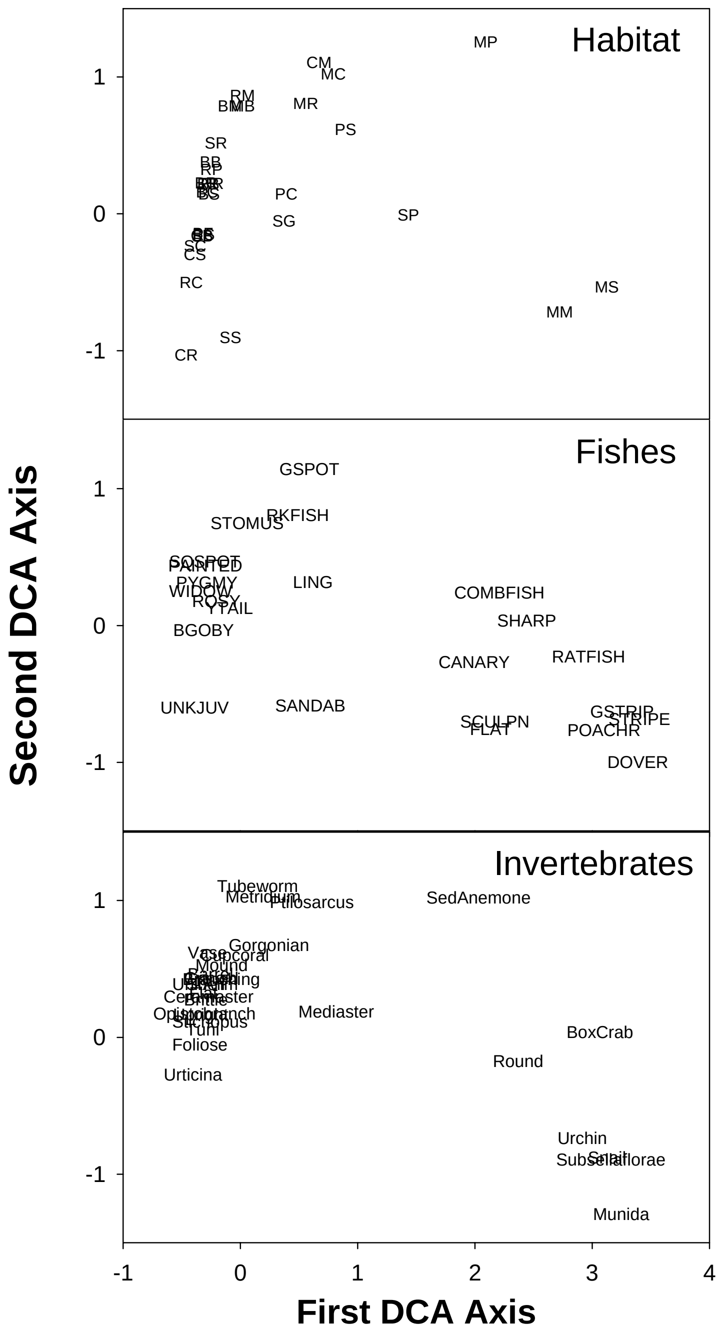


Figure 11. Density (#/h) with standard error by pooled substrate type for fishes at Cordell Bank.



(a)

Figure 12. (a) Ordination of species and habitat along Dimension 1 and 2 as a result of Detrended Correspondence Analysis incorporated to identify and compare associations of megafaunal invertebrates and fishes with the physical habitats of Cordell Bank.

(b)

Fishes	
DCA Code	**Scientific Name**
POACHR	unknown agonidae
SANDAB	*Citharichthys spp.*
RATFISH	*Hydrolagus colliei*
SCULPN	unknown sculpin
BGOBY	*Coryphopterus nicholsii*
PAINTED	*Oxylebius pictus*
LING	*Ophiodon elongatus*
COMBFISH	*Zaniolepis spp.*
DOVER	*Microstomus pacificus*
FLAT	unknown flatfish
GSPOT	*Sebastes chlorostictus*
GSTRIP	*Sebastes elongatus*
WIDOW	*Sebastes entomelas*
YTAIL	*Sebastes flavidus*
SQSPOT	*Sebastes hopkinsi*
CANARY	*Sebastes pinniger*
ROSY	*Sebastes rosaceus*
STRIPE	*Sebastes saxicola*
PYGMY	*Sebastes wilsoni*
SHARP	*Sebastes zacentrus*
STOMUS	unknown *Sebastomus*
UNKJUV	juvenile *Sebastes spp.*
RKFISH	*Sebastes spp.*

(c)

Invertebrates	
DCA Code	**Scientific Name**
Barrel	barrel sponge
Branching	branching sponge
Flat	flat sponge
Foliose	foliose sponge
Mound	mound sponge
Round	round yellow sponge
Shelf	shelf sponge
Upright	upright sponge
Vase	vase sponge
Gorgonian	Gorgonacea
Ptilosarcus	*Ptilosarcus spp.*
Subsellaflorae	Subselliflorae sea pen
Metridium	*Metridium gigantium*
SedAnemone	unknown sand anemone
UnkAnm	unknown anemone
Urticina	*Urticina piscivora*
Cupcoral	*Balanophyllia elegans*
Snail	Prosobranchia
Opistobranch	Opistobranchia
Tubeworm	Serpulid worm
BoxCrab	*Lopholithodes foraminatus*
Munida	*Munida quadrispina*
Urchin	*Allocentrotus fragilis*
Brittle	Ophiacanthidae
Crinoid	*Florometra serratissima*
Ceramaster	*Ceramaster spp.*
Mediaster	*Mediaster aequalis*
Stichopus	*Parastichopus spp.*
Tuni	Urochordata

Figure 12. (Continued) DCA fish codes (b), and invertebrate codes (c).

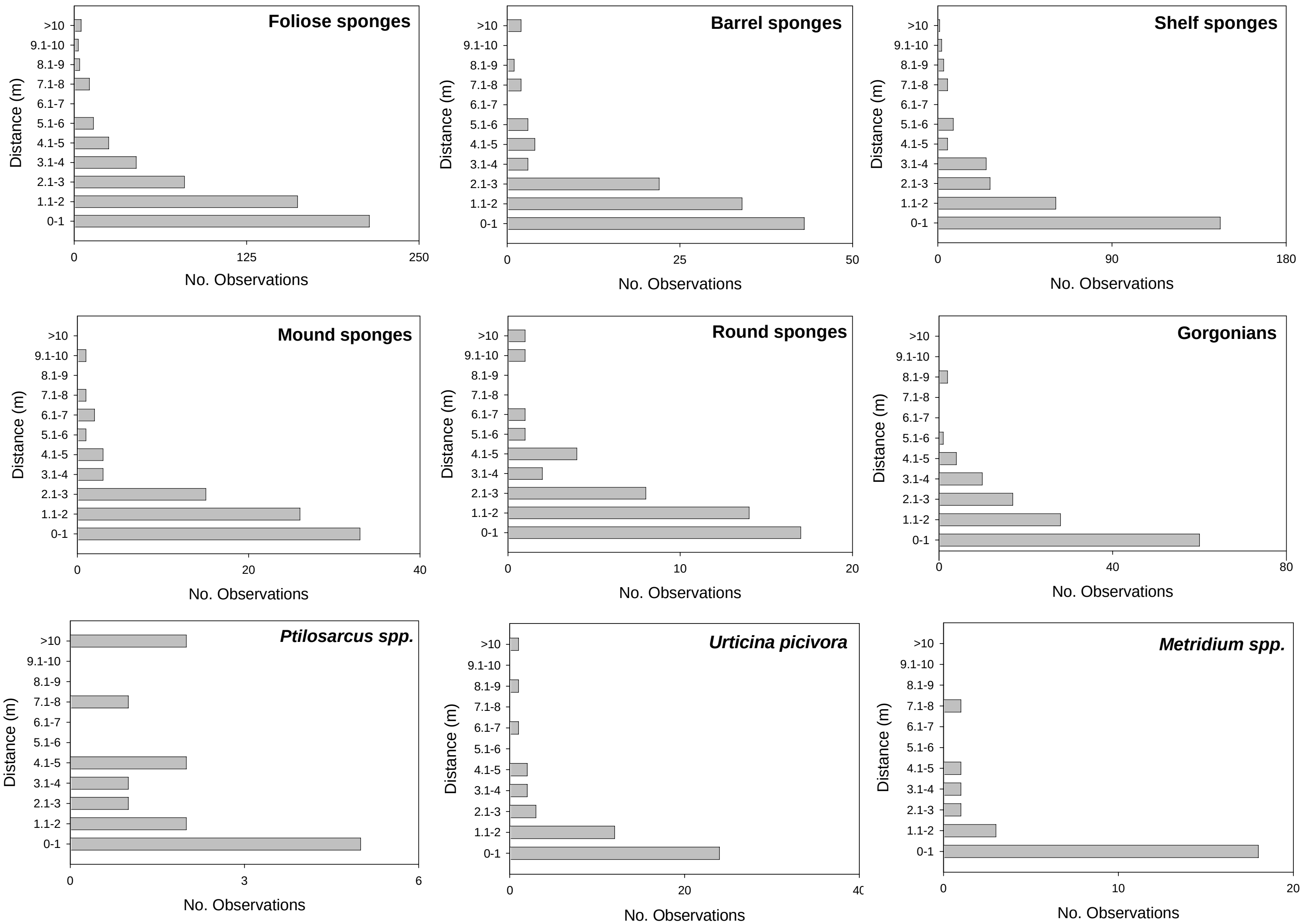
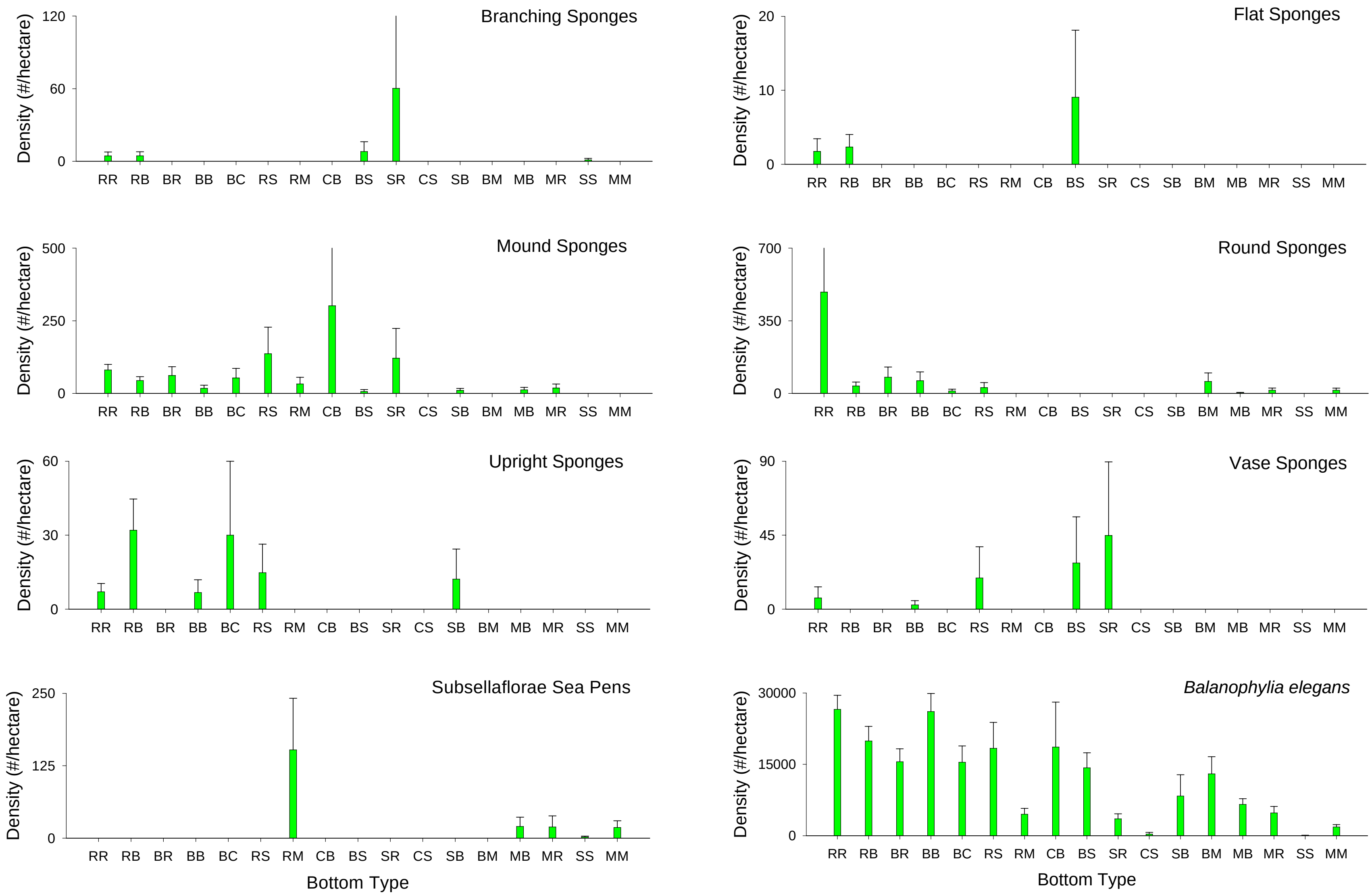
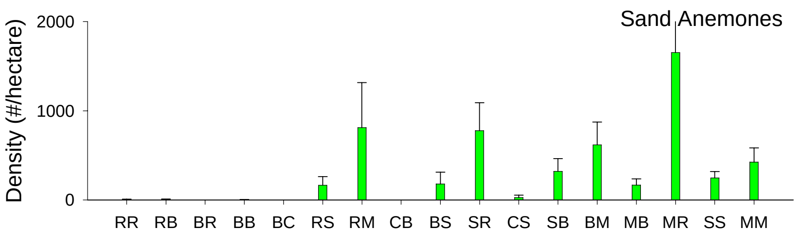


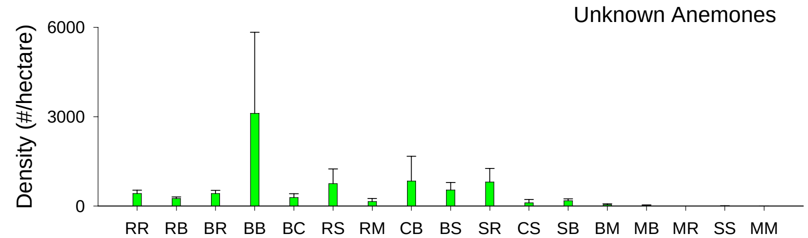
Figure 13: Nearest neighbor distances of fishes to sponges, gorgonians, *Ptilosarcus spp.* sea pens, and the anemones *Urticina picivora*, and *Metridium gigantium*.

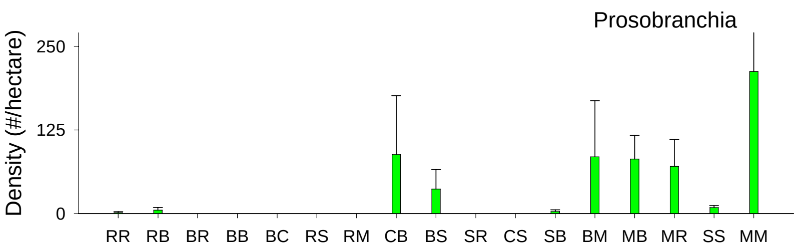
Appendix A. Invertebrate density (#/h) with standard error by pooled substrate type at Cordell Bank, California during September, 2002.

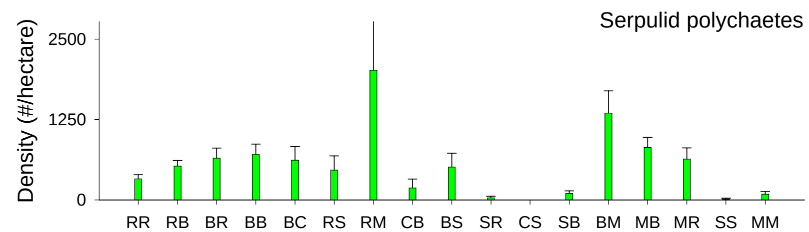


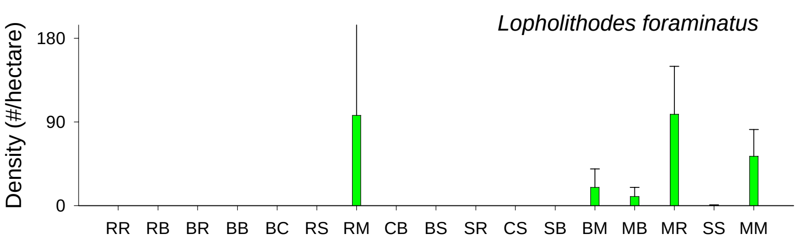
Appendix A. Continued

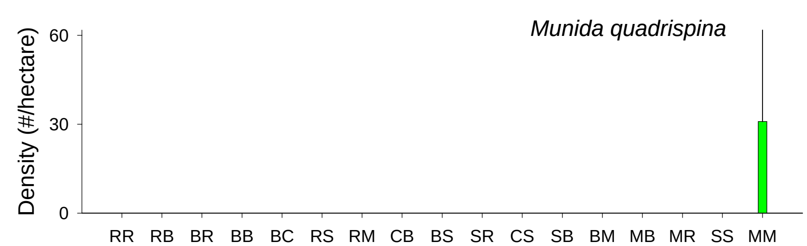


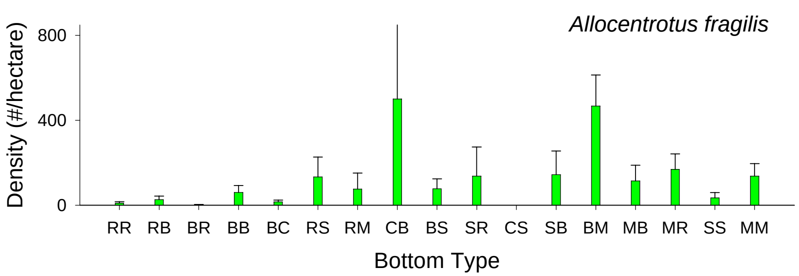


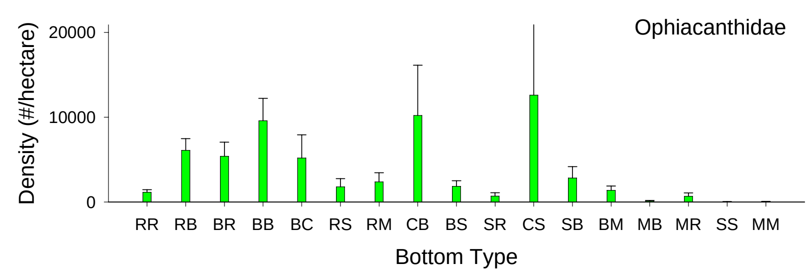




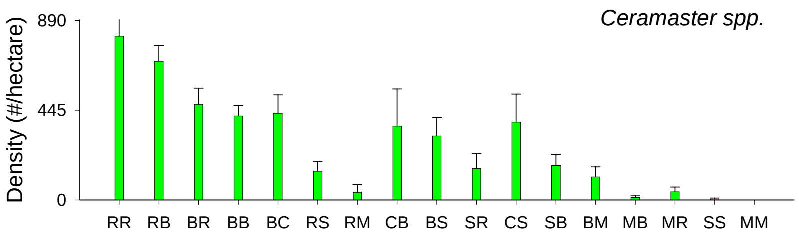


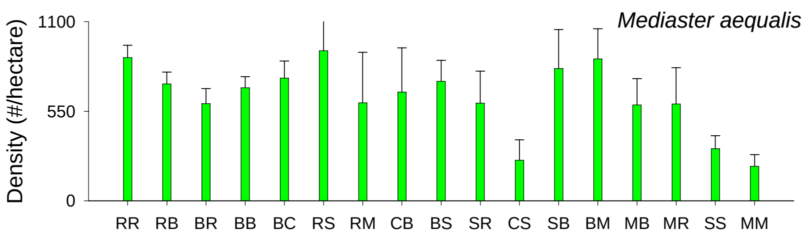


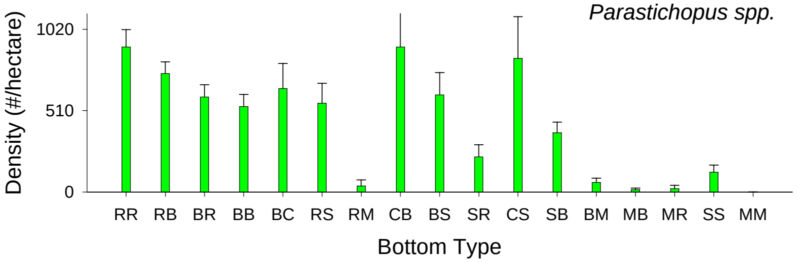


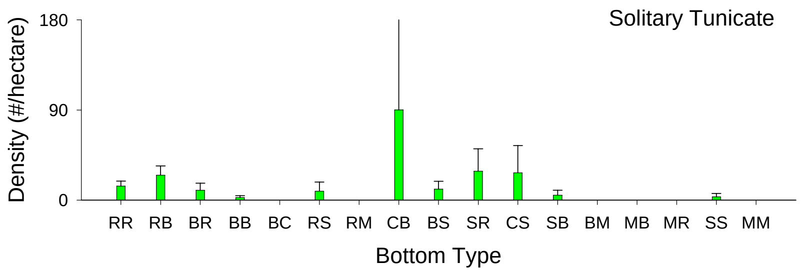


Appendix A. Continued

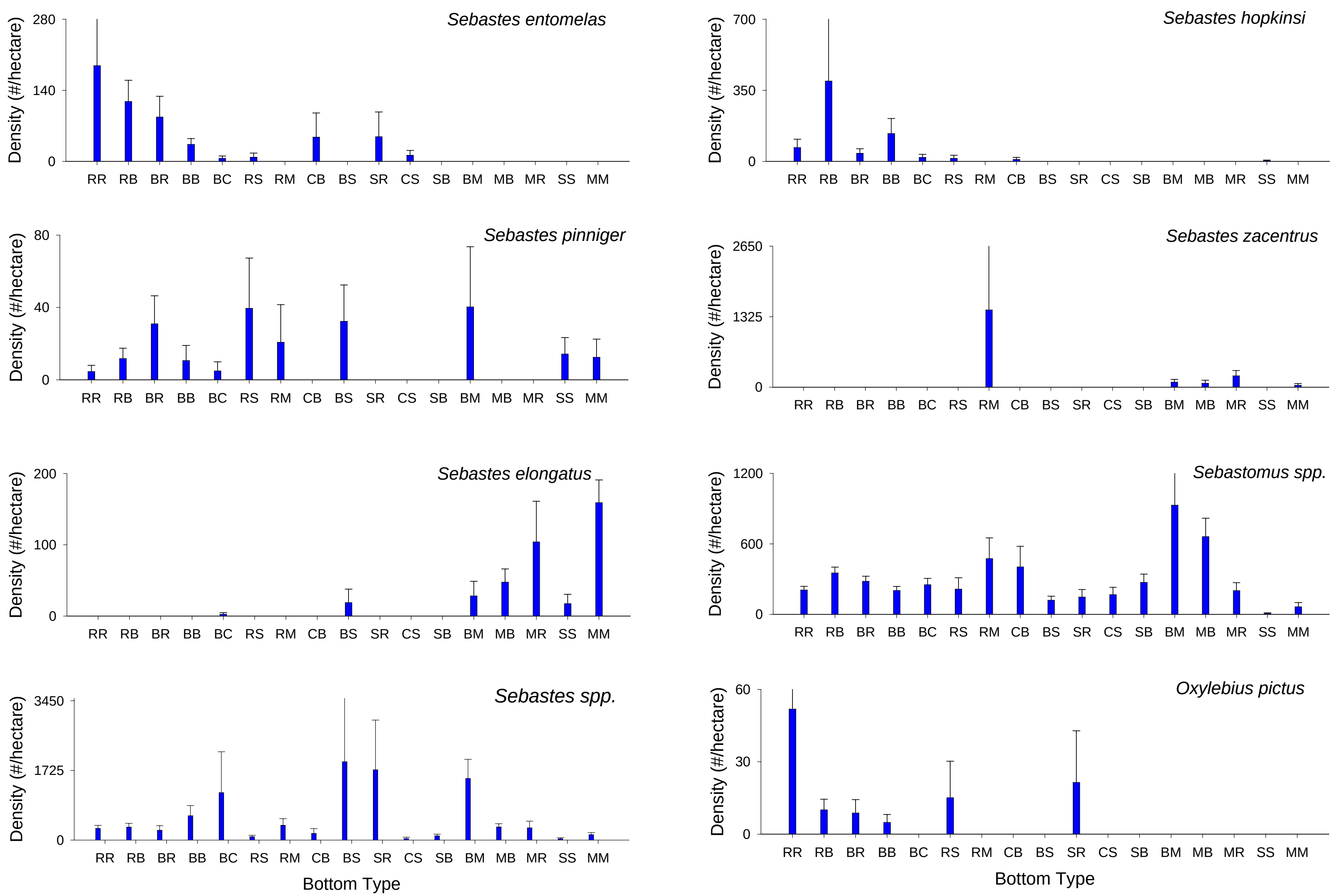








Appendix B. Density (#/h) of fishes with standard error by pooled substrate type at Cordell Bank, California during September, 2002.



Appendix B. Continued