# ABUNDANCE AND DISTRIBUTION OF MEGAFAUNAL INVERTEBRATES IN NE PACIFIC SUBMARINE CANYONS AND THEIR ECOLOGICAL ASSOCIATIONS WITH DEMERSAL FISHES

By

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the thesis of CAMELIA BIANCHI find it satisfactory and recommend that it be accepted.

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Abstract

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Submarine canyons can influence the physical, chemical, and biological processes of coastal regions, thereby creating ecologically important areas of elevated production. Megafaunal invertebrates are diverse, long-lived organisms that play important ecological roles in marine ecosystems. Recent observations have assessed that a subgroup of megafaunal invertebrates called structure-forming invertebrates (e.g., large deep-sea corals and sponges) may have a functional role as living components of habitat for demersal fishes by providing relief and adding complexity to substrata in continental shelf and slope regions. We examined megafaunal invertebrate composition, substratum complexity, and associations between fishes and structure-forming invertebrates within three submarine canyons in the Northeast Pacific. We made 31 submersible dives at water depths ranging from 90 to 1358 m and classified substrata consisting of high-relief rock walls and outcrops to low-relief mud. Mud dominated the substrata in all three canyons; even in areas of high- and moderate-relief, such as rock ridge and boulders, sediment covered many surfaces. We identified 130,125 individual megafaunal invertebrates from 68 taxa and 7 phyla. A community composition analysis revealed that spatial patterns of habitat and distribution of invertebrates are likely driven by variation in invertebrate densities and high

aggregations of unique fauna in one canyon relative to the others. For example, *Myxoderma* sea stars were the most abundant organisms in Astoria Canyon, hermit crabs in Ascension Canyon, and spot prawns (*Pandalus platyceros*) in Carmel Canyon. The differences in topography, geology, and location among our study sites indicated that a broad range of unique pockets of microhabitat were formed in canyons and were able to support high aggregations of the organisms best adapted to changes in the physical environment and rates of disturbance. Structure-forming invertebrates were associated with few demersal fishes in close proximity with most of the associations occurring at ≥1 m away. However, fishes were seen resting inside and underneath these invertebrates (e.g., foliose sponges, vase sponges, barrel sponges, shelf sponges, and black corals) which were among the largest of all observed structure-forming invertebrates in our study, suggesting that their shapes created a suitable hiding place. The nature of the coexistence of fishes and invertebrates in similar habitats warrants further examination to determine if structure-forming invertebrates play a functional role as living components of habitat. Nonetheless, deep-sea corals, sponges, and other invertebrates are important organisms and deserve adequate protection. Management policies that take into account the whole ecosystem should be considered.

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## Introduction

Submarine canyons have important effects on the physical, chemical, and biological processes of coastal regions (Chen and Allen, 1996). The abrupt, steep topography of canyons intensifies currents and turbulence (Bosley et al., 2004), causing large quantities of sediment and organic matter to transfer from the shore to the deep basin (Palanques et al., 2005). During upwelling-favorable conditions on the shelf, the nutrient-rich water within submarine canyons is enhanced, resulting in even higher biological productivity in and around the canyons (Mirshak and Allen, 2005; Skliris et al., 2004; Ryan et al., 2005; Shanmugam, 2003; Hickey, 1997). The lateral transport of matter and vertical flux of detritus within submarine canyons create ecologically important patches that can attract high densities of plankton, invertebrates, and fish populations compared to patches at similar depths adjacent to canyons (Vetter and Dayton, 1999; Vetter and Dayton, 1998; Macquart-Moulin and Patriti, 1996). The complex geological features in submarine canyons, such as rock ledges, outcrops, and boulder talus piles, impede some types of fishing activities, thereby providing a natural refuge for certain depleted fish populations (Yoklavich et al., 2000).

Megafaunal invertebrates are a diverse group of animals that play important ecological roles, and can be indicators of long-term environmental conditions (Brusca and Brusca, 1990; Tissot et al, 2006). Observations have assessed that a subgroup of invertebrates called structure-forming invertebrates, such as corals or sponges, may function as living components of demersal fish habitat by adding relief and complexity to substrata (Heifetz, 2002; Auster, 2005; Stone, 2006; Tissot et al., 2006, 2007). In the Northeastern U.S. region, certain species of fish were found more often in the vicinity of corals than in areas without corals (Packer et al., 2007), and in Alaska more than a third of the economically important juvenile and adult fish species observed on transect exhibited high use of corals and other emergent epifauna (Stone and Shotwell, 2007). While the variation of coral form and morphology within a landscape, together with the availability and complexity of noncoral habitat, may determine if fishes use corals for shelter and refuge (Auster, 2005; Packer et al., 2007), the nature of these ecological relationships is not fully understood. It is possible that invertebrates play an important functional role in the habitats of fish.

Ecosystem-based management practices that include invertebrates as components of habitat will help reduce the risk of irreversible changes to natural assemblages of species and ecosystem processes. This is an integrated management approach that considers all elements affecting marine ecosystems including the role of humans (Lester et al., 2010). Benthic communities have long suffered effects from certain commercial fishing practices (e.g., bottom trawling) which alter benthic habitat that fish and other marine organisms rely on (NRC, 2002). Other anthropogenic effects upon benthic communities include pollution and ocean acidification.

Few fish-invertebrate associations have been documented in submarine canyons; most fine-scale association studies have focused on rocky banks of continental shelf and slopes. Hecker et al. (1980) observed fishes using the bases of large anemones for protection in three major East Coast submarine canyons, and Brodeur (2001) observed dense aggregations of rockfishes (*Sebastes alutus*) inhabiting a forest of sea whips in Alaska's Pribilof Canyon.

Our study examines invertebrate composition and substrata complexity, and quantifies ecological associations between fishes and invertebrates, on the U.S. west coast off Oregon and California. Our objectives are to (1) determine the taxonomic composition and describe and compare the abundance and distribution of megafaunal invertebrates, (2) identify invertebrates with potential to add structure and complexity to the physical habitat, and (3) investigate ecological associations of demersal fishes with structure-forming invertebrates. Specifically, we are testing the hypothesis that invertebrates in submarine canyons play an important and unique ecological role in providing structure and complexity within fish habitats.

## Methodology

We assessed invertebrate composition, habitat complexity, and ecological associations with structure-forming invertebrates and fishes in three submarine canyons.

*Data collection*

*Study sites*

*Astoria Submarine Canyon*

Astoria Submarine Canyon (Astoria Canyon) lies within a major upwelling region approximately 14 km west of the mouth of the Columbia River, along the coast of Washington and Oregon (Fig. 1; Appendix N). The head of the canyon lies at a depth of approximately 100 m. The canyon extends west-southwest for approximately 104 km to a depth of 2,085 m. At the head of the canyon, the floor is narrow and the walls have the distinguished relief described by a V-shape canyon profile (Nelson et al., 1970). In contrast, the mid- to lower reaches of the canyon have a U-shape profile, with a wider floor and lower walls of a more even height, consisting of a less consolidated rock (Nelson et al., 1970). Astoria Canyon has been found to have depositional trends of high-density turbidity currents that carry coarse traction loads to the upper fan valleys and fine debris and clay silt to its lower fan valleys (Nelson et al., 1970).

*Ascension Submarine Canyon*

Ascension Submarine Canyon (Ascension Canyon) is located off the central California coast between Santa Cruz and Año Nuevo (Fig. 1; Appendix O), approximately 64 km north of Monterey. The head of the canyon lies approximately 120 m below the shelf break, beyond littoral drift. Ascension Canyon is a V-shape canyon with steep walls of sandstone near its head, and has a narrow (less than 0.5 km) and straight channel (Greene et al., 2002). The sharp, steep relief of the canyon suggests active erosion (Greene et al., 2002).

*Carmel Submarine Canyon*

Carmel Submarine Canyon (Carmel Canyon) is a relatively straight arm of the Monterey Canyon located off the central California coast (Fig. 1; Appendix P). Carmel Canyon has three heads, one of which extends to the shoreline and connects to the river drainage of the Carmel River and San Jose Creek in Carmel Bay (Greene et al. 2002). Although the outermost, deep part of this canyon is relatively wide and bowl-shaped, our dive sites were located inside Carmel Bay where the canyon has a V-shape profile and relatively steep walls. Granitic rock is present on both the north and south sides of this canyon (Eittreim et al., 2002).

*Submersible surveys*

*ROPOS Surveys*

Using nonextractive video-transect and direct-observation methodologies, we assessed demersal fishes, invertebrate assemblages, and associated habitat in Astoria Canyon from June 28 through July 3, 2001, with the remotely operated vehicle (ROV) *ROPOS* (see Wakefield et al., in prep, for details on methodology). We completed seven *ROPOS* dives at Astoria Canyon in daylight and at night, with dive duration varying from 2.5 to 4 hrs (Table 1; Appendix A). *ROPOS* is an electrohydraulic work-class ROV containing a 30 HP motor with a maximum operating depth of 5,000 m. *ROPOS* was equipped with 10 cm lasers that projected onto the seafloor, providing a scale reference for measuring objects and allowing us to accurately estimate the distance traveled along a transect and area of substratum patches. The support vessel tracked the navigational path of the vehicle using GPS, ORE Offshore TrackPoint II ultra-short baseline, and the Workboat computer navigation system. To record the transect, two external video cameras—a forward-looking broadcast-quality 3-chip DXC 950 color video camera and a forward-looking low-light wide-angle SIT video camera—were mounted on *ROPOS*. The scientists on the support vessel were able to watch the recordings in real time and annotate them with observations of fishes, invertebrates, and substratum type. We used the mechanical arm attached to the vehicle to collect specimens, which were identified by taxonomic experts.

*Delta Surveys*

We assessed demersal fishes, invertebrate assemblages, and associated habitat in Ascension and Carmel Canyons from September 20 through September 26, 1994, with the occupied submersible *Delta* (see Yoklavich et al., 2000, for details on methodology). We completed twelve *Delta* dives in Ascension Canyon and twelve in Carmel Canyon. All *Delta* dives took place during daylight and generally lasted just over an hour (Table 1; Appendix A). *Delta* has an operating depth of up to 365 m and travels at a cruising speed of 1.5 knots. The support vessel tracked the navigational path of the vehicle using an acoustic track-point system and differential GPS. The submersible traveled along the canyon walls and floor, following strip transects conducted 1–2 m off the bottom at 0.4–0.9 knots. To maintain a constant depth, we kept the duration of each transect to 10 minutes. A High-8 color video camera mounted externally on the starboard viewing port of the vehicle recorded each transect. The scientist inside the submersible annotated the tapes with observations of fishes and substratum type in real time. Two parallel lasers located 20 cm apart and mounted on the external video camera projected visible laser points onto the seafloor. These projections were recorded on the videotape, providing a scale reference for measuring objects encountered and allowing us to accurately estimate the distance traveled along a transect and the area of substratum patches.

*Data analysis*

We used dive videotapes to collect quantitative information on substratum type, invertebrates, and fishes. Based on these videotapes, we identified and described aspects of demersal habitats using the Stein et al. (1992) classification scheme of nine substratum categories, listed in order of increasing particle size: mud (M), sand (S), gravel (G), pebble (P), cobble (C), boulder (B), continuous flat rock (F), rock ridge (R), and pinnacles (T). We assigned a binary code to each designated substratum patch, consisting of a primary character representing at least 50% of the substratum in the patch and a second character accounting for at least 20% of the substratum in the patch (e.g., "MB" represents a substratum patch with at least 50% mud cover and at least 20% boulder cover). When a distinct substratum change occurred with a duration of at least 10 seconds (*Delta*) or at least 30 seconds (*ROPOS)*, we defined a new substratum patch. The difference in duration was due to the slower speed of *ROPOS* relative to *Delta*. Using the geographic position at the start and end of each transect, we quantified the area of each substratum patch by multiplying the transect width by the length of the substratum patch. We used a transect width of 2 m for *Delta*; the transect width varied for ROPOS, depending on the primary substratum type assessed: 2.6 m for ridge, 2.4 m for boulder, 2.3 m for cobble, and 2.0 m for mud. The sampling unit was defined at the substratum patch level (Stein et al., 1992). To assist in graphing, we pooled 31 substrata classification codes that were similar (>85%) in a cluster analysis (Euclidean distance, group average method) based on the 20 most common invertebrate taxa. This resulted in a total of 12 substrata classification codes, listed in order of highest to lowest vertical relief: hard (RR, RB, RM, BB, BC, BM), mixed (CB), and soft (MR, MB, MC, MP, MM) (Tissot et al., 2006).

We identified megafaunal invertebrates (>5 cm in height), "structure-forming invertebrates" (i.e., those megafaunal invertebrates with complex morphology and/or large size [>20 cm in height]; Tissot et al., 2006), and other potentially key indicators species (e.g., hermit crabs) to the lowest taxonomic level possible and quantified them within each substratum patch.

We categorized sponges by growth form: foliose, barrel, vase, shelf, mound, branching, and upright. Most deep-sea corals were categorized to the level of order with the exception of a few Gorgonians (*Swiftia* and *Paragorgia*) in Astoria Canyon that were identified by G. Williams (California Academy of Sciences). M. Yoklavich (NOAA NMFS SWFSC) identified, counted, and measured the fishes in Carmel and Ascension Canyons, following methodology described in Yoklavich et al. (2000). Fish data were not available for Astoria Canyon. In addition, we recorded the time of observation and estimated the maximum height of each structure-forming invertebrate. To calculate densities, we divided the total number of individuals by the area of their corresponding substratum patch. For each study site, we calculated richness (S) and Shannon-Wiener's diversity index (H', $\log^e$) with DIVERSE in PRIMER v5 (Clarke and Gorley, 2001), using the sum for each taxon within associated substratum patches.

We analyzed sites, substratum type, and invertebrate abundance (total number of individuals) using a multivariate correspondence analysis to assist in describing community composition and structure within and among canyons on a multidimensional scale. We used invertebrate taxa that accounted for 98% of overall abundance in the multivariate analysis and we log-transformed data prior to running the test. To further compare community composition, we ran a one-way analysis of variance (ANOVA) to test for differences among the scores of each axis generated from the correspondence analysis. We tested for all the assumptions of ANOVA and transformed the data when necessary (Zar, 1999).

Furthermore, to compare and contrast the distribution and densities of invertebrates across substratum types at the three study sites, we stratified data by depth. We ran a three-way ANOVA to test the significance of site, substratum type (hard, mixed and soft), and depth (using only those common to all three sites) for three of the most abundant invertebrates (mound sponges, *Ophiurina* and *Ophiacantha* brittle stars, and *Florometra* crinoids) observed at all sites and depth categories. Furthermore, we calculated an electivity index to measure preference versus avoidance of substratum types by these invertebrates (Krebs, 1989). We divided the depths common to all three canyons into at least two categories, resulting in four depth categories: shallow (<148 m), mid-shallow (≥148 and <234 m), mid-deep (≥234 and <320 m) and deep (≥320 m). The shallow and deep categories included only dives from Carmel Canyon and Astoria Canyon, respectively.

We quantified invertebrate-fish associations through direct video observations, classifying them into five types that described the activity and proximity of the fish to the closest structure-forming invertebrate (Pirtle, 2005; Stone, 2006). The association types included 0=no close association (fishes seen at rest or in water column >1 m from a structure-forming invertebrate); 1=fish in the water column or at rest at a distance ≤1 m from a structure-forming invertebrate; 2=fish in the water column at a distance ≤1 fish-body-length from a structure-forming invertebrate; 3=fish at rest at a distance ≤1 fish-body-length from a structure-forming invertebrate; and 4=fish in physical contact with a structure-forming invertebrate. In addition for Ascension and Carmel Canyons, we conducted a nearest neighbor analysis using ArcGIS® to estimate the frequencies and distances of fishes observed closest to structure-forming invertebrates along each transect (Tissot et al., 2006). We used a Mann-Whitney test to identify statistical differences between observed frequencies (total number of fishes observed closest to structure-forming invertebrates) and expected frequencies (total number of fishes observed along each transect).

## Results

### *Habitat analysis*

We quantified 390 substratum patches (Fig. 2, A) equaling 1.5 ha of area (Fig. 2, B) in Astoria Canyon, 521 substratum patches (Fig. 2, A) equaling 1.9 ha of area (Fig. 2, B) in Ascension Canyon, and 566 substratum patches (Fig. 2, A) equaling 1.3 ha of area (Fig. 2, B) in Carmel Canyon. Although high-relief rocky ridge substrata were present at all sites, mud and other low- to medium-relief substratum types dominated all canyons. Mud was the most frequently occurring substrata in three canyons (Fig. 2, A-B). The second substratum type varied among the sites: ridge-mud in Astoria Canyon, mud-boulder in Ascension Canyon, and boulder-mud in Carmel Canyon (Fig. 2, A-B). Carmel and Ascension Canyons contained more diverse substrata, consisting of more high- and moderate-relief mixed sediment (Fig. 2, C) when compared to Astoria Canyon.

We were able to assess deeper ranges in Astoria Canyon (148–1,358 m) by using the *ROPOS* ROV than we were in Ascension (182–319 m) or Carmel (90–305 m) Canyons, due to the depth limitations of the *Delta* submersible (Table 1; Appendix A). The depth category containing the most surveyed area varied from canyon to canyon: 1.1 ha of area at deep depths (>320 m) in Astoria Canyon, 1.3 ha of area at mid-deep depths (≥234 to <320 m) in Ascension Canyon, and 0.6 ha of area at mid-shallow depths (≥148 to <234 m) in Carmel Canyon (Figs. 3, B-D). Substrata in Carmel Canyon changed from hard to soft as depth increased (Fig. 3). Conversely, in Astoria and Ascension Canyons, the soft substratum types were present with higher frequency across all depths (Fig. 3), except at mid-deep depths in Astoria Canyon (Fig. 3, C) where hard substratum (rock-mud ridge) occurred more frequently.

*Invertebrate diversity, abundance, and distribution*

We identified a total of 130,125 individual megafaunal invertebrates and structure-forming invertebrates from 68 taxa and 7 phyla (Appendices B and C). Of these, the most frequently occurring phyla were Echinodermata (84% in Astoria Canyon and 67% in Ascension Canyon) and Arthropoda (50% in Carmel Canyon) (Appendix C). Although there were more individual invertebrates quantified in Astoria Canyon (*n*=85,965) than in Ascension (*n*=14,009) and Carmel (*n*=30,151) Canyons, overall species diversity was slightly higher in Carmel Canyon (S=47, H'=1.7) than in Astoria (S=56, H'=1.3) and Ascension (S=42, H'=1.5) Canyons (Appendix B).

*Astoria Canyon*

The majority of the invertebrates in Astoria Canyon were distributed in deep depths, with an overall density of 1043/100 $m^2$ (Table 2). The red sea star (*Myxoderma*) was the most abundant taxon (*n*=33,007) and was distributed only in mud on the canyon floor (Fig. 4, A). This taxon was also most plentiful in deep depths, with densities of 178/100 $m^2$ (Table 2). The second most abundant taxon (*n*=20,455), the brittle star (*Ophiurina*), was distributed across mixed substratum types consisting of mud, boulders, cobbles, and pebbles (Fig. 4, A), and was densest (362/100 $m^2$) in deep depths (Table 2). The third most abundant taxon (*n*=11,392), the psolid sea cucumber (*Psolus squamatus*), was distributed in substratum types similar to those inhabited by the brittle star. However, the population of *Psolid* sea cucumber was densest in boulder-mud (Fig. 4, A) but was also observed burrowed in the mud walls of the canyon in deep depths, with an overall density of 288/100 $m^2$ (Table 2). The fourth most abundant taxon, the spot prawn (*Pandalus*) (*n*=7,474), was observed in mud-ridge and in deep depths, with an overall density of 74/100 $m^2$. The fifth most abundant taxon, the white deep-sea cucumber (*Pannychia*) (*n*=4,061), was densest in mud and in deep depths, with an overall density of 24/100 $m^2$ (Table 2; Fig. 4, A).

*Ascension Canyon*

The majority of the invertebrates in Ascension Canyon were observed in mid-deep depths with an overall density of 94/100 $m^2$ (Table 2). The brittle star (*Ophiacantha*) was the most abundant taxon (*n*=4,943). Brittle stars were distributed across all substratum types (Fig. 4, B) and in mid- to deep depths with an overall density of 25/100 $m^2$ (Table 2). This taxon was common in substratum types containing boulders, boulder-mud, boulder-cobble, and mud-cobble (Fig. 4, B). The second most abundant taxon, the hermit crab (*n*=2,952), was distributed evenly across all substratum types (Fig. 4, B) and was densest in mid-deep depths (29/100 $m^2$) (Table 2). The third most abundant taxon, the psolid sea cucumber (*n*=2,050), was distributed in mixed substratum consisting of boulders and mud (Fig. 4, B) and was densest in mid-deep depths (14/100 $m^2$) (Table 2). The fourth and fifth most abundant taxa were the fragile pink urchin (*Allocentrotus fragile*) (*n*=920) and the crinoid (*Florometra serratissima*) ( *n*=796), which were common on all substratum types, except cobble-boulder, and across all depths (Table 2; Fig. 4, B).

*Carmel Canyon*

The majority of invertebrates in Carmel Canyon were distributed in shallow depths and mid-deep depths with overall densities of 251/100 $m^2$ and 254/100 $m^2$, respectively (Table 2). The spot prawn (*Pandalus platyceros*) was the most abundant taxon (*n*=9,097). Populations of spot prawns were observed in mud-pebble and mud substratum types (Fig. 4, C) and were densest in mid-shallow depths (61/100 $m^2$) (Table 2). The second most abundant taxon, the brittle star (*n*=6,582), was distributed across mixed boulder-mud substratum types (Fig. 4, C) and was densest in mid-deep depths (68/100 $m^2$) (Table 2). The third most abundant invertebrate (*n*=5,879), the squat lobster (*Galatheidae*), was distributed across all substratum types (Fig. 4, C) and was densest in mid-deep depths (103/100 $m^2$) (Table 2). The fourth and fifth most abundant taxa were crinoids (*n*=3,402) and vermillion sea stars (*Mediaster aequalis*) (*n*=1,636). They were distributed across all substratum types, but were densest in hard substratum types and in shallow depths (Table 2; Fig. 4, C).

*Distribution patterns across depths and sites*

Mound sponges, crinoids and brittle stars preferred hard substratum and did not necessarily occupy the substrata with the most area (Fig. 5; Appendix E). Mound sponges were observed more frequently on hard substratum types in all three canyons and at all depths, except in Astoria Canyon's mid-deep depths, where it exhibited a preference for soft substratum types (Fig. 5; Appendix E). Brittle stars were statistically denser in Ascension Canyon than at the other two study sites and on hard substrata (Table 3). This taxon was observed more frequently in hard substratum types at mid-shallow to mid-deep depths in Ascension Canyon and Carmel Canyon (Fig. 5, B-C; Appendix E) and in soft substratum types at deep depths in Astoria Canyon (Fig. 5, D). Crinoids were statistically denser in Astoria Canyon at mid-shallow depths and in Carmel Canyon at mid-deep depths (Table 3; Fig. 5, B-C). This taxon preferred hard substratum types across all depths and all sites, except for exhibiting a preference to soft substrata in Carmel Canyon's mid-shallow depths. (Fig. 5; Appendix E).

*Community composition*

We used a correspondence analysis to assess community composition and structure within and among canyons. We plotted weighted-average scores along two axes, and the ordination of the scores showed similarities in megafaunal invertebrate abundances along potential environmental gradients (Jongman et al., 1987). The correspondence analysis revealed strong differences among sites in both habitat and invertebrate abundances (Fig. 6). The spatial pattern of substratum type was significantly different among locations on the first and second axes (two-way ANOVA: substrata and sites; respectively; axis 1: $F$=1.4, 103.8; df=22, 2; $P$=0.23, <0.001; axis 2: $F$=1.9, 85.2; df=22, 2; $P$=0.07, <0.001) (Fig. 6, A). Axis 1 showed the differences between Astoria Canyon and both California canyons, whereas axis 2 showed differences between Carmel and Ascension Canyons. These patterns were driven by the unique invertebrate fauna we observed in each canyon (Fig. 6, B). Those taxa that we found in greater numbers in Astoria Canyon (e.g., red sea stars, black crinoids, *Caryophyllidae* anemones, and brittle stars) had positive scores on axis 1, while those taxa observed in greater numbers in Ascension Canyon (e.g., box crabs [*Lopholithodes foraminatus*] and hermit crabs) had negative scores on both dimensions. In Carmel Canyon, squat lobsters and serpulid worms were dense and had positive multivariate scores on axis 2 (Fig. 6, B). Deposit feeders (e.g., white deep-sea cucumbers and red sea stars) and motile invertebrates (e.g., box and hermit crabs and fragile sea urchins) were located among the negative scores on axis 2. In contrast, filter-feeding invertebrates (e.g., crinoids and clear anemones) and sessile invertebrates (e.g., corals and sponges) had positive scores on axis 2 (Fig. 6, B).

*Fish-invertebrate associations*

Overall, an average of 29% ($n$=16,903) of all fish-invertebrate observations showed that fishes and structure-forming invertebrates were associated with each other at some level < 1m or < 1 fish body length (24% of total percent associations in Astoria Canyon, 24% in Ascension Canyon, and 39% in Carmel Canyon; Table 4). Of these fish-invertebrate associations, the most common was where fishes were observed ≤1 m away in the water column from an invertebrate (18% in Astoria Canyon, 19% in Ascension Canyon, 30% in Carmel Canyon) and the least common was where fishes were observed in physical contact with an invertebrate (0.3%, 0.4%, 0.4%, respectively; Table 4). Of the associations where fishes were ≤1 fish-body-length away from an invertebrate either in the water column (1%, 1%, 4%, respectively) or at rest (5%, 3%, 4%, respectively), the at-rest associations were more common (Table 4).

Although close associations (types 3 and 4) were generally rare, there were some noteworthy exceptions (Table 4). For example, in Astoria Canyon, we saw *Sebastes*/*Sebastomus* and flatfishes on and under black corals (3% of the total black coral observations [*n*=93]), branching sponges (2% [*n*=52]), and foliose sponges (2% [*n*=226]). The same Astoria Canyon fish taxa were observed at rest next to black corals (11%), barrel sponges (12% [*n*=92]), *Anthomastus ritteri* octocorals (8% [*n*=158]), sand anemones (8% [*n*=244]), branching sponges (8%), and vase sponges (8% [*n*=50]). In Ascension Canyon, we saw *Sebastes*/*Sebastomus* fishes (e.g., darkblotched rockfish, splitnose rockfish, and rosethorn rockfish) inside vase sponges (2% [*n*=66]), and under swimming anemones (1% [*n*=321]), foliose sponges (1% [*n*=405]), and upright sponges (1% [*n*=100]). The Ascension Canyon fish taxa were seen at rest next to Gorgonian corals (47% [*n*=15]), branching sponges (11% [*n*=19]) and vase sponges (9%). In Carmel Canyon, we observed *Sebastes*/*Sebastomus* fishes (e.g., pygmy rockfish, half-banded rockfish, darkblotched rockfish, and greenstriped rockfish) under vase sponges (6% [*n*=107]), barrel sponges (1% [*n*=507]), and upright sponges (1% [*n*=534]). The same Carmel Canyon fish taxa were seen at rest next to basket stars (6% [*n*=16]) and vase sponges (5%). In Carmel Canyon, we also observed Dover and/or English sole underneath plumed sea pens (4% [*n*=23]) and next to Subselliflorae sea pens (16% [*n*=676]).

The nearest neighbor analysis consisted of two steps. During the first step, we identified which fishes were statistically more commonly observed near structure-forming invertebrates than would be expected by chance (based on their abundance) in Ascension and Carmel Canyons. In the second step, for these fishes we calculated their mean distances to their nearest structure-forming invertebrates. Our results showed that overall the frequency of fishes observed near structure-forming invertebrates was not significantly different from a random distribution (Appendices H-L). However, in Carmel Canyon there were several statistically significant associations: lingcod (*Ophiodon elongatus*) with mound sponges in hard and mixed substrata; squarespot rockfish (*Sebastes hopkinsi*) with mound sponges in mixed substrata; and combfish (*Zaniolepis*) with Subselliflorae sea pen in soft substrata.

Additional results showed that the mean distances of fishes to their nearest structure-forming invertebrates were similar across both California canyons and all substratum types (ANOVA, factors: site [Carmel, Ascension], substrata [hard, soft], $n$=387, F=0.3, 2.9, P=0.6, 0.1) (Appendix M). In Ascension Canyon, those fish <1 m mean distance from structure-forming invertebrates in hard substrata included stripetail (*Sebastes saxicola*), greenstriped rockfish (*Sebastes elongates*), and greenspotted (*Sebastes chlorostictus*). Those in soft substrata included lingcod, yelloweye (*Sebastes ruberrimus*), greenblotched (*Sebastes rosenblatti*), darkblotched (*Sebastes crameri*), red-banded (*Sebastes babcocki*), greenspotted, and greenstriped rockfishes (Appendix M). In Carmel Canyon, the fish observed <1 m mean distance from structure-forming invertebrates in hard substrata included rougheye (*Sebastes aleutianus*), swordspine (*Sebastes ensifer*), half-banded (*Sebastes semicinctus)*, speckled (*Sebastes ovalis*), starry (*Sebastes constellatus*), greenspotted, stripetail, and greenstriped rockfishes (Appendix M). Those in mixed substrata included unidentified *Sebastes* and pygmy; and those in soft substrata included unidentified *Sebastomus*, blackeyed goby (*Coryphopterus nicholsii*), longspine combfish (*Zaniolepis latipinnis*), bocaccio (*Sebastes paucispppinis*), flag (*Sebastes rubrivinctus*), tiger

(*Sebastes nigrocinctus*), squarespot, greenstriped, and swordspine rockfishes (Appendix M). These fish taxa were observed <1 m mean distance away from swimming anemones, white deep-sea corals, foliose sponges, barrel sponges, vase sponges, and upright sponges in Ascension Canyon, and white plumed anemones, swimming anemones, Gorgonian corals, white deep-sea corals, barrel sponges, mound sponges, and upright sponges in Carmel Canyon (Fig. 7).

## Discussion

The three submarine canyons we studied displayed a wide diversity of habitats at varying depths, each associated with distinct invertebrate communities. Two distinct habitat assemblages, consisting of soft substrata and hard substrata were present in all three canyons. Motile invertebrates (e.g., brittle stars, sea stars, *Pannychia* sea cucumbers, and arthropods) were among the most abundant taxa and were broadly distributed across all habitats while filter feeders (e.g., crinoids, sponges, corals, and *Psolus* sea cucumbers) were more commonly observed on hard substrata. Similar invertebrate distributional patterns have been described in continental shelf studies of California and Oregon. For example, in Heceta Bank, Oregon (Tissot et al., 2004, 2007), Cordell Bank, California (Pirtle, 2005), central California (Graiff, 2008), and Southern California (Tissot et al., 2006), scientists found crinoids and brittle stars to be distributed across all habitat types. The same studies observed that Gorgonians and other deep-sea corals were densest on ridges and other habitat dominated by hard substratum types, whereas sea urchins, sea cucumbers, and sea pens were densest in mud-dominated habitat. These studies observed similar dominant taxa, such as crinoids, brittle stars, and sea urchins, at all sites. In our study, however, we observed that the most abundant taxa differed from canyon to canyon. The overall diversity and community structure of invertebrates we observed are associated with the diverse depths and habitats in canyons, which offer high variation in the physical and biological environment. High densities of filter feeders, for example, may occur in response to the canyons' enhanced currents and greater availability of hard substrate. Conversely, generalist organisms, such as motile invertebrates and bottom dwellers, can thrive in habitats dominated by unconsolidated mud, the most widespread substratum type at our study sites.

*Uniqueness of community structure*

Although many megafaunal invertebrates were common to our study sites, we observed several taxa in higher numbers, or only unique to one canyon relative to another. Likewise, some taxa observed in high aggregations in the canyons were not as abundant in continental shelf studies. Overall invertebrate densities were higher in Astoria Canyon (589/100 $m^2$) and Carmel Canyon (239/100 $m^2$) compared to continental shelf sites at Heceta Bank, Oregon (164/100 $m^2$; Tissot et al., 2007), Cordell Bank (91/100 $m^2$; Pirtle, 2005), central California (28 to 150/100 $m^2$; Graiff, 2008), and Southern California (200/100 $m^2$; Tissot et al., 2006). Similarly, Vetter and Dayton (1999) found greater species richness in Del Mar Submarine Canyon compared to adjacent shelf and slope areas in Southern California, concluding that organic enrichment in canyons led to greater densities of megafaunal invertebrates.

Our community structure analysis showed that each submarine canyon had distinct species assemblages. Kampf and Fohrmann (2000) and Bosley et al. (2004) and reported that it is not uncommon for submarine canyons to have density-driven, down-canyon flows. Furthermore, these flows are able to change habitats along the canyon floor temporarily by scouring the seafloor and increasing turbidity through sediment deposition (Kampf and Fohrmann, 2000; Bosley et al. 2004), and that species composition appeared to vary in the water column both vertically and spatially (Bosley et al.; 2004). The taxa observed in high aggregations in our study indicate good conditions for filter feeders that thrive in all depths and in habitats with high detritus, disturbance, currents, sediment transport, and particle loads. Vetter and Dayton (1998) observed that disturbance in submarine canyons generally decreased with depth. At our study sites, changes in the physical environment and rates of disturbance may have affected the distribution and settlement of invertebrates at various depths and across habitats. In Ascension

Canyon, mound sponges, crinoids, and brittle stars avoided the mid-deep depths (≥234 to <320 m), which were the most common depths we surveyed and which consisted of soft substratum types. Similarly, in Carmel Canyon, brittle stars avoided mid-deep depths, the largest area we surveyed that consisted of mud-dominant substrata. Brittle stars have the ability to live on, under, and between rocks, shells, other living organisms, and sediments at all depths, yet these organisms avoided areas featuring mixed substratum types and soft-dominant substrata. This suggests that high disturbance, heavy sedimentation, low food availability, greater risks of predation, or other factors affected their distribution. At the same time, we observed diverse and abundant species assemblages in Carmel Canyon at shallower depths, as well as at deeper depths (>320 m) in Astoria Canyon. In Astoria Canyon, the abundance and diversity of cnidarians and sponges occurring at deep depths containing mud-dominant habitats may have indicated favorable feeding conditions as well as low sediment loading and disturbance, as these organisms are sensitive to high particle loads.

Several studies have observed diverse species assemblages in submarine canyons (Schlacher et al., 2007; Packer et al., 2007; Yoklavich et al., 2000; Vetter and Dayton, 1999; Vetter and Dayton, 1998). This diversity could result from the unique habitats created by the complexity, instability, material processing, hydrodynamics, and topography of canyons (Schlacher et al., 2007). It is therefore not surprising that we found dissimilarities in both substrata and species diversity among the canyons in this study. The California canyons, although geographically close to one another, are significantly different in their geomorphology and their subsequent influence on the biological and physical environments. Astoria Canyon, located at the mouth of the largest river on the West Coast of North America, is exposed to high fluctuations in currents and sediment loading. Ascension Canyon, somewhat isolated from coastal influences, is exposed to open-ocean currents. Carmel Canyon is protected within Carmel Bay and positioned at the mouth of a relatively small river. The walls of Astoria and Ascension Canyons consist of softer clays and limestones, whereas the Carmel Canyon walls are composed largely of granodiorite rock. The differences we observed in the topography, geology, and location of our study sites, when combined with our findings of species diversity, indicate that a broad range of microhabitats are formed in canyons.

*Fish-invertebrate associations*

Submarine canyons appear to have similar frequencies of fish-invertebrate associations to those of nearby continental shelves and slopes. An average of 29% of the total structure-forming invertebrates observed were associated with fishes at some level in this study compared to 17% in Southern California (Bright, 2007) and 46% in Cordell Bank (Pirtle, 2005). Furthermore, some of the most frequently observed close associations (< 1 fish length or in physical contact) involved the same organisms. For example, we observed fishes in contact with black corals, branching sponges, foliose sponges, and vase sponges, and resting ≤1 fish-body-length away from branching sponges, barrel sponges, vase sponges and gorgonian corals. Similarly, fish-invertebrate contact associations were observed with black corals and vase sponges in Southern California (Bright, 2007), and with barrel sponges in Cordell Bank (Pirtle 2005), and fishes were resting ≤1 fish-body-length away from branching sponges, barrel sponges, vase sponges and gorgonian corals in Southern California (Bright, 2007). In our study sites, fishes were seen resting inside and underneath these invertebrates, which were among the largest of all observed structure-forming invertebrates in our study, suggesting that their shapes created a suitable hiding place.

Those fish species with statistically significant, nonrandom associations at relatively close median distances to structure-forming invertebrates in Ascension and Carmel Canyons included combfish, lincod, and squarespot rockfish. In Carmel Canyon, combfish were seen adjacent to Subselliflorae sea pens in low-relief mud habitats. Another study observed dense aggregations rockfishes (*Sebastes alutus*) inhabiting a forest of sea whips (*Halipteris willemoesi*) (Brodeur, 2001). In the Brodeur study, fewer rockfishes were seen within areas with damaged sea whips and no rockfish were observed in areas without sea whips. We also found lingcod adjacent to mound sponges on hard and mixed substratum types, and we found squarespot rockfish, which are known to feed on krill, zooplankton, and copepods, more in mixed substratum types adjacent to mound sponges. Both lingcod and squarespot rockfish are often associated with habitat containing rocky ridges, and patches with boulders and cobbles on Heceta Bank, Oregon (Tissot et al., 2007), Cordell Bank, California (Pirtle, 2005), and in central California (Anderson and Yoklavich, 2007). Pirtle (2005) also observed significant associations between squarespot rockfish and foliose and barrel sponges; combfish near mound sponges and shelf sponges; and lingcod near shelf sponges and barrel sponges. In general, sponges favor areas with strong currents and hard substrata. Likewise, lingcod males establish nest sites in strong current areas with crevices and ledges (DFO, 2001). Lingcod are also known to feed on invertebrates as well as on fish, and although we did not directly observe many organisms on mound sponges, we did observe megafaunal invertebrates inside, on top of, underneath, or near corals, sponges, and other structure-forming invertebrates, thereby creating foraging opportunities for fishes and other organisms. The mean distances in our study were relatively close for lingcod (median=≤1 m, range=0.3–3 m) or squarespot rockfish (median= ≤1 m, range=0.2–8 m), and the total mean nearest neighbor distances for all fish we observed on transects were also relatively low (Ascension Canyon [hard substrata: average=2 m, range=0.4–47 m; soft substrata: average=2 m, range=0.1–12 m] and Carmel Canyon [hard substrata: average=1 m, range=0.1–30 m; mixed substrata: average=1 m, range=0.3–6 m; soft substrata: average=1 m, range=0.1–30 m]).

We found fewer significant nearest neighbor relationships than the other two studies using the same methodology (Pirtle, 2005; Tissot et al., 2006). However, those studies had greater fish densities (151/100m$^2$ and 274/100m$^2$, respectively) compared to our study (20/100m$^2$ in Ascension Canyon and 73/100m$^2$ in Carmel Canyon). Tissot et al. (2006) and Pirtle (2005) concluded that the coexistence of fishes and invertebrates in the same habitats may not necessarily imply a functional relationship between species. Other studies concluded that deep-sea corals affected the distribution and abundance of fishes (Stone, 2006; Stone and Shotwell, 2007) and that deep-sea corals or sponges may have affected fish distribution only when functionally equivalent habitats are infrequently encountered or absent (Auster, 2005). In our study, there were no statistical differences in the mean distances for fish observed on hard or soft substrata, suggesting that invertebrates in canyons do not influence the occurrence of fishes even in low-relief, mud-dominated substrata. One possibility is that many areas of the canyon walls were smooth and lacked crevices, so although they had high vertical relief, they were functionally similar to low-relief mud habitats. The high incidence of unconsolidated sediment (silt and detritus) in canyons can cover boulders, cobbles, and other rocky surfaces, thereby reducing the complexity of the structural relief. Seasonal observations on the fluctuations of sedimentation on rocky surfaces due to higher rainfall or other weather conditions could provide insight on the role of sediments in these ecosystems.

Another factor that may have impacted the taxa densities in our study is commercial fishing activities. Brodeur (2001) and Hixon and Tissot (2007) observed lower densities of fishes and megafaunal invertebrates in low-relief areas with damaged sea pens. Deep-sea corals, sea pens, and sponges are slow-growing and long-lived, and it has been well documented that these fragile organisms can be easily damaged by fishing activities (Tissot and Hixon, 2007; Freese, 2001; Krieger, 2001).

All three canyons have been subjected to various fishing activities—spot prawn fishery in Carmel Canyon and groundfish fishery in Ascension and Astoria Canyons. From 1987–2002, the commercial fishing gear types (number of tows and percent of tows) recorded in the PACFIN database for Washington, Oregon and California were as follows: groundfish trawl=363,709 tows (54.4%), flatfish trawl=138,856 tows (20.8%), roller trawl=126,478 tows (18.9%), midwater trawl=33,157 tows (5%), other trawl=3674 tows (0.5%), and no gear given=2173 tows (0.3%) (NMFS, 2005). The average groundfish fishery landings in Astoria, Oregon accounted for 11.1 million pounds between 2000–2004 (NMFS, 2005) and 19.5 million pounds in Monterey Bay, California between 1981–2000 (Starr et al., 2002). Since 1992, the spot prawn landings increased and peaked in 1998 at about 372,000 pounds in Monterey Bay, California with the majority of the landings taken by traps in the early 1990s and trawling by 1996 (Starr et al., 2002). Although there were no obvious signs of damaged structure-forming invertebrates, we encountered fishing gear in both California canyons (e.g., nets [n=15], lines [n=3] and traps [n=2] in Ascension Canyon, and lines [n=4], and traps [n=2] in Carmel Canyon). Ascension Canyon is heavily trawled compared to the other two canyons (personal communication with Mary Yoklavich, Southwest Fisheries Science Center) which was the canyon with the least fish and megafaunal invertebrate densities; however, it is difficult to determine the extent that fishing gear or fishing effort may have had to the taxa densities and sizes in our study sites.

Further studies, including manipulative in situ experiments, are needed to determine the nature of the associations of fishes and invertebrates in our study areas and other regions. Observations of fish-invertebrate associations during both day and night would create an opportunity to examine temporal variability in these ecological relationships. Hart et al. (2010) found an increase in the abundance and activity of some fishes during the day compared to night, particularly in shallower cobble, boulder, and rock ridge substratum types on Heceta Bank, Oregon. This suggests that demersal fish may use structure-forming invertebrates as hiding places when they are less active at night, particularly in mud-dominant habitats where there is little to no relief.

*Conclusion*

The topography of submarine canyons enhances biological and chemical processes, thereby creating unique environments inside canyons, which in turn create unique community structures. We observed diverse habitats at varying depths containing species assemblages distinct to each submarine canyon. Our study is the first to systematically quantify fine-scale ecological associations between fishes and invertebrates in submarine canyons. Although we observed few associations, structure-forming invertebrates may have a functional role as living components of habitat for relatively few demersal fishes by adding structure, relief, and complexity to existing substrata. Thus, ecosystem-based fishery management practices that include corals, sponges, and other invertebrates will help reduce the risk of irreversible ecological changes to natural assemblages of species and ecosystem processes.

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Table 1. Submersible dive information by study site with total area (ha) and depth (minimum and maximum range, and mean (SE) calculated by patch). (*ROPOS*=remotely operated vehicle, *Delta*=occupied submersible)

| Canyon | No. of Dives | Vehicle | Date | Total Area (ha) | Depth (M) | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Min | Max | Mean | SE |
| Astoria | 7 | *ROPOS* | Jun 28-Jul 3, 2001 | 1.5 | 148 | 1358 | 594 | 15 |
| Ascension | 12 | *Delta* | Sep 20-23, 1994 | 1.9 | 182 | 319 | 253 | 2 |
| Carmel | 12 | *Delta* | Sep 24-26, 1994 | 1.3 | 90 | 305 | 182 | 3 |

Table 2. Mean densities (number of individuals/patch area [100 $m^2$]) of megafaunal invertebrates identified in each canyon at shallow (< 148 m), mid-shallow (≥ 148 and < 234 m), mid-deep (≥ 234 and < 320 m) and deep depths (≥ 320 m).

| | | Astoria Canyon | | | | | | Ascension Canyon | | | | Carmel Canyon | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Mid-shallow | | Mid-deep | | Deep | | Mid-shallow | | Mid-deep | | Shallow | | Mid-shallow | | Mid-deep | |
| Phylum | Taxon Name | Mean density | SE | Mean density | SE | Mean density | SE | Mean density | SE | Mean density | SE | Mean density | SE | Mean density | SE | Mean density | SE |
| Porifera | Barrel sponges | - | - | 1 | *1* | 2 | *1* | <0.1 | *0* | 0.5 | *0* | 2 | *1* | 2 | *0* | 1 | *0* |
| | Branching sponges | 0.2 | *0* | 3 | *2* | <0.1 | *0* | <0.1 | *0* | <0.1 | *0* | 0.2 | *0* | 1 | *0* | 0.1 | *0* |
| | Foliose sponges | 1 | *1* | 6 | *3* | 1 | *1* | 0.4 | *0* | 1 | *0* | 5 | *1* | 7 | *1* | 4 | *1* |
| | Mound sponges | 14 | *4* | 114 | *31* | 20 | *5* | 2 | *1* | 1 | *0* | 8 | *1* | 2 | *1* | 5 | *3* |
| | Shelf sponges | - | - | 0.1 | *0* | 1 | *0* | 0.4 | *0* | 1 | *0* | 1 | *0* | 0.3 | *0* | <0.1 | *0* |
| | Upright sponges | - | - | 0.3 | *0* | 0.3 | *0* | 0.7 | *0* | 0.3 | *0* | 3 | *1* | 2 | *0* | 0.2 | *0* |
| | Vase sponges | <0.1 | *0* | <0.1 | *0* | 1 | *0* | <0.1 | *0* | 0.2 | *0* | 0.2 | *0* | 0.4 | *0* | 1 | *0* |
| Cnidaria | Black corals (Antipatharia) | - | - | - | - | 1 | *0* | - | - | - | - | - | - | - | - | - | - |
| | Gorgonian corals | 1 | *0* | - | - | 9 | *2* | - | - | <0.1 | *0* | 1 | *0* | 1 | *0* | 1 | *1* |
| | White deep sea corals | 2 | *1* | 1 | *1* | 0.2 | *0* | 0.4 | *0* | 0.4 | *0* | 1 | *1* | 2 | *1* | 0.3 | *0* |
| | Dog toy octocorals (*Anthomastus ritteri*) | <0.1 | *0* | 2 | *1* | 3 | *1* | - | - | - | - | 0.3 | *0* | 2 | *0* | 1 | *0* |
| | Droopy sea pens (*Umbellula*) | - | - | - | - | 1 | *1* | - | - | - | - | - | - | - | - | - | - |
| | Subselliflorae sea pens | 1 | *1* | - | - | 17 | *5* | - | - | <0.1 | *0* | 1 | *1* | 0.4 | *0* | 0.5 | *0* |
| | Plumed sea pens (*Ptilosarcus*) | - | - | - | - | 2 | *1* | <0.1 | *0* | - | - | 0.4 | *0* | - | - | - | - |
| | Clear anemones (Caryophyllidae) | 6 | *3* | 37 | *16* | 1 | *1* | - | - | - | - | - | - | - | - | - | - |
| | Pom Pom anemones (*Liponema*) | - | - | 0.1 | *0* | 0.1 | *0* | - | - | - | - | - | - | - | - | - | - |
| | Transparent purple anemones (*Corralamorphus*) | 1 | *1* | 4 | *2* | 1 | *1* | - | - | - | - | - | - | - | - | - | - |
| | Swimming anemones (*Stomphia*) | 0.1 | *0* | 2 | *2* | 2 | *1* | 1 | *0* | 1 | *0* | 0.2 | *0* | 0.5 | *0* | 1 | *0* |
| | White plumed anemones (*Metridium*) | - | - | - | - | <0.1 | *0* | - | - | 1 | *1* | 0.1 | *0* | 0.2 | *0* | 1 | *1* |
| | Venus fly trap anemones (Hormathidae) | - | - | - | - | 1 | *0* | - | - | - | - | - | - | - | - | - | - |
| | Sand anemones | - | - | - | - | 2 | *1* | - | - | - | - | - | - | - | - | - | - |
| Annelida | Serpulid worms | - | - | - | - | - | - | 1 | *0* | 0.1 | *0* | 1 | *1* | 6 | *1* | 3 | *1* |
| Arthropoda | Shrimps (*Pandalus*) | 19 | *6* | 3 | *3* | 74 | *8* | - | - | - | - | - | - | - | - | - | - |
| | Spot prawns (*Pandalus platyceros*) | - | - | - | - | - | - | 0.5 | *0* | 1 | *0* | 7 | *2* | 61 | *12* | 24 | *8* |

Table 2. (continued).

| | | Astoria Canyon | | | | | | Ascension Canyon | | | | Carmel Canyon | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Mid-shallow | | Mid-deep | | Deep | | Mid-shallow | | Mid-deep | | Shallow | | Mid-shallow | | Mid-deep | |
| Phylum | Taxon Name | Mean density | *SE* | Mean density | SE | Mean density | *SE* | Mean density | *SE* | Mean density | *SE* | Mean density | *SE* | Mean density | *SE* | Mean density | *SE* |
| Arthropoda | Squat lobsters (Galatheidae c.f. *Munida*) | - | - | - | - | - | - | 2 | *0* | 2 | *0* | 31 | *14* | 51 | *5* | 103 | *9* |
| | Box crabs *(Lopholithodes foraminatus)* | <.01 | *0* | - | - | - | - | 5 | *2* | 1 | *0* | - | - | <.01 | *0* | - | - |
| | Crabs (*Cancer)* | - | - | - | - | 0.2 | *0* | <0.1 | *0* | - | - | <0.1 | *0* | <0.1 | *0* | 0.2 | *0* |
| | Hermit crabs | 0.1 | *0* | - | - | 1 | *0* | 6 | *1* | 29 | *2* | - | - | <0.1 | *0* | - | - |
| | Moss crabs (*Loxorhynchus crispatus*) | - | - | - | - | - | - | - | - | - | - | - | - | <0.1 | *0* | <0.1 | *0* |
| | Decorator crabs | - | - | - | - | - | - | - | - | - | - | - | - | <0.1 | *0* | - | - |
| | King crabs (*Paralithodes californica*) | - | - | - | - | - | - | - | - | - | - | - | - | <0.1 | *0* | <0.1 | *0* |
| | Spider crabs | - | - | - | - | 1 | *0* | - | - | - | - | - | - | - | - | - | - |
| | Tanner crabs (*Chionoecetes*) | - | - | - | - | 0.5 | *0* | - | - | - | - | - | - | - | - | - | - |
| | Unknown crabs | - | - | - | - | 0.1 | *0* | <0.1 | *0* | <0.1 | *0* | - | | 0.1 | *0* | 0.2 | *0* |
| Mollusca | Unknown gastropods (*Neptunea*) | 0.4 | *0* | 0.3 | *0* | 1 | *0* | - | - | - | - | - | - | - | - | - | - |
| | Hairy gastropods (*Fusitriton orgonensis*) | - | - | - | - | <0.1 | *0* | - | - | - | - | - | - | - | - | - | - |
| | Unknown Octopus (*Octopus*) | <0.1 | *0* | - | - | <0.1 | *0* | - | - | - | - | - | - | - | - | - | - |
| | White nudibranch (Dorididae) | - | - | - | - | 0.3 | *0* | - | - | - | - | - | - | - | - | - | - |
| Echino-dermata | Crinoids *(Florometra serratissima)* | 42 | *16* | 13 | *6* | 26 | *12* | 7 | *2* | 6 | *2* | 97 | *20* | 5 | *1* | 31 | *8* |
| | Black crinoids | - | - | 0.1 | *0* | 7 | *2* | - | - | - | - | - | - | - | - | - | - |
| | Fragile pink urchins *(Allocentrotus fragilis)* | 1 | *0* | 1 | *1* | 5 | *2* | 1 | *1* | 5 | *1* | <0.1 | *0* | <0.1 | *0* | 1 | *0* |
| | Purple sea urchins (*Strongylocentrotus*) | - | - | - | - | - | - | - | - | - | - | 1 | *1* | <0.1 | *0* | 0.1 | *0* |
| | Unknown urchins | - | - | - | - | 0.2 | *0* | - | - | - | - | - | - | - | - | - | - |
| | Psolid sea cucumbers *(Psolus squamatus)* | 4 | *3* | 158 | *63* | 288 | *57* | 0.1 | *0* | 14 | *3* | 0.2 | *0* | <0.1 | *0* | - | - |
| | Spined sea cucumbers *(Parastichopus*) | 2 | *1* | - | - | <0.1 | *0* | 0.1 | *0* | 0.2 | - | 1 | *0* | 0.1 | *0* | <0.1 | *0* |
| | White deep sea cucumbers *(Pannychia*) | - | - | - | - | 24 | *6* | - | - | - | - | - | - | - | - | - | - |
| Echino-dermata | Basket stars *(Gorgonocephalus eucnemis)* | - | - | - | - | <0.1 | *0* | <0.1 | *0* | - | - | 0.4 | *0* | <0.1 | *0* | - | - |
| | *Ophiacantha* brittle stars | - | - | - | - | - | - | 25 | *4* | 25 | *3* | 53 | *7* | 54 | *7* | 68 | *12* |
| | Ophiurina brittle stars | 5 | *2* | 14 | *4* | 362 | *67* | - | - | - | - | - | - | - | - | - | - |
| | *Asteronyx* brittle stars | - | - | - | - | 0.3 | *0* | - | - | - | - | - | - | - | - | - | - |

Table 2. (continued).

| | | Astoria Canyon | | | | | | Ascension Canyon | | | | Carmel Canyon | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Mid-shallow | | Mid-deep | | Deep | | Mid-shallow | | Mid-deep | | Shallow | | Mid-shallow | | Mid-deep | |
| Phylum | Taxon Name | Mean density | SE | Mean density | SE | Mean density | SE | Mean density | SE | Mean density | SE | Mean density | SE | Mean density | SE | Mean density | SE |
| Echino-dermata | Bat stars *(Asterina miniata)* | - | - | - | - | <0.1 | 0 | 0.1 | 0 | <0.1 | 0 | 2 | 1 | - | - | 0.1 | 0 |
| | Blood sea stars (*Henricia*) | 0.4 | 0 | - | - | 1 | 0 | 0.3 | 0 | 0.5 | 0 | 1 | 0 | 0.2 | 0 | 0.1 | 0 |
| | Cookie cutter stars *(Ceramaster*) | - | - | - | - | <0.1 | 0 | 0.1 | 0 | <0.1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| | Fish eating stars *(Stylasterias)* | <0.1 | 0 | - | - | - | - | 0.3 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| | Red sea stars *(Myxoderma)* | - | - | - | - | 178 | 44 | - | - | - | - | - | - | - | - | - | - |
| | Sand stars *(Luidia)* | 0.4 | 0 | 0.1 | 0 | 0.1 | 0 | <0.1 | 0 | <0.1 | 0 | 1 | 0 | 0.4 | 0 | 0.2 | 0 |
| | Sunflower stars *(Pycnopodia/Rathbunaste*) | 1 | 0 | 3 | 2 | 1 | 1 | 0.3 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0.3 | 0 |
| | Vermilion sea stars *(Mediaster aequalis)* | 1 | 0 | - | - | - | - | 1 | 0 | 0.3 | 0 | 29 | 3 | 11 | 3 | 3 | 1 |
| | Sun stars (*Solaster*) | - | - | - | - | 2 | 0 | - | - | - | - | - | - | - | - | - | - |
| | Spiny sea stars (*Poraniopsis inflata*) | - | - | - | - | - | - | - | - | - | - | 0.1 | 0 | 0.1 | 0 | 0.3 | 0 |
| | Wrinkled sea stars (*Pteraster militaris*) | <0.1 | 0 | - | - | <0.1 | 0 | <0.1 | 0 | 0.2 | 0 | 0.1 | 0 | 0.1 | 0 | 1 | 0 |
| | Cushion stars (*Pteraster tesselatus*) | 0.1 | 0 | - | - | - | - | - | - | - | - | - | - | <0.1 | 0 | - | - |
| | Rose sea stars (*Crossaster papposus*) | 0.3 | 0 | - | - | - | - | - | - | - | - | <0.1 | 0 | - | - | - | - |
| | Spiny red stars (*Hippasterias*) | - | - | - | - | - | - | - | - | <0.1 | 0 | 0.1 | 0 | 0.2 | 0 | 1 | 1 |
| | Six ray stars (*Leptasterias*) | - | - | - | - | - | - | <0.1 | 0 | <0.1 | 0 | - | - | <0.1 | 0 | - | - |
| | Unknown sea stars | 6 | 3 | 3 | 1 | 3 | 1 | 0.2 | 0 | 0.2 | 0 | 0.2 | 0 | 0.1 | 0 | <0.1 | 0 |
| Chordata | Tunicates (*Urochordata*) | 0.1 | 0 | - | - | <0.1 | 0 | - | - | 0.1 | 0 | - | - | 1 | 1 | <0.1 | 0 |
| | Sea squirts (*Ascidiacea*) | - | - | - | - | - | - | - | - | - | - | 0.1 | 0 | 0.5 | 0 | - | - |
| Mean density by depth (no. individuals/patch area [100m$^2$]) | | 109 | 20 | 365 | 89 | 1043 | 96 | 56 | 6 | 94 | 6 | 251 | 24 | 211 | 13 | 254 | 20 |
| Mean density by site (no. individuals/patch area [100m$^2$]) | | 589 | | | | | | 75 | | | | 239 | | | | | |

Table 3. Results of statistical tests comparing the density of three abundant invertebrates among study sites, substratum types (hard, mixed and soft) and depths (mid-shallow and mid-deep). Bold p-values are those significant at $p < 0.05$.

| Taxon | Test | *n* | Site (S) | Substratum Type (H) | Depth (D) | S*H | S*D | H*D |
|---|---|---|---|---|---|---|---|---|
| Mound sponges | ANOVA | 71 | F =1.4<br>p =0.3 | F =0.6<br>p =0.5 | F =1.0<br>p =0.3 | F =0.9<br>p =0.4 | F =2.7<br>p =0.1 | F =0.9<br>p =0.4 |
| Brittle stars* | ANOVA | 71 | F =5.7<br>**p =<0.01** | F =4.1<br>**p =0.02** | F =0.3<br>p =0.6 | F =0.7<br>p =0.6 | F =0.4<br>p =0.7 | F =0.6<br>p =0.6 |
| Crinoids | ANOVA | 71 | F =0.3<br>p =0.8 | F =2.4<br>p =0.1 | F=0.04<br>p =0.8 | F=0.5<br>p =0.7 | F=6.4<br>**p =<0.01** | F=0.1<br>p =0.9 |

* Indicates where a log (x+1) transformation was used.

Table 4. Total number of structure-forming invertebrates (*n*), their maximum size (cm), and percent of direction observations of fish-invertebrate associations in each canyon. Fish associations are listed by category: (0) no close association with invertebrate; (1) in the water column <1 m from invertebrate; (2) in the water column <1 fish body length from invertebrate; (3) at rest <1 fish body length from invertebrate; (4) in physical contact with invertebrate. We used all videotaped data to assess fish-invertebrate associations, which included taxa observed along the 2 m-wide strip transect, as well as beyond the width of the transect and in between the end and start of a new transect.

| | | **Astoria Canyon** | | | | | | | **Ascension Canyon** | | | | | | | **Carmel Canyon** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Max | | Percent Association Type | | | | | Max | | Percent Association Type | | | | | Max | | Percent Association Type | | | | |
| Taxon Name | *n* | Size (cm) | *n* | 0 | 1 | 2 | 3 | 4 | Size (cm) | *n* | 0 | 1 | 2 | 3 | 4 | Size (cm) | *n* | 0 | 1 | 2 | 3 | 4 |
| Basket stars | 68 | 40 | 1 | 0 | 100 | 0 | 0 | 0 | 40 | 51 | 100 | 0 | 0 | 0 | 0 | 60 | 16 | 63 | 13 | 19 | 6 | 0 |
| Clear anemones | 354 | 40 | 354 | 91 | 8 | 0 | 1 | 0 | 40 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Transparent purple anemones | 135 | 25 | 135 | 84 | 13 | 0 | 2 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Venus fly trap anemones | 206 | 40 | 206 | 70 | 24 | 1 | 5 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| White plumed anemones | 422 | 40 | 1 | 0 | 100 | 0 | 0 | 0 | 30 | 345 | 68 | 32 | 0 | 0 | 0 | 130 | 76 | 72 | 24 | 4 | 0 | 0 |
| Sand anemones | 336 | 20 | 244 | 57 | 34 | 1 | 8 | 0 | 30 | 92 | 100 | 0 | 0 | 0 | 0 | - | - | - | - | - | - | - |
| Swimming anemones | 667 | 20 | 208 | 71 | 23 | 2 | 3 | 0.5 | 30 | 321 | 67 | 21 | 4 | 6 | 1 | 30 | 138 | 58 | 38 | 4 | 0 | 1 |
| Pom Pom anemones | 14 | 50 | 12 | 75 | 17 | 8 | 0 | 0 | - | - | - | - | - | - | - | 20 | 2 | 100 | 0 | 0 | 0 | 0 |
| Droopy sea pens | 74 | 70 | 74 | 80 | 19 | 0 | 1 | 0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Plumed sea pens | 499 | 100 | 465 | 63 | 31 | 0 | 7 | 0 | 40 | 11 | 100 | 0 | 0 | 0 | 0 | 30 | 23 | 61 | 17 | 13 | 4 | 4 |
| Subselliflorae sea pens | 2,441 | 140 | 1,695 | 78 | 18 | 0 | 4 | 0.2 | 20 | 70 | 94 | 4 | 0 | 1 | 0 | 140 | 676 | 42 | 38 | 4 | 16 | 0 |
| Dog toy octocorals | 392 | 40 | 158 | 62 | 30 | 0 | 8 | 0 | 20 | 5 | 60 | 40 | 0 | 0 | 0 | 40 | 229 | 66 | 27 | 3 | 4 | 0 |
| Black corals | 93 | 160 | 93 | 65 | 20 | 1 | 11 | 3 | - | - | - | - | | - | - | - | - | - | - | - | - | - |
| Gorgonian corals | 1,246 | 200 | 1,050 | 72 | 20 | 2 | 6 | 1 | 10 | 15 | 47 | 0 | 7 | 47 | - | 50 | 181 | 53 | 35 | 9 | 2 | 0 |
| White deep sea corals | 612 | 90 | 108 | 85 | 7 | 0 | 6 | 1 | 60 | 206 | 71 | 19 | 2 | 7 | 0 | 40 | 298 | 77 | 21 | 2 | 0.3 | 0.3 |
| Barrel sponges | 784 | 100 | 92 | 70 | 17 | 1 | 12 | 0 | 100 | 185 | 71 | 18 | 3 | 7 | 1 | 130 | 507 | 50 | 36 | 9 | 4 | 1 |
| Branching sponges | 177 | 140 | 52 | 73 | 17 | 0 | 8 | 2 | 20 | 19 | 68 | 21 | 0 | 11 | 0 | 40 | 106 | 54 | 42 | 1 | 4 | 0 |
| Foliose sponges | 2,980 | 160 | 226 | 71 | 19 | 1 | 7 | 2 | 90 | 405 | 77 | 16 | 1 | 5 | 1 | 140 | 2,349 | 57 | 37 | 3 | 2 | 0.3 |
| Mound sponges | 4,101 | 60 | 2,028 | 83 | 13 | 0 | 3 | 0 | 60 | 1,076 | 81 | 18 | 0 | 1 | 0 | 60 | 997 | 95 | 2 | 3 | 1 | 0 |
| Shelf sponges | 407 | 100 | 89 | 69 | 22 | 1 | 7 | 1 | 80 | 188 | 70 | 26 | 1 | 4 | 1 | 65 | 130 | 39 | 44 | 13 | 4 | 0 |
| Upright sponges | 672 | 100 | 38 | 71 | 21 | 5 | 3 | 0 | 100 | 100 | 78 | 17 | 0 | 4 | 1 | 60 | 534 | 49 | 38 | 9 | 3 | 1 |
| Vase sponges | 223 | 80 | 50 | 78 | 10 | 4 | 8 | 0 | 140 | 66 | 74 | 11 | 5 | 9 | 2 | 110 | 107 | 50 | 28 | 12 | 5 | 6 |
| **Total number of structure-forming invertebrate s** | **16,903** | | **7,379** | **76** | **18** | **1** | **5** | **0.3** | | **3,155** | **76** | **19** | **1** | **3** | **0.4** | | **6,369** | **61** | **30** | **4** | **4** | **0.4** |

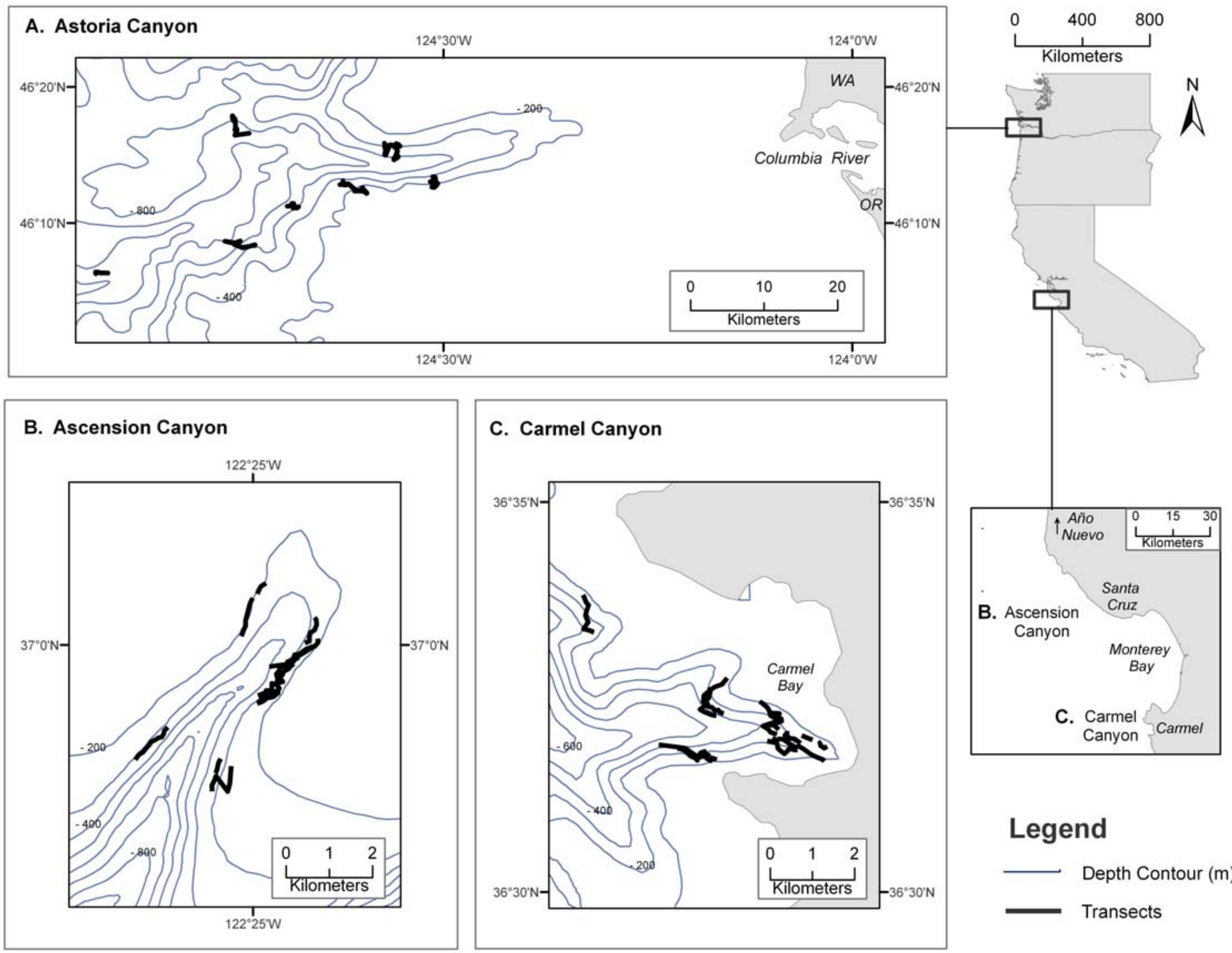



Fig. 1 Study sites: Astoria Canyon, Ascension Canyon, and Carmel Canyon. Thick lines denote submersible transects.

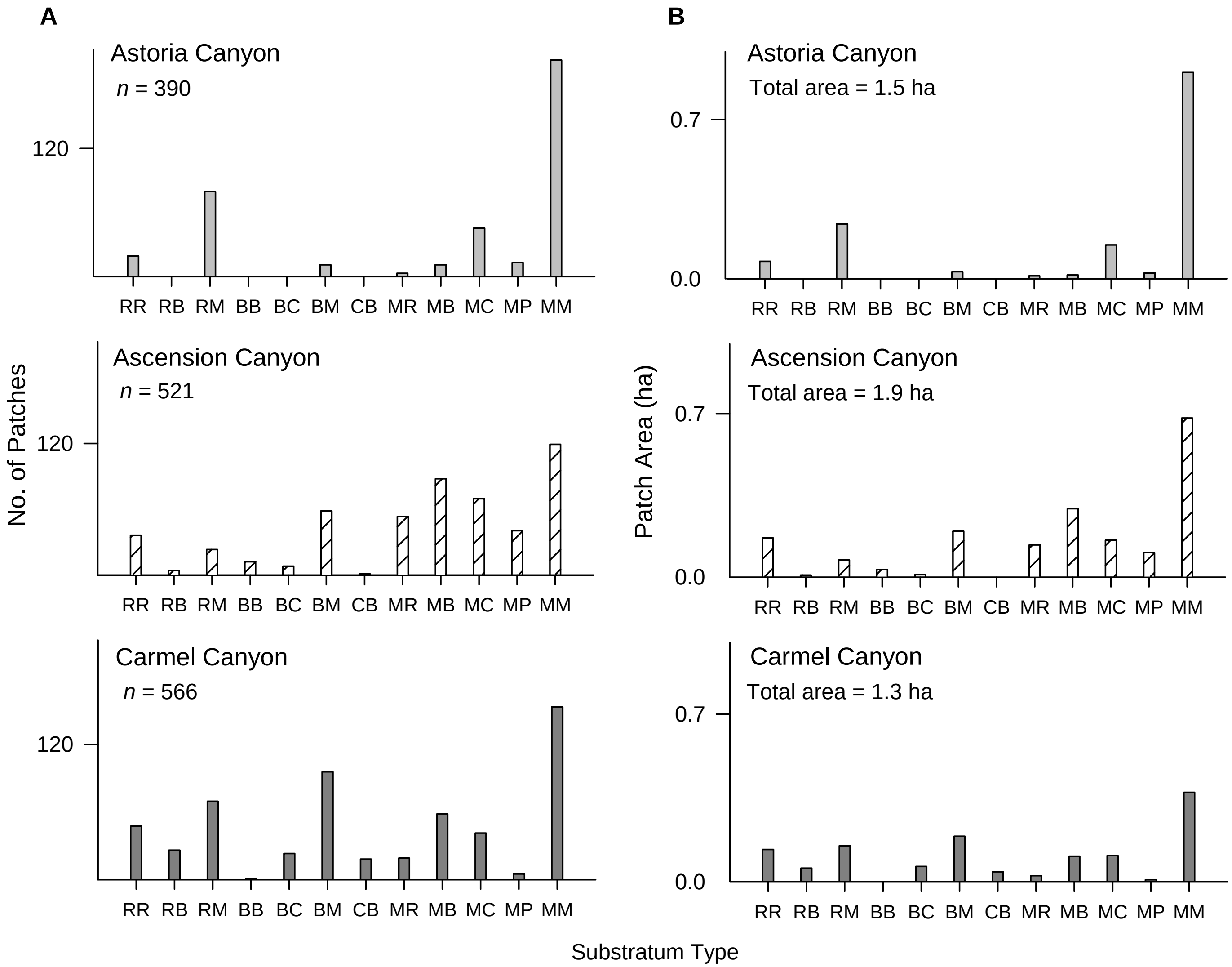



Fig. 2. The (A) frequency of substratum patches and (B) total patch area of each substratum type (ha).

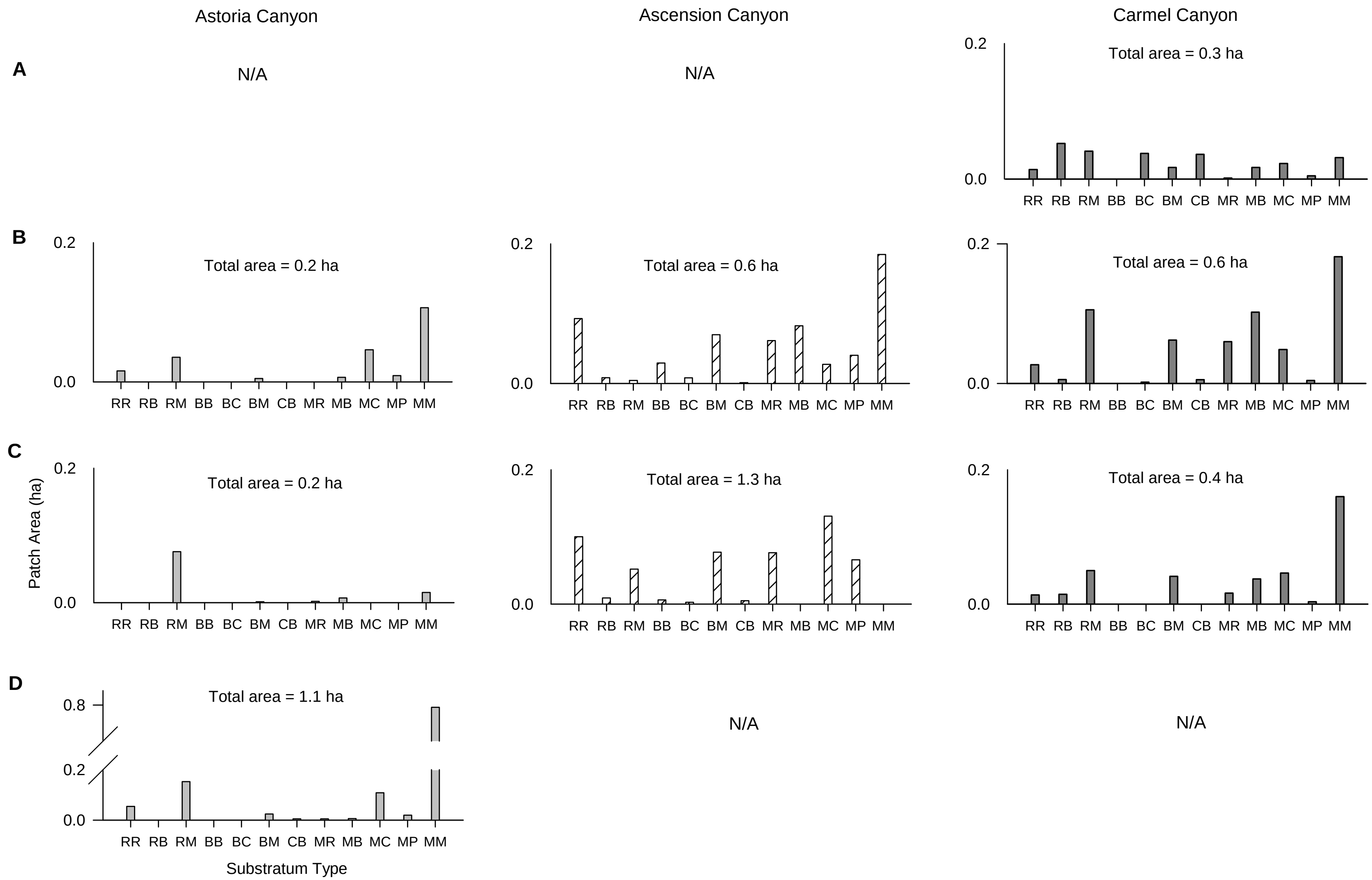



Fig. 3. Patch area (ha) of each substratum type in each canyon at varying depths (A: shallow [<148 m]; B: mid-shallow [≥148 and <234 m]; C: mid-deep [≥234 and <320 m]; D: deep [≥320]).

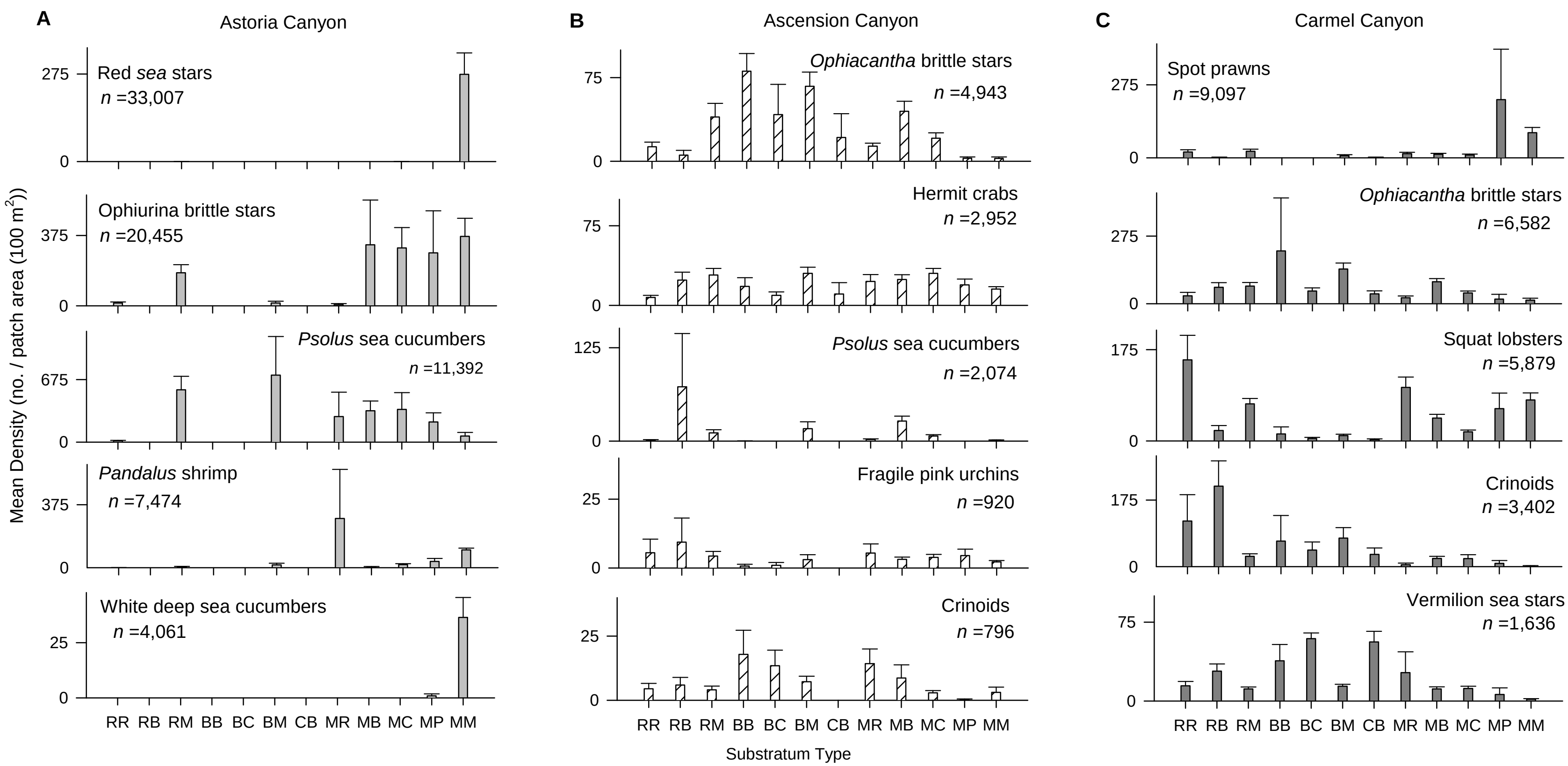



Fig. 4. Mean densities (no. of individuals/patch area (100 m$^2$)) of the five most abundant megafaunal invertebrates distributed across substratum type.

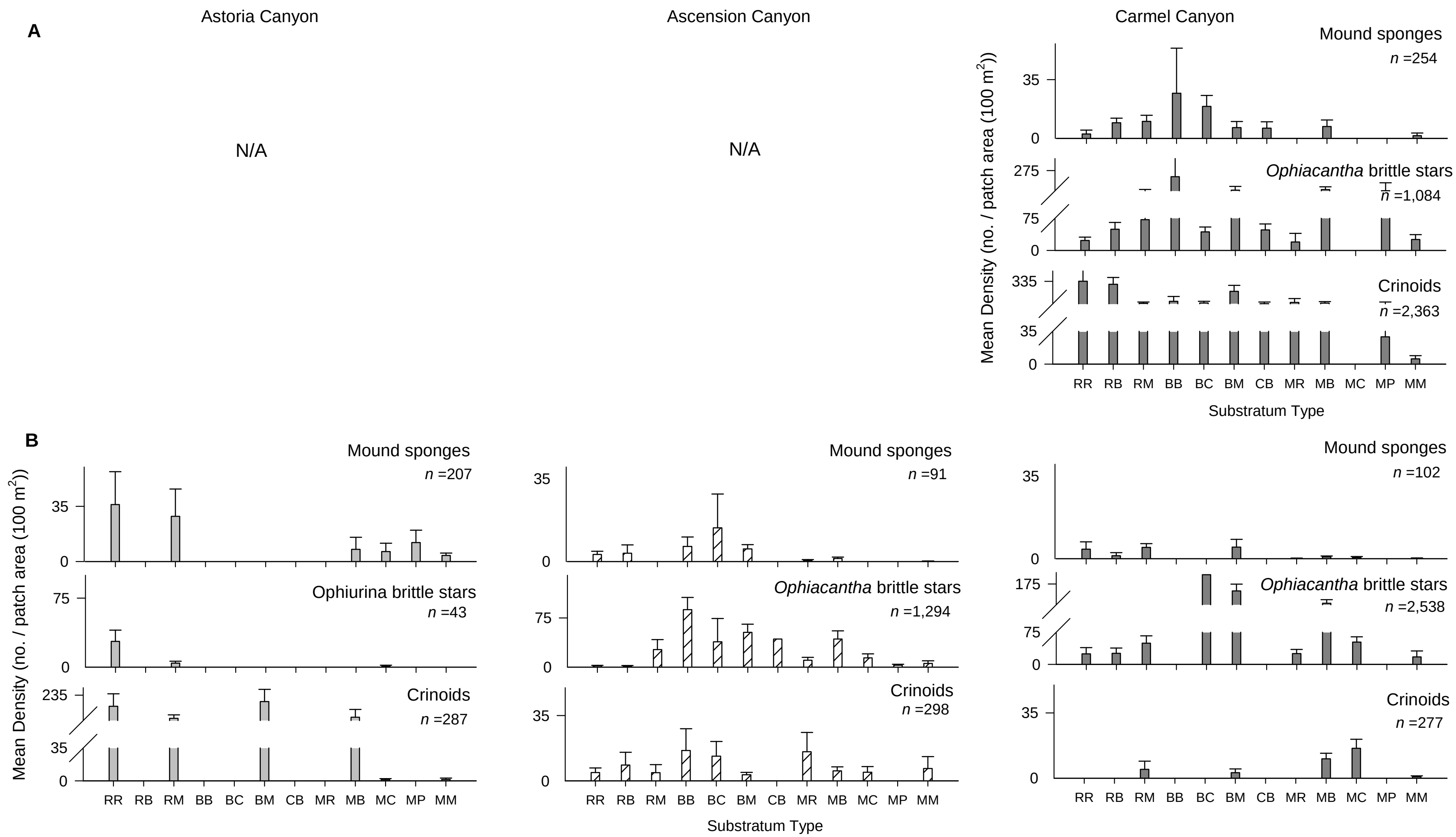



Fig. 5. Mean densities (no. of individuals/ patch area (100 $m^2$)) of megafaunal invertebrates distributed across substratum type at varying depths and by canyon (A: shallow [<148 m]; B: mid-shallow [≥148 and <234 m]).

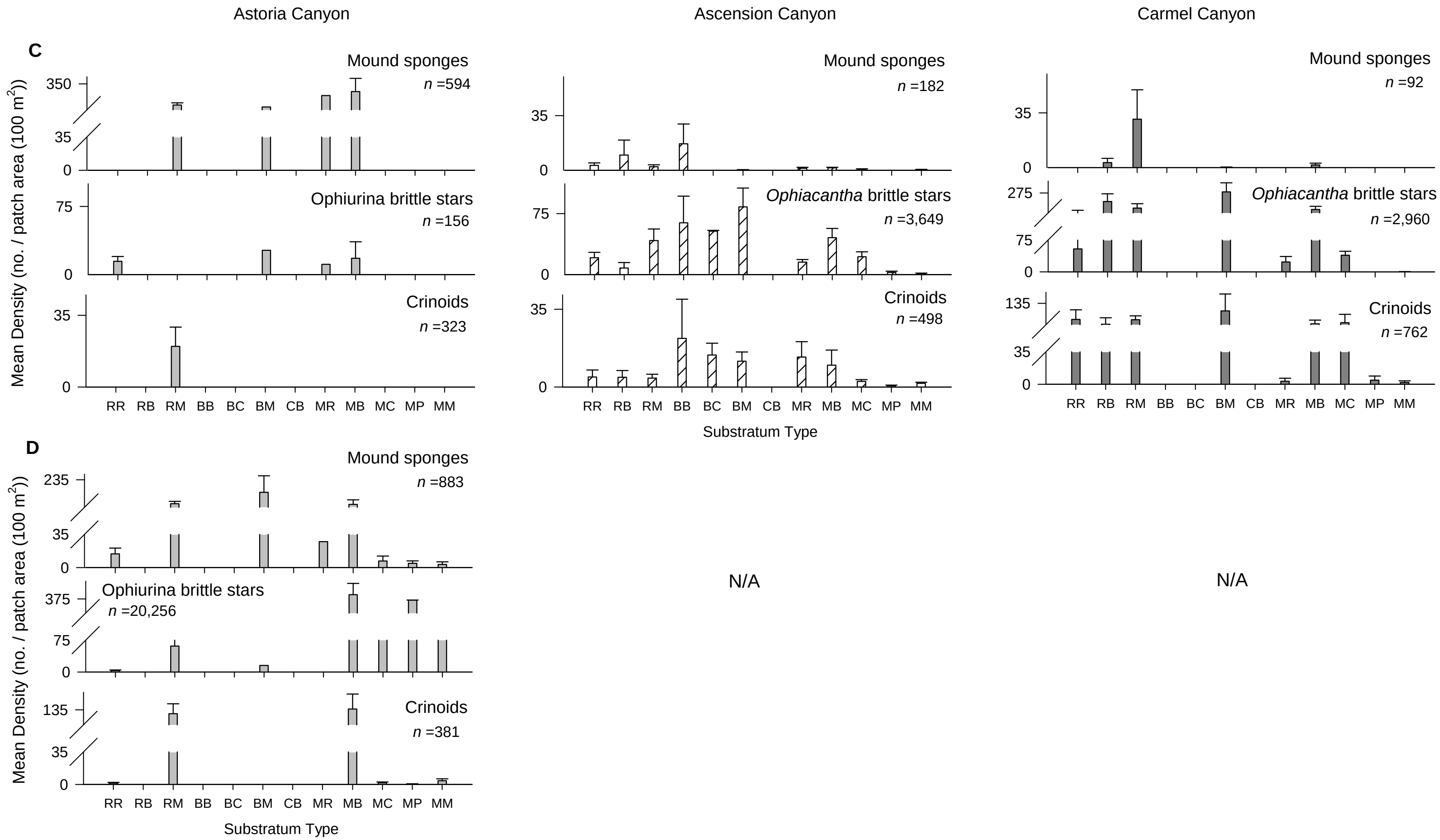
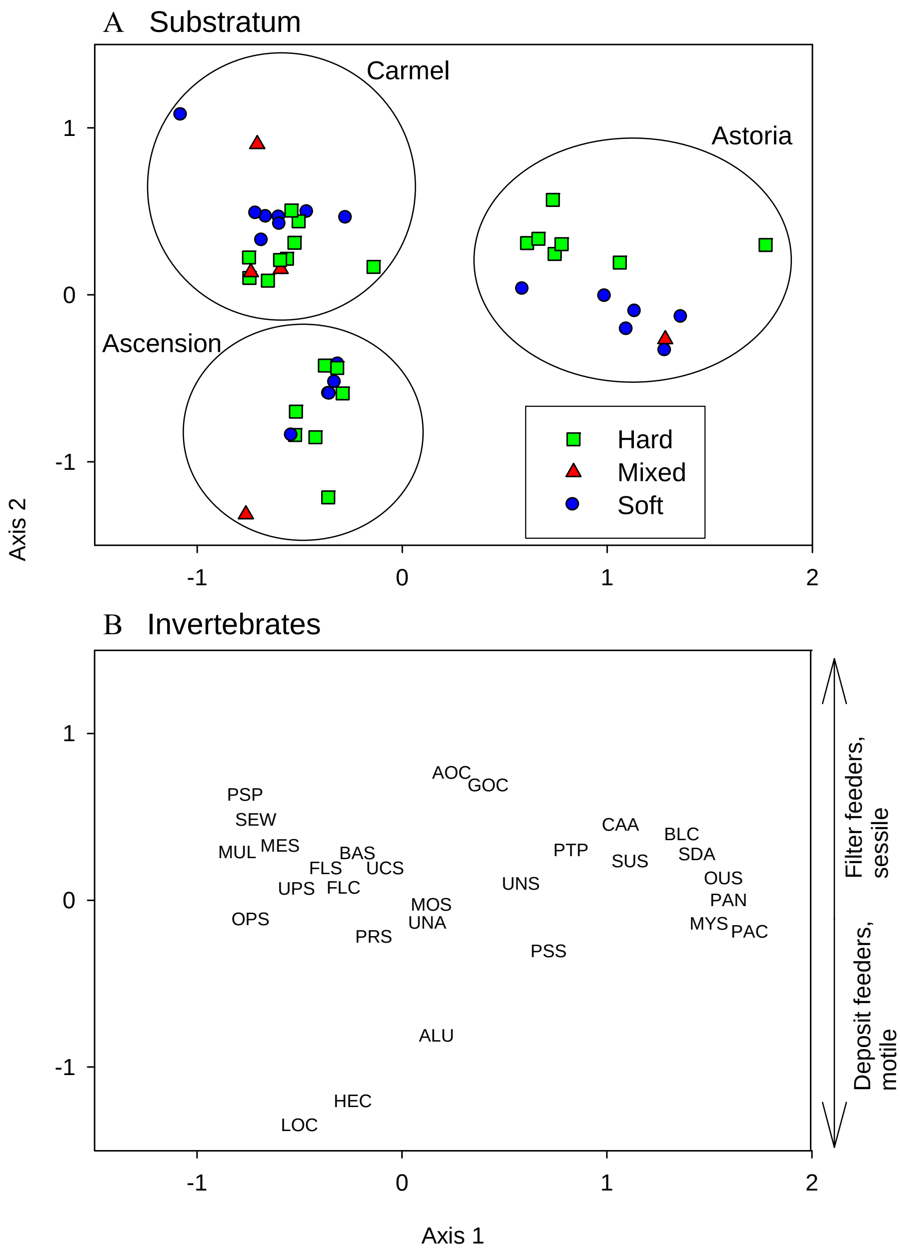



Fig. 5. (continued). Mean densities (no. of individuals/ patch area (100 $m^2$)) of megafaunal invertebrates distributed across substratum type at varying depths and by canyon (C: mid-deep [≥234 and <320 m]; D: deep [≥320]).




Invertebrates

| Code | Common Name |
|---|---|
| ALU | Fragile pink urchins |
| AOC | Dog toy corals |
| BAS | Barrel sponges |
| BLC | Black crinoids |
| CAA | Clear anemones |
| FLC | Crinoids |
| FLS | Foliose sponges |
| GOC | Gorgonian corals |
| HEC | Hermit crabs |
| LOC | Box crabs |
| MES | Vermilion sea stars |
| MOS | Mound sponges |
| MUL | Squat lobsters |
| MYS | Red sea stars |
| OPS | *Ophiacantha* brittle stars |
| OUS | Ophiurina brittle stars |
| PAC | White deep-sea cucumbers |
| PAN | Bat stars |
| PRS | Spot prawns |
| PSP | Shrimps |
| PSS | *Psolus* sea cucumbers |
| PTP | Plumed sea pens |
| SDA | Sand anemones |
| SEW | Serpulid worms |
| SUS | Subselliflorae sea pens |
| UCS | White deep-sea corals |
| UNA | Swimming anemones |
| UNS | Unknown sea stars |
| UPS | Upright sponges |

Fig. 6. Results of multivariate correspondence analysis illustrating patterns of overall community composition (substrata of each canyon and total invertebrate abundance within substratum type).

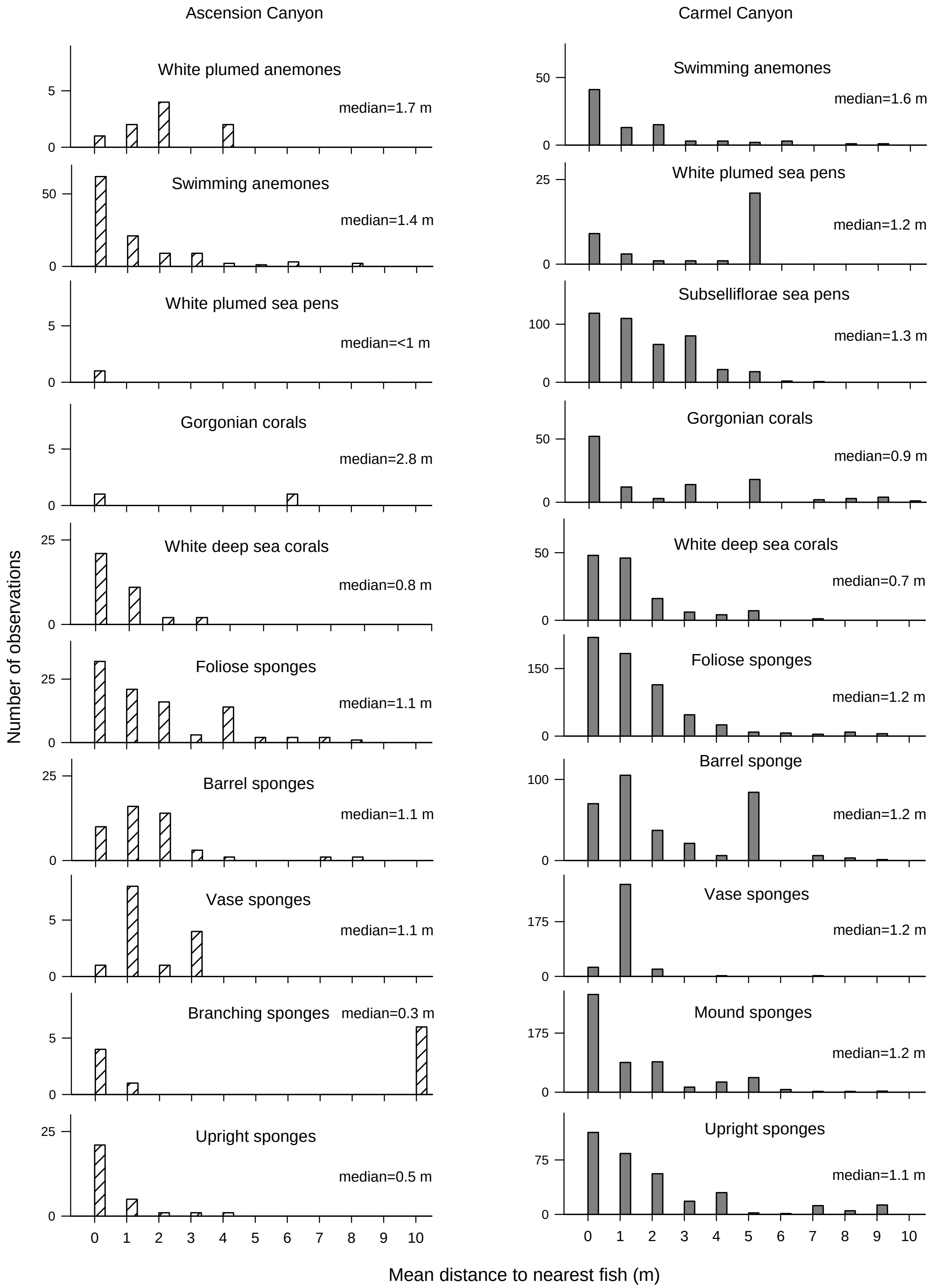



Fig. 7. Nearest neighbor distances of selected fishes observed near structure-forming invertebrates in both California canyons.

# Appendices

Appendix A. Submersible information by dive with total area (ha), number of substratum patches, and depth (minimum and maximum range, and mean (SE) calculated by patch).

| Canyon | Dive number | Location (canyon wall) | Date | Total area (ha) | No. of substrata patches | Depth (m) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Min | Max | Mean | SE |
| Astoria | 596 | South | Jun 28, 2001 | 0.1 | 44 | 172 | 593 | 389 | 23 |
| | 597 | South | Jun 28 – 29, 2001 | 0.2 | 49 | 728 | 972 | 860 | 9 |
| | 598 | South | Jun 29 – 30, 2001 | 0.4 | 117 | 194 | 655 | 414 | 12 |
| | 599 | North | Jun 30 – Jul. 1, 2001 | 0.4 | 62 | 148 | 699 | 273 | 19 |
| | 600 | North | Jul 1 – 2, 2001 | 0.2 | 46 | 646 | 882 | 744 | 10 |
| | 601 | South | Jul 2, 2001 | 0.1 | 23 | 649 | 837 | 778 | 12 |
| | 602 | South | Jul 2 – 3, 2001 | 0.2 | 49 | 886 | 1358 | 1123 | 19 |
| Ascension | 3433 | East | Sep 20, 1994 | 0.2 | 64 | 219 | 280 | 245 | 3 |
| | 3434 | East | Sep 20, 1994 | 0.2 | 78 | 199 | 283 | 255 | 4 |
| | 3435 | East | Sep 20, 1994 | 0.1 | 30 | 251 | 283 | 264 | 3 |
| | 3436 | East | Sep 21, 1994 | 0.2 | 68 | 215 | 280 | 253 | 3 |
| | 3437 | East | Sep 21, 1994 | 0.1 | 35 | 214 | 251 | 242 | 2 |
| | 3439 | West | Sep 21, 1994 | 0.1 | 23 | 183 | 184 | 183 | 0 |
| | 3440 | West | Sep 21, 1994 | 0.2 | 25 | 182 | 207 | 189 | 1 |
| | 3441 | East | Sep 22, 1994 | 0.1 | 18 | 314 | 319 | 316 | 0 |
| | 3442 | East | Sep 22, 1994 | 0.2 | 21 | 251 | 316 | 307 | 3 |
| | 3444 | East | Sep 22, 1994 | 0.2 | 66 | 241 | 302 | 283 | 3 |
| | 3445 | East | Sep 22, 1994 | 0.1 | 57 | 215 | 225 | 220 | 0 |
| | 3450 | West | Sep 23, 1994 | 0.2 | 36 | 287 | 301 | 291 | 1 |
| Carmel | 3452 | SE | Sep 24, 1994 | 0.1 | 68 | 97 | 305 | 185 | 11 |
| | 3453 | SE | Sep 24, 1994 | 0.1 | 45 | 148 | 254 | 194 | 7 |
| | 3454 | SE | Sep 24, 1994 | 0.2 | 53 | 97 | 302 | 207 | 10 |
| | 3455 | SE | Sep 24, 1994 | 0.1 | 65 | 147 | 254 | 200 | 6 |
| | 3456 | NE | Sep 25, 1994 | 0.1 | 50 | 95 | 301 | 198 | 9 |
| | 3457 | NE | Sep 25, 1994 | 0.1 | 56 | 150 | 252 | 184 | 5 |
| | 3458 | NE | Sep 25, 1994 | 0.1 | 42 | 90 | 304 | 152 | 11 |
| | 3459 | NE | Sep 25, 1994 | 0.1 | 43 | 139 | 230 | 170 | 5 |
| | 3460 | NE | Sep 25, 1994 | 0.1 | 17 | 141 | 153 | 150 | 1 |
| | 3462 | NE | Sep 26, 1994 | 0.03 | 26 | 95 | 130 | 102 | 1 |
| | 3464 | NE | Sep 26, 1994 | 0.1 | 42 | 147 | 261 | 203 | 7 |
| | 3465 | NW | Sep 26, 1994 | 0.1 | 59 | 96 | 304 | 169 | 9 |

Appendix B. Summary fish and invertebrate data: total number observed primary phyla, and primary taxon in each canyon, and species richness and diversity. The species diversity indexes were calculated at patch level. *Fish data are not yet available for all Astoria Canyon dives.

| | Astoria Canyon | Ascension Canyon | Carmel Canyon |
|---|---|---|---|
| Fishes (*n*) | * | 3,736 | 9,254 |
| Invertebrates (*n*) | 85,965 | 14,009 | 30,151 |
| Phyla total | 6 | 7 | 6 |
| Primary phylum | Echinodermata (84%) | Echinodermata (67%) | Arthropoda (50%) |
| Primary taxon | Red sea stars (38%) | Brittle stars (35%) | Spot prawns (30%) |
| Species Richness Index (S) | 56 | 42 | 47 |
| Mean Species Diversity Index (H’) | 1.3 (SE=0.1) | 1.5 (SE=0.1) | 1.7 (SE=0.1) |

Appendix C. Number of individual observations, percent of total observations, and cumulative percent for phyla identified in each canyon.

| Astoria Canyon | | | | | Ascension Canyon | | | | | Carmel Canyon | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phyla | No. Taxa | *n* | Percent Total | Percent Cum. | Phyla | No. Taxa | *n* | Percent Total | Percent Cum. | Phyla | No. Taxa | *n* | Percent Total | Percent Cum. |
| Echinodermata | 23 | 72,064 | 84 | 84 | Echinodermata | 17 | 9,420 | 67 | 67 | Arthropoda | 9 | 14,996 | 50 | 50 |
| Arthropoda | 7 | 7,764 | 9 | 93 | Arthropoda | 6 | 3,586 | 26 | 93 | Echinodermata | 21 | 12,166 | 40 | 90 |
| Cnidaria | 13 | 3,980 | 5 | 97 | Porifera | 7 | 626 | 4 | 97 | Porifera | 7 | 1904 | 6 | 96 |
| Porifera | 7 | 2,062 | 2 | 100 | Cnidaria | 6 | 295 | 2 | 99 | Cnidaria | 7 | 537 | 2 | 98 |
| Mollusca | 4 | 92 | <0.1 | 100 | Annelida | 1 | 72 | 1 | 100 | Annelida | 1 | 454 | 2 | 100 |
| Chordata | 1 | 3 | <0.1 | 100 | Chordata | 1 | 10 | <0.1 | 100 | Chordata | 2 | 94 | <0.1 | 100 |
| Grand total | 55 | 85,965 | | | Grand total | 38 | 14,009 | | | Grand total | 47 | 30,151 | | |

Appendix D. The ten most common invertebrates identified in each submarine canyon, ranked by abundance.

| Taxon Name/Phylum | Ranking of Abundance | | |
|---|---|---|---|
| | Astoria Canyon | Ascension Canyon | Carmel Canyon |
| Red sea stars *(Echinodermata)* | 1 | - | - |
| Brittle stars *(Echinodermata)* | 2 | 1 | 2 |
| Spot prawns *(Arthropoda)* | 4 | 13 | 1 |
| Hermit crabs *(Arthropoda)* | 30 | 2 | 47 |
| Sessile sea cucumbers *(Echinodermata)* | 3 | 3 | 41 |
| Squat lobsters *(Arthropoda)* | - | 7 | 3 |
| Crinoids *(Echinodermata)* | 8 | 5 | 4 |
| Fragile pink urchins *(Echinodermata)* | 11 | 4 | 27 |
| White deep sea cucumbers *(Echinodermata)* | 5 | - | - |
| Vermilion sea stars *(Echinodermata)* | 45 | 14 | 5 |
| Mound sponges *(Porifera)* | 6 | 6 | 8 |
| Foliose sponges *(Porifera)* | 20 | 11 | 6 |
| Subselliflorae sea pens *(Cnidaria)* | 7 | 32 | 12 |
| Serpulid worms *(Annelida)* | - | 17 | 7 |
| Sunflower stars *(Echinodermata)* | 28 | 8 | 19 |
| Black crinoids *(Echinodermata)* | 9 | - | - |
| Box crabs *(Arthropoda)* | 59 | 9 | 44 |
| Upright Sponges *(Porifera)* | 32 | 22 | 9 |
| Gorgonian corals *(Cnidaria)* | 10 | - | - |
| Fish eating stars *(Echinodermata)* | 54 | 10 | 18 |
| Barrel sponges *(Porifera)* | 29 | 19 | 10 |

Appendix E. Results of electivity index. Electivity varies from -1.0 to +1.0, with values between 0 and +1 indicating preference and values between 0 and -1 indicating avoidance.

| Substratum Type | Taxa | Astoria Canyon | | | Ascension Canyon | | Carmel Canyon | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mid-shallow | Mid-deep | Deep | Mid-shallow | Mid-deep | Shallow | Mid-shallow | Mid-deep |
| Hard | Mound sponges | 0.5 | -0.5 | 0.5 | 0.5 | 0.6 | 0.2 | 0.5 | 0.5 |
| Soft | Mound sponges | -0.4 | 0.5 | -0.4 | -0.8 | -0.8 | -0.5 | -0.7 | -0.9 |
| Hard | Brittle stars | 0.6 | 0.3 | -0.1 | -0.2 | 0.6 | 0.1 | 0.4 | 0.4 |
| Soft | Brittle stars | -0.9 | -0.5 | 0.3 | 0 | -0.5 | 0 | -0.4 | -0.5 |
| Hard | Crinoids | 0.5 | 0.1 | 0.4 | 0.3 | 0.6 | 0.2 | -0.4 | 0.4 |
| Soft | Crinoids | -0.7 | -1.0 | -0.2 | -0.2 | -0.4 | -0.4 | 0.1 | -0.4 |

Appendix F. Summary of mean patch area (ha), depth and primary observations of substratum type, fish and invertebrates per transect. Transects where only one substratum type occurred are denoted by * symbol. AS =Astoria Canyon, AC =Ascension Canyon, CC=Carmel Canyon.

| | | | | | | | Most abundant organisms | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Site | Dive | Tran-sect | Mean Area (ha) | Mean Depth (m) | Invertebrates (*n*) | Fish (*n*) | Bottom Type | Invertebrate | Structure-forming Invertebrate | Fish |
| AS | 596 | 2 | 0.04 | 575 | 5,764 | 142 | MM* | sea star | sea pen | thornyhead |
| AS | 596 | 3 | 0.01 | 498 | 2,398 | 33 | MM* | sea star | sea pen | thornyhead |
| AS | 596 | 4 | 0.01 | 375 | 1,142 | 30 | RM | sea star | mound sponge | thornyhead |
| AS | 596 | 5 | 0.03 | 230 | 1,173 | 58 | RM | sea cucumber | mound sponge | thornyhead |
| AS | 597 | 1 | 0.01 | 961 | 54 | 8 | MM* | shrimp | sea pen | thornyhead |
| AS | 597 | 2 | 0.05 | 920 | 315 | 88 | MM* | shrimp | sea pen | thornyhead |
| AS | 597 | 3 | 0.07 | 863 | 788 | 70 | MM* | shrimp | sea pen | thornyhead |
| AS | 597 | 4 | 0.01 | 818 | 6,219 | 26 | MM* | brittle star | sea pen | thornyhead |
| AS | 597 | 5 | 0.01 | 807 | 3,354 | - | MM* | brittle star | soft coral | thornyhead |
| AS | 597 | 6 | 0.01 | 742 | 350 | - | MM* | shrimp | sea pen | thornyhead |
| AS | 598 | 1 | 0.05 | 397 | 3,263 | - | RM | sea cucumber | mound sponge | No fish data |
| AS | 598 | 2 | 0.08 | 209 | 545 | - | MM | crinoid | mound sponge | |
| AS | 598 | 3 | 0.003 | 383 | 45 | - | MM* | shrimp | sea pen | |
| AS | 598 | 4 | 0.11 | 500 | 5,335 | - | MM | shrimp | mound sponge | |
| AS | 598 | 5 | 0.003 | 352 | 934 | - | RM | sea cucumber | mound sponge | |
| AS | 598 | 6 | 0.06 | 506 | 1,210 | - | MM | sea star | mound sponge | |
| AS | 598 | 7 | 0.04 | 482 | 5,691 | - | RM | sea cucumber | mound sponge | |
| AS | 598 | 8 | 0.02 | 388 | 378 | - | RM | sea cucumber | fly trap anemone | |
| AS | 599 | 1 | 0.06 | 681 | 23,558 | - | MM* | sea star | sea pen | |
| AS | 599 | 2 | 0.08 | 438 | 3,712 | - | MM | sea star | mound sponge | |
| AS | 599 | 3 | 0.002 | 192 | 111 | - | RR* | crinoid | mound sponge | |
| AS | 599 | 4 | 0.05 | 154 | 181 | - | MM* | shrimp | fly trap anemone | |
| AS | 599 | 5 | 0.04 | 234 | 462 | - | FM, RM | shrimp | mound sponge | |
| AS | 599 | 6 | 0.04 | 172 | 76 | - | FM | shrimp | foliose sponge | |
| AS | 599 | 7 | 0.01 | 154 | 47 | - | RR | brittle star | white deep sea coral | |
| AS | 599 | 8 | 0.03 | 154 | 109 | - | MM, MP | shrimp | foliose sponge | |

Appendix F. (continued).

| Site | Dive | Tran-sect | Mean Area (ha) | Mean Depth (m) | Invertebrates (n) | Fish (n) | Most abundant organisms: Bottom Type | Most abundant organisms: Invertebrate | Most abundant organisms: Structure-forming Invertebrate | Most abundant organisms: Fish |
|---|---|---|---|---|---|---|---|---|---|---|
| AS | 599 | 10 | 0.09 | 399 | 1,085 | - | MM | sea cucumber | fly trap anemone | No fish data |
| AS | 600 | 1 | 0.03 | 860 | 1,160 | - | MM* | shrimp | sea pen | |
| AS | 600 | 2 | 0.05 | 782 | 450 | - | FM, MM | shrimp | sea pen | |
| AS | 600 | 3 | 0.06 | 743 | 1,067 | - | MM, RM | crinoid | sea pen | |
| AS | 600 | 4 | 0.001 | 739 | 255 | - | MM* | brittle star | sea pen | |
| AS | 600 | 5 | 0.09 | 682 | 9,271 | - | MM | brittle star | sea pen | |
| AS | 600 | 6 | 0.003 | 655 | 267 | - | MS* | fragile pink urchin | sea pen | |
| AS | 601 | 1 | 0.03 | 828 | 453 | - | MM* | shrimp | sea pen | |
| AS | 601 | 2 | 0.03 | 760 | 2,250 | - | MM | brittle star | sea pen | |
| AS | 602 | 1 | 0.004 | 1357 | 355 | 35 | MM, RM | brittle star | sand anemone | thornyhead |
| AS | 602 | 2 | 0.05 | 1293 | 312 | 38 | RR | sea star | fly trap anemone | thornyhead |
| AS | 602 | 3 | 0.03 | 1156 | 782 | 22 | RM | brittle star | Gorgonian coral | thornyhead |
| AS | 602 | 4 | 0.10 | 1021 | 1,028 | 67 | MM | spider crab | soft coral | thornyhead |
| AS | 602 | 5 | 0.01 | 927 | 16 | - | MM* | shrimp | - | thornyhead |
| AC | 3433 | 1 | 0.05 | 278 | 1,216 | 105 | RM | brittle star | plumed anemone | bank |
| AC | 3433 | 2 | 0.08 | 252 | 226 | 186 | MB | sea cucumber | foliose sponge | stripetail |
| AC | 3433 | 3 | 0.09 | 221 | 214 | 109 | MB, MM | brittle star | foliose sponge | stripetail |
| AC | 3434 | 1 | 0.10 | 280 | 1,473 | 98 | MC | sea cucumber | anemone | hagfish |
| AC | 3434 | 2 | 0.07 | 266 | 218 | 94 | MC | hermit crab | mound sponge | hagfish |
| AC | 3434 | 3 | 0.06 | 201 | 924 | 327 | MB | brittle star | anemone | darkblotched |
| AC | 3435 | 1 | 0.06 | 281 | 120 | 150 | MM | hermit crab | sea pen | flatfish |
| AC | 3435 | 2 | 0.06 | 252 | 53 | 97 | MM | brittle star | white deep sea coral | darkblotched |
| AC | 3436 | 1 | 0.06 | 278 | 1,551 | 232 | MB | brittle star | barrel sponge | splitnosed |
| AC | 3436 | 2 | 0.06 | 249 | 560 | 196 | MM | hermit crab | mound sponge | darkblotched |
| AC | 3436 | 3 | 0.07 | 219 | 171 | 147 | MR, RR | squat lobster | foliose sponge | greenspotted |
| AC | 3437 | 1 | 0.07 | 250 | 712 | 100 | MM | fragile pink urchin | white deep sea coral | unid. rockfish |
| AC | 3437 | 2 | 0.06 | 220 | 101 | 269 | MR | crinoid | shelf sponge | bank |
| AC | 3439 | 1 | 0.07 | 183 | 363 | 174 | MM | brittle star | mound sponge | darkblotched |

Appendix F. (continued).

| Site | Dive | Tran-sect | Mean Area (ha) | Mean Depth (m) | Invertebrates (*n*) | Fish (*n*) | Most abundant organisms | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Bottom Type | Invertebrate | Structure-forming Invertebrate | Fish |
| AC | 3440 | 1 | 0.07 | 186 | 119 | 232 | MM | brittle star | mound sponge | darkblotched |
| AC | 3440 | 2 | 0.08 | 195 | 171 | 128 | MR | crinoid | mound sponge | bank |
| AC | 3441 | 1 | 0.08 | 316 | 621 | 176 | MB | sea cucumber | mound sponge | splitnosed |
| AC | 3442 | 1 | 0.08 | 310 | 654 | 155 | MB | sea cucumber | shelf sponge | splitnosed |
| AC | 3442 | 2 | 0.12 | 251 | 387 | 151 | MM* | fragile pink urchin | - | splitnosed |
| AC | 3444 | 1 | 0.05 | 298 | 436 | 81 | MR, RR | brittle star | white deep sea coral | splitnosed |
| AC | 3444 | 2 | 0.05 | 297 | 437 | 65 | RR | brittle star | white deep sea coral | splitnosed |
| AC | 3444 | 3 | 0.05 | 245 | 948 | 50 | MC | hermit crab | plumed anemone | rosethorn |
| AC | 3445 | 1 | 0.05 | 223 | 513 | 87 | BM | brittle star | mound sponge | bocaccio |
| AC | 3445 | 2 | 0.05 | 218 | 246 | 95 | BM | brittle star | mound sponge | darkblotched |
| AC | 3450 | 1 | 0.09 | 291 | 1,228 | 94 | MM | sea cucumber | white deep sea coral | bank |
| AC | 3450 | 2 | 0.11 | 290 | 347 | 138 | MM | hermit crab | mound sponge | dover sole |
| CC | 3452 | 1 | 0.02 | 302 | 577 | 417 | MM | squat lobster | plumed anemone | dover sole |
| CC | 3452 | 2 | 0.03 | 197 | 1,134 | 127 | MM | squat lobster | octocoral | dover sole |
| CC | 3452 | 3 | 0.04 | 99 | 567 | 206 | MM | crinoid | foliose sponge | pygmy |
| CC | 3453 | 1 | 0.03 | 253 | 612 | 302 | MM | squat lobster | octocoral | dover sole |
| CC | 3453 | 2 | 0.03 | 199 | 2,628 | 267 | MM | spot prawn | branching sponge | dover sole |
| CC | 3453 | 3 | 0.03 | 150 | 354 | 131 | MM | brittle star | barrel sponge | half-banded |
| CC | 3454 | 1 | 0.06 | 298 | 2,457 | 72 | MM | brittle star | foliose sponge | hagfish |
| CC | 3454 | 2 | 0.06 | 201 | 963 | 57 | MR | squat lobster | foliose sponge | unid. rockfish |
| CC | 3454 | 3 | 0.04 | 98 | 412 | 700 | BC | crinoid | upright sponge | pygmy |
| CC | 3455 | 1 | 0.08 | 253 | 1,084 | 50 | MB | brittle star | foliose sponge | splitnosed |
| CC | 3455 | 2 | 0.03 | 197 | 481 | 53 | MR | squat lobster | foliose sponge | unid. rockfish |
| CC | 3455 | 3 | 0.03 | 149 | 632 | 122 | MM | brittle star | upright sponge | unid. rockfish |
| CC | 3456 | 1 | 0.04 | 293 | 616 | 91 | MB, MM | brittle star | white deep sea coral | shortspine-thornyhead |
| CC | 3456 | 2 | 0.05 | 199 | 616 | 118 | MC | brittle star | foliose sponge | darkblotched |
| CC | 3456 | 3 | 0.04 | 99 | 732 | 1,629 | BC, CB | brittle star | sea pen | pygmy |

Appendix F. (continued).

| Site | Dive | Tran-sect | Mean Area (ha) | Mean Depth (m) | Invertebrates (*n*) | Fish (*n*) | Most abundant organisms<br>Bottom Type | Invertebrate | Structure-forming Invertebrate | Fish |
|---|---|---|---|---|---|---|---|---|---|---|
| CC | 3457 | 1 | 0.03 | 247 | 409 | 90 | MM | squat lobster | sea pen | dover sole |
| CC | 3457 | 2 | 0.04 | 199 | 494 | 95 | MM | brittle star | foliose sponge | stripetail |
| CC | 3457 | 3 | 0.05 | 152 | 868 | 256 | MC | brittle star | sea pen | half-banded |
| CC | 3458 | 1 | 0.05 | 301 | 245 | 611 | MM | squat lobster | sea pen | rex/dover sole |
| CC | 3458 | 2 | 0.04 | 199 | 3,450 | 383 | MM, RM | spot prawn | Gorgonian coral | rex/dover sole |
| CC | 3458 | 3 | 0.05 | 100 | 584 | 791 | BC | sea star | mound sponge | pygmy |
| CC | 3459 | 1 | 0.03 | 229 | 680 | 172 | MB, MM, RM | squat lobster | foliose sponge | rex/dover sole |
| CC | 3459 | 2 | 0.03 | 178 | 1,839 | 230 | MM | spot prawn | barrel sponge | rex/dover sole |
| CC | 3459 | 3 | 0.02 | 140 | 328 | 277 | MM | brittle star | mound sponge | shortbelly/chilipepper |
| CC | 3460 | 1 | 0.05 | 150 | 737 | 115 | MM | spot prawn | foliose sponge | unid. rockfish |
| CC | 3462 | 1 | 0.01 | 104 | 492 | - | RR | squat lobster | foliose sponge | - |
| CC | 3462 | 2 | 0.03 | 101 | 967 | 722 | MB | crinoid | mound sponge | squarespot |
| CC | 3464 | 1 | 0.05 | 256 | 1,157 | 206 | MM | squat lobster | mound sponge | rex/dover sole |
| CC | 3464 | 2 | 0.04 | 199 | 616 | 196 | MM | squat lobster | mound sponge | rex sole |
| CC | 3464 | 3 | 0.03 | 154 | 373 | 191 | MM | spot prawn | sea pen | darkblotched |
| CC | 3465 | 1 | 0.04 | 301 | 371 | 113 | MS | brittle star | mound sponge | shortspine-thornyhead |
| CC | 3465 | 2 | 0.05 | 198 | 929 | 79 | BM | brittle star | foliose sponge | rosethorn |
| CC | 3465 | 3 | 0.05 | 99 | 1,747 | 385 | SM | crinoid | mound sponge | pygmy |

Appendix G. List of fishes observed for the nearest neighbor analysis.

| Common name | Scientific Name |
|---|---|
| Aurora | *Sebastes aurora* |
| Bank | *Sebastes rufus* |
| Blackeyed goby | *Coryphopterus nicholsii* |
| Blue | *Sebastes mystinus* |
| Bocaccio | *Sebastes paucispppinis* |
| Canary | *Sebastes pinniger* |
| Chilipepper | *Sebastes goodei* |
| Copper | *Sebastes caurinus* |
| Cowcod | *Sebastes levis* |
| Darkblotched | *Sebastes crameri* |
| Flag | *Sebastes rubrivinctus* |
| Gopher | *Sebastes carnatus* |
| Greenblotched | *Sebastes rosenblatti* |
| Greenspotted | *Sebastes chlorostictus* |
| Greenstriped | *Sebastes elongatus* |
| Half-banded | *Sebastes semicinctus* |
| Lingcod | *Ophiodon elongatus* |
| Longspine combfish | *Zaniolepis latipinnis* |
| Pygmy | *Sebastes wilsoni* |
| Quillback | *Sebastes maliger* |
| Red-banded | *Sebastes babcocki* |
| Rosethorn | *Sebastes helvomaculatus* |
| Rosy | *Sebastes rosaceus* |
| Rougheye | *Sebastes aleutianus* |
| Semaphore | *Sebastes melanosema* |
| Sharphcin | *Sebastes zacentrus* |
| Shortbelly | *Sebastes jordani* |
| Shortspine combfish | *Zaniolepis frenata* |
| Shortspine thornyhead | *Sebastolobus alascanus* |
| Speckled | *Sebastes ovalis* |
| Splitnosed | *Sebastes diploproa* |
| Squarespot | *Sebastes hopkinsi* |
| Starry | *Sebastes constellatus* |
| Stripetail | *Sebastes saxicola* |
| Swordspine | *Sebastes ensifer* |
| Tiger | *Sebastes nigrocinctus* |
| Unid. Combfish | *Zaniolepis* |
| Unidentified rockfish | *Sebastes* |
| Unidentified *Sebastomus* | *Sebastomus* |
| Vermillion | *Sebastes miniatus* |
| Widow | *Sebastes entomelas* |
| Yelloweye | *Sebastes ruberrimus* |
| Yellowtail | *Sebastes flavidus* |

Appendix H. Total percentage of selected fishes near structure-forming invertebrates relative to fishes counted along transects consisting of hard substratum type in Ascension Canyon.

| Taxon name | Total Percent of Fish on Transect (Hard Substrata) | Total Percent of Fish Near Structure-forming Invertebrates | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Sponges | | | | | | | Corals | | | Sea Pens | | Anemones | |
| | | foliose | vase | barrel | mound | branching | upright | shelf | white deep sea corals | gorgonian corals | dog toy octocoral | white plumed sea pens | subselli-florae sea pens | white plumed anemones | swimming anemone |
| Darkblotched | 27 | 1 | 0 | 4 | 19 | 0 | 0 | 28 | 63 | 0 | 0 | - | - | 0 | 7 |
| Bank | 14 | 3 | 9 | 2 | 5 | 0 | 0 | 0 | 7 | 0 | 0 | - | - | 0 | 3 |
| Rosethorn | 12 | 57 | 36 | 4 | 26 | 6 | 21 | 9 | 7 | 0 | 0 | - | - | 63 | 15 |
| Splitnosed | 8 | 12 | 18 | 18 | 10 | 13 | 21 | 13 | 13 | 100 | 0 | - | - | 0 | 26 |
| Unknown *Sebastes* | 8 | 14 | 18 | 47 | 12 | 75 | 0 | 8 | 0 | 0 | 0 | - | - | 37 | 7 |
| Greenspotted | 7 | 7 | 0 | 6 | 4 | 0 | 14 | 4 | 0 | 0 | 0 | - | - | 0 | 7 |
| Unknown *Sebastomus* | 6 | 2 | 18 | 2 | 17 | 6 | 36 | 21 | 0 | 0 | 100 | - | - | 0 | 15 |
| Stripetail | 5 | 0 | 0 | 8 | 0 | 0 | 7 | 8 | 0 | 0 | 0 | - | - | 0 | 0 |
| Bocaccio | 4 | 1 | 0 | 6 | 5 | 0 | 0 | 8 | 3 | 0 | 0 | - | - | 0 | 9 |
| Greenblotched | 3 | 1 | 0 | 2 | 1 | 0 | 0 | 2 | 3 | 0 | 0 | - | - | 0 | 3 |
| Shortspine thornyhead | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | - | 0 | 1 |
| Lingcod | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | - | 0 | 0 |
| Yelloweye | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | - | 0 | 2 |
| Greenstriped | 1 | 1 | 0 | 0 | <1 | 0 | 0 | 0 | 3 | 0 | 0 | - | - | 0 | 0 |
| Cowcod | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | - | 0 | 0 |
| Red-banded | <1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | - | 0 | 2 |

Appendix I. Total percentage of selected fishes near structure-forming invertebrates relative to fishes counted along transects consisting of soft substratum type in Ascension Canyon.

| Taxon name | Total Percent of Fish on Transect (Soft Substrata) | Total Percent of Fish Near Structure-forming Invertebrates | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Sponges | | | | | | | Corals | | | Sea Pens | | Anemones | |
| | | foliose | vase | barrel | mound | branching | upright | shelf | white deep sea corals | gorgonian corals | dog toy octocoral | white plumed sea pens | subselli-florae sea pens | white plumed anemones | swimming anemone |
| Darkblotched | 24 | 16 | 0 | 5 | 3 | 13 | 39 | 7 | 17 | 0 | 0 | 0 | 0 | - | 12 |
| Splitnosed | 22 | 18 | 47 | 47 | 18 | 25 | 31 | 38 | 25 | 0 | 100 | 100 | 0 | - | 6 |
| Bank | 13 | 7 | 11 | 16 | 64 | 0 | 6 | 13 | 1 | 0 | 0 | 0 | 0 | - | 30 |
| Stripetail | 11 | 12 | 0 | 3 | <1 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | - | 0 |
| Shortspine thornyhead | 9 | 4 | 5 | 4 | 1 | 0 | 0 | 3 | 4 | 0 | 0 | 0 | 0 | - | 3 |
| Unknown Sebastes | 5 | 10 | 0 | 6 | 1 | 25 | 8 | 8 | 5 | 0 | 0 | 0 | 0 | - | 5 |
| Rosethorn | 5 | 15 | 26 | 8 | 7 | 13 | 8 | 11 | 3 | 100 | 0 | 0 | 100 | - | 9 |
| Greenspotted | 5 | 5 | 0 | 4 | <1 | 0 | 0 | 5 | 31 | 0 | 0 | 0 | 0 | - | 27 |
| Greenstriped | 2 | 2 | 0 | 0 | <1 | 0 | 3 | 2 | 5 | 0 | 0 | 0 | 0 | - | 1 |
| Sebastomus | 2 | 1 | 0 | 1 | 1 | 13 | 3 | 0 | 5 | 0 | 0 | 0 | 0 | - | 1 |
| Red-banded | 1 | 2 | 11 | 5 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | - | 1 |
| Greenblotched | 1 | 3 | 0 | 1 | <1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | - | 3 |
| Lingcod | <1 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 |
| Sharphcin | <1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 |
| Cowcod | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 |
| Bocaccio | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 |

Appendix J. Total percentage of selected fishes near structure-forming invertebrates relative to fishes counted along transects consisting of hard substratum type in Carmel Canyon. Species that occurred statistically more often near these invertebrates are indicated with bold font and * symbol ($p \leq 0.05$).

| Taxon name | Total Percent of Fish on Transect (Hard Substrata) | Total Percent of Fish Near Structure-forming Invertebrates | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Sponges | | | | | | | Corals | | | Sea Pens | | Anemones | |
| | | foliose | vase | barrel | mound | branching | upright | shelf | white deep sea corals | gorgonian corals | dog toy octocoral | white plumed sea pens | subselli-florae sea pens | white plumed anemones | swimming anemone |
| Pygmy | 61 | 15 | 45 | 37 | 63 | 36 | 52 | 46 | 0 | 19 | 0 | 0 | - | 0 | 0 |
| Squarespot | 16 | 12 | 2 | <1 | 1 | 0 | 12 | 3 | 7 | 3 | 0 | 0 | - | 0 | 0 |
| Unknown *Sebastes* | 4 | 37 | 16 | 12 | 3 | 20 | 8 | 2 | 19 | 42 | 23 | 0 | - | 32 | 15 |
| Rosethorn | 4 | 16 | 5 | 14 | 11 | 2 | 4 | 14 | 9 | 1 | 17 | 100 | - | 11 | 27 |
| Bank | 3 | 4 | 3 | 7 | 3 | 20 | 5 | 10 | 12 | 3 | 14 | 0 | - | 0 | 9 |
| Greenspotted | 2 | 3 | 0 | 5 | 3 | 7 | 7 | 9 | 38 | 17 | 6 | 0 | - | 11 | 3 |
| Half-banded | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 |
| Rosy | 1 | 1 | 3 | 6 | 1 | 0 | 4 | 6 | 4 | 3 | 0 | 0 | - | 0 | 0 |
| Darkblotched | 1 | 3 | 3 | 2 | 5 | 2 | <1 | 2 | 2 | 0 | 6 | 0 | - | 21 | 6 |
| Splitnosed | 1 | 2 | 7 | 1 | 1 | 11 | <1 | 1 | 2 | 8 | 6 | 0 | - | 11 | 12 |
| Unknown *Sebastomus* | 1 | 2 | 0 | 2 | 1 | 0 | 1 | 0 | 2 | 1 | 3 | 0 | - | 5 | 3 |
| Blackeyed goby | 1 | 1 | 0 | 1 | <1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | - | 0 | 0 |
| Stripetail | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 3 | 2 | 0 | 20 | 0 | - | 0 | 3 |
| Bocaccio | <1 | 1 | 0 | <1 | <1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | - | 0 | 0 |
| Greenblotched | <1 | 1 | 7 | 5 | 1 | 0 | 2 | 3 | 0 | 4 | 0 | 0 | - | 11 | 0 |
| Starry | <1 | 0 | 0 | 0 | <1 | 0 | <1 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 |

Appendix J. (continued).

| Taxon name | Total Percent of Fish on Transect (Hard Substrata) | Total Percent of Fish Near Structure-forming Invertebrates | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Sponges | | | | | | | Corals | | | Sea Pens | | Anemones | |
| | | foliose | vase | barrel | mound | branching | upright | shelf | white deep sea corals | gorgonian corals | dog toy octocoral | white plumed sea pens | subselli-florae sea pens | white plumed anemones | swimming anemone |
| Shortspine thornyhead | <1 | <1 | 0 | 1 | 1 | 0 | <1 | 0 | 1 | 0 | 0 | 0 | - | 0 | 6 |
| Lingcod | <1 | 1 | 0 | 0 | 1* | 0 | <1 | 0 | 0 | 0 | 0 | 0 | - | 0 | 3 |

Appendix K. Total percentage of selected fishes near structure-forming invertebrates relative to fishes counted along transects consisting of mixed substratum type in Carmel Canyon. Species that occurred statistically more often near these invertebrates are indicated with bold font and * symbol ($p \leq 0.05$).

| | | Total Percent of Fish Near Structure-forming Invertebrates | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Sponges | | | | | | | Corals | | | Sea Pens | | Anemones | |
| Taxon name | Total Percent of Fish on Transect (Mixed Substrata) | foliose | vase | barrel | mound | branching | upright | shelf | white deep sea corals | gorgonian corals | dog toy octocoral | white plumed sea pens | subselli-florae sea pens | white plumed anemones | swimming anemone |
| Pygmy | 92 | 0 | 100 | 60 | 46 | - | 22 | 0 | 0 | - | - | 91 | - | - | - |
| Unknown *Sebastes* | 2 | 0 | 0 | 0 | 0 | - | 11 | 0 | 80 | - | - | 0 | - | - | - |
| Squarespot | 2 | 33 | 0 | 20 | **38*** | - | 28 | 0 | 0 | - | - | 0 | - | - | - |
| Rosy | 2 | 67 | 0 | 0 | 13 | - | 6 | 60 | 0 | - | - | 0 | - | - | - |
| Rosethorn | 1 | 0 | 0 | 20 | 0 | - | 22 | 10 | 0 | - | - | 4 | - | - | - |
| Lingcod | <1 | 0 | 0 | 0 | **3*** | - | 11 | 30 | 20 | - | - | 4 | - | - | - |
| Greenspotted | <1 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | - | - | 0 | - | - | - |
| Unknown *Sebastomus* | <1 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | - | - | 0 | - | - | - |
| Greenstriped | <1 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | - | - | 0 | - | - | - |
| Bank | <1 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | - | - | 0 | - | - | - |

Appendix L. Total percentage of selected fishes (individual abundance near structure-forming invertebrates relative to fishes counted along transects consisting of soft substratum type in Carmel Canyon. Species that occurred statistically more often near these invertebrates are indicated with bold font and * symbol ($p \leq 0.05$).

| Taxon name | Total Percent of Fish on Transect (Soft Substrata) | Total Percent of Fish Near Structure-forming Invertebrates | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Sponges | | | | | | | Corals | | | Sea Pens | | Anemones | |
| | | foliose | vase | barrel | mound | branching | upright | shelf | white deep sea corals | gorgonian corals | dog toy octocoral | white plumed sea pens | subselli-florae sea pens | white plumed anemones | swimming anemone |
| Unknown *Sebastes* | 21 | 22 | 11 | 14 | 6 | 5 | 8 | 0 | 27 | 30 | 24 | 13 | 9 | 0 | 3 |
| Stripetail | 16 | 6 | 11 | 5 | 14 | 10 | 2 | 6 | 1 | 26 | 2 | 9 | 2 | 20 | 14 |
| Pygmy | 14 | 12 | 0 | 3 | 4 | 38 | 6 | 53 | 18 | 17 | 1 | 78 | 66 | 0 | 7 |
| Darkblotched | 11 | 22 | 11 | 43 | 25 | 0 | 0 | 0 | 8 | 9 | 55 | 0 | 4 | 0 | 34 |
| Half-banded | 9 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 4 | 1 | 0 | 14 | 0 | 14 |
| Splitnosed | 5 | 2 | 6 | 4 | 0 | 0 | 3 | 0 | 3 | 0 | 3 | 0 | <1 | 0 | 2 |
| Rosethorn | 5 | 13 | 39 | 12 | 2 | 10 | 53 | 29 | 5 | 9 | 5 | 0 | 0 | 60 | 3 |
| Unknown *Sebastomus* | 4 | 6 | 0 | 4 | 10 | 14 | 6 | 0 | 6 | 0 | 0 | 0 | 1 | 0 | 0 |
| Shortspine thornyhead | 4 | 3 | 11 | 1 | 0 | 0 | 1 | 0 | 19 | 0 | 0 | 0 | 0 | 0 | 0 |
| Greenspotted | 3 | 4 | 0 | 3 | 4 | 0 | 4 | 6 | 4 | 4 | 4 | 0 | 2 | 0 | 3 |
| Bank | 2 | 8 | 6 | 5 | 6 | 10 | 11 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 7 |
| Greenstriped | 1 | 1 | 6 | 3 | 20 | 14 | 5 | 6 | 1 | 0 | 4 | 0 | <1 | 20 | 12 |
| Blackeyed goby | 1 | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Rosy | <1 | 1 | 0 | 0 | 10 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Aurora | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Longspine combfish | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |

Appendix L. (continued).

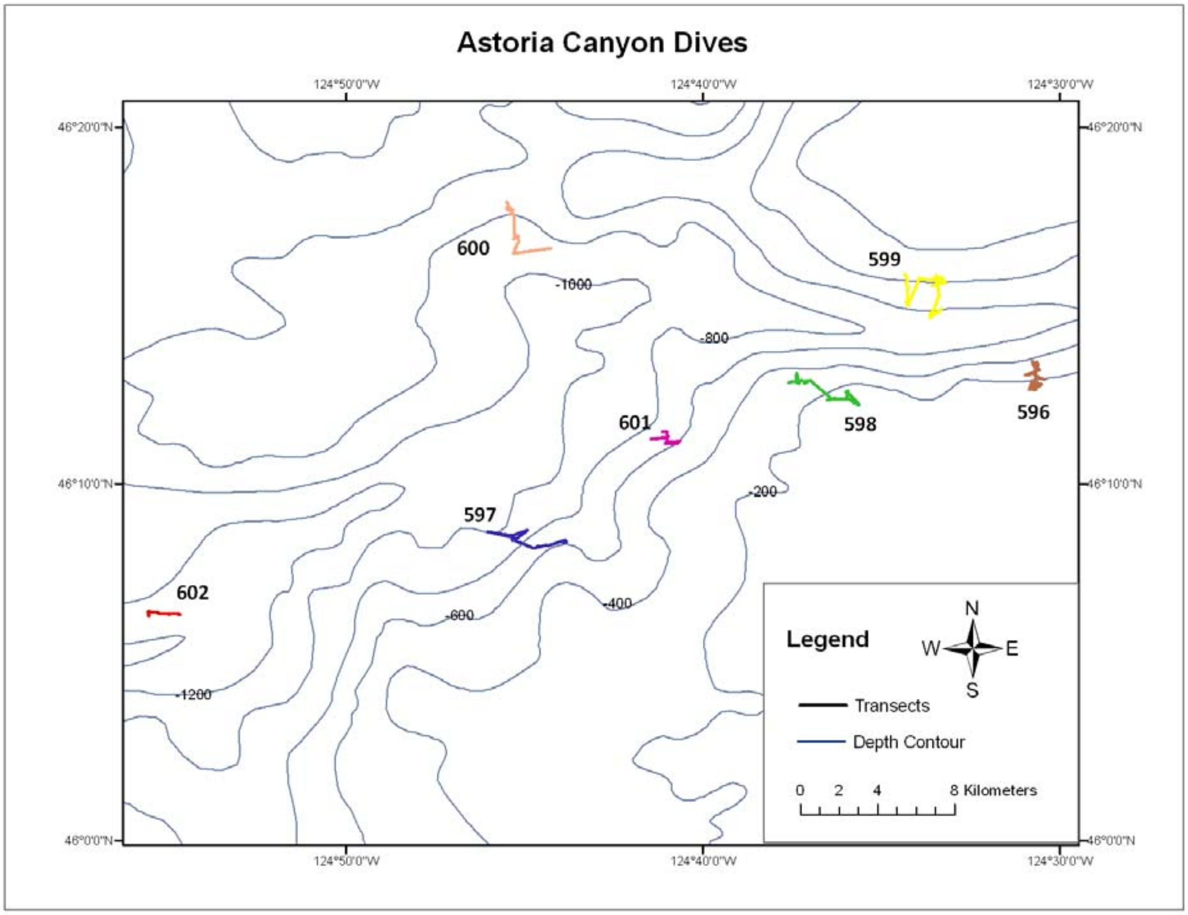
| Taxon name | Total Percent of Fish on Transect (Soft Substrata) | Total Percent of Fish Near Structure-forming Invertebrates | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Sponges | | | | | | | Corals | | | Sea Pens | | Anemones | |
| | | foliose | vase | barrel | mound | branching | upright | shelf | white deep sea corals | gorgonian corals | dog toy octocoral | white plumed sea pens | subselli-florae sea pens | white plumed anemones | swimming anemone |
| Lingcod | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cowcod | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Bocaccio | <1 | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Greenblotched | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Unknown *Zaniolepis* | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **1*** | 0 | 0 |

Appendix M. Mean distances and range (m) of selected fishes from nearest neighbor analysis.

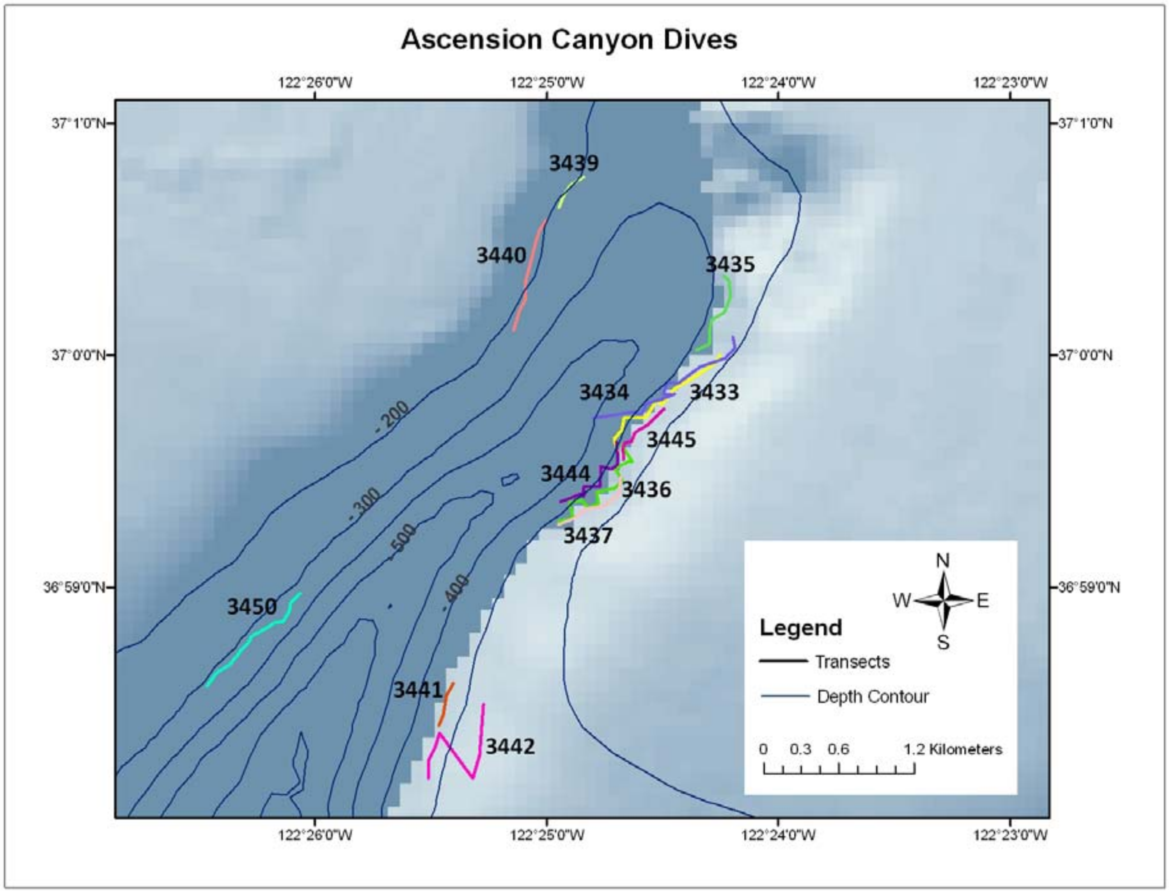
| | Ascension Canyon | | | | Carmel Canyon | | | |
|---|---|---|---|---|---|---|---|---|
| | | Distance (m) | | | | Distance (m) | | |
| | Taxa Name | Median | Average | Range | Taxa Name | Median | Average | Range |
| Hard Substratum Type | Greenblotched | <1 | 1 | <1–1 | Rougheye | <1 | <1 | <1 |
| | Red-banded | <1 | 1 | <1–2 | Swordspine | <1 | <1 | <1 |
| | Rosethorn | <1 | 1 | 0.2–5 | Greenspotted | <1 | <1 | 0.2–3 |
| | Unknown *Sebastomus* | <1 | 1 | 0.3–4.5 | Stripetail | <1 | <1 | 0.4–6 |
| | Darkblotched | <1 | 1 | 0.7–3 | Greenstriped | <1 | 0.8 | 0.4–1 |
| | Splitnosed | <1 | 3 | 0.3–14 | Shortspine thornyhead | <1 | 1 | <1–4 |
| | Stripetail | 0.6 | 0.8 | 0.4–1 | Unknown *Sebastes* | <1 | 1 | 0.1–15 |
| | Greenstriped | 0.8 | 0.8 | 0.7–1 | Rosy | <1 | 1 | 0.1–9 |
| | Greenspotted | 0.8 | <1 | 0.4–1 | Bank | <1 | 1 | 0.2–6 |
| | Yelloweye | 1 | 1 | 0.7–1 | Squarespot | <1 | 1 | 0.2–8 |
| | Shortspine thornyhead | 1 | 2 | 1–6 | Pygmy | <1 | 1 | 0.2–9 |
| | Bank | 1 | 3 | 0.9–6.5 | Darkblotched | <1 | 1 | 0.3–4 |
| | Unknown *Sebastes* | 1.5 | 3 | 0.3–10 | Unknown *Sebastomus* | <1 | 1 | 0.4–4 |
| | Bocaccio | 1.5 | 3 | 1–47 | Lingcod | <1 | 1 | 0.5–3 |
| | Cowcod | 2 | 2 | 2 | Splitnosed | <1 | 3 | 0.2–9 |
| | Vermillion | 3 | 3 | 3 | Yelloweye | <1 | 3 | 0.3–8 |
| | | | | | Half-banded | 0.2 | 0.6 | 0.2–2 |
| | | | | | Speckled | 0.7 | 0.7 | 0.2–2.8 |
| | | | | | Starry | 0.7 | 0.7 | 0.5–1 |
| | | | | | Sharphcin | 1 | 1 | 1 |
| | | | | | Bocaccio | 1 | 1 | 0.2–2 |
| | | | | | Blackeyed goby | 1 | 1 | 0.2–4 |
| | | | | | Rosethorn | 1 | 1 | 0.2–8 |
| | | | | | Greenblotched | 1 | 2 | 0.2–8 |
| | | | | | Cowcod | 1 | 2 | 0.8–8 |
| | Total | 2 | 2 | 0.4–47 | Total | <1 | 1 | 0.1–30 |
| Mixed Substratum Type | N/A | | | | Unknown *Sebastes* | <1 | <1 | <1 |
| | | | | | Lingcod | <1 | 1 | 0.3–2 |
| | | | | | Rosethorn | <1 | 1 | 0.3–5 |
| | | | | | Pygmy | 0.7 | 0.8 | 0.3–5 |
| | | | | | Rosy | 0.7 | 1.5 | 0.3–6 |
| | | | | | Squarespot | 2 | 1 | 0.3–6 |
| | | | | | Total | 0.4 | 1 | 0.3–6 |

Appendix M. (continued).

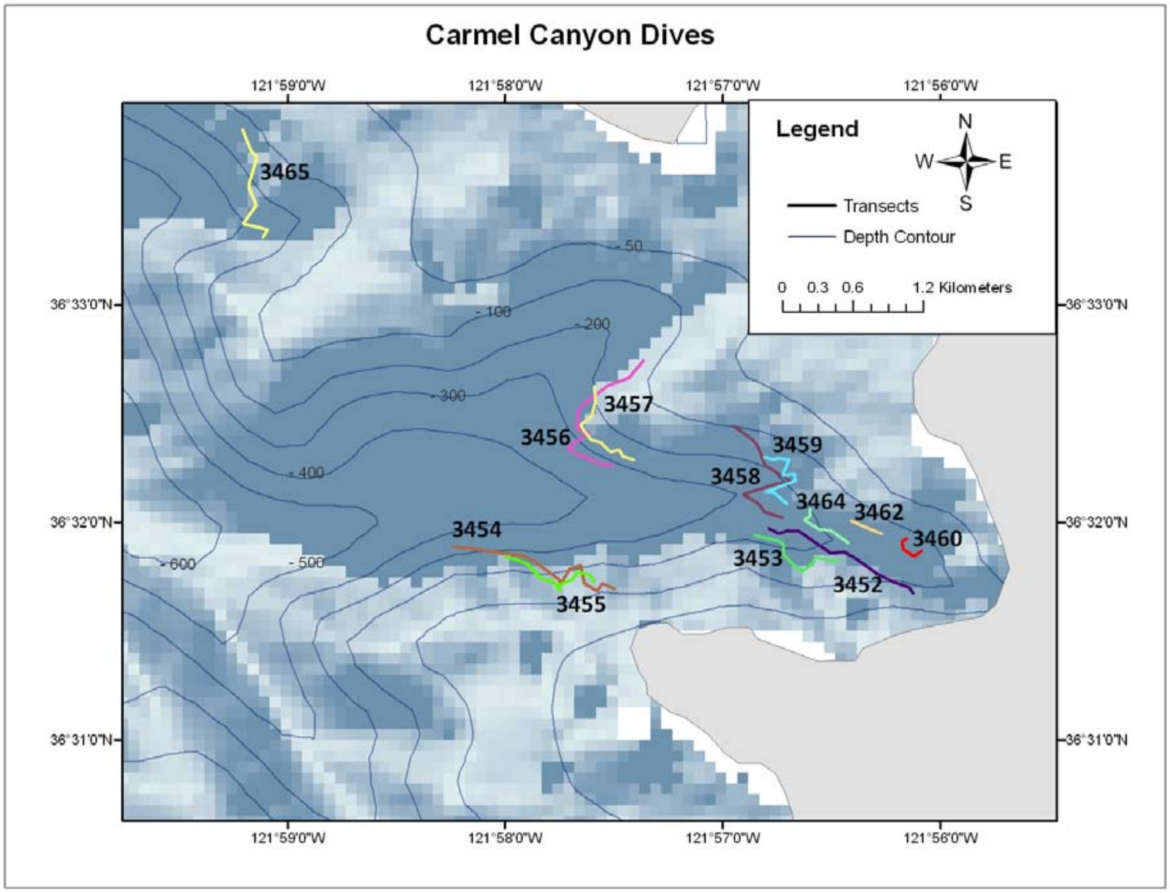
| Substratum Type | Ascension Canyon | | | | Carmel Canyon | | | |
|---|---|---|---|---|---|---|---|---|
| | | Distance (m) | | | | Distance (m) | | |
| | Taxa Name | Median | Average | Range | Taxa Name | Median | Average | Range |
| Soft | Yelloweye | <1 | <1 | <1 | Blackeyed goby | <1 | <1 | <1 |
| | Greenblotched | <1 | <1 | <1– 1 | Squarespot | <1 | <1 | <1 |
| | Darkblotched | <1 | <1 | 0.1–4 | Bocaccio | <1 | <1 | <1 |
| | Red-banded | <1 | <1 | 0.3–1 | Longspine combfish | <1 | <1 | <1 |
| | Greenspotted | <1 | <1 | 0.6–2 | Greenstriped | <1 | <1 | <1–1 |
| | Rosethorn | <1 | 1 | 0.1–6 | Unknown *Sebastomus* | <1 | <1 | 0.1–2 |
| | Unknown *Sebastes* | <1 | 1 | 0.3–3 | Greenspotted | <1 | 1 | 0.1–3 |
| | Splitnosed | <1 | 1 | 0.3–7 | Unknown *Sebastes* | <1 | 1 | 0.1–5 |
| | Unknown *Sebastomus* | <1 | 1 | 0.4–2 | Splitnosed | <1 | 1 | 0.1–5 |
| | Lingcod | 0.3 | 0.3 | 0.3 | Darkblotched | <1 | 1 | 0.1–7 |
| | Greenstriped | 0.4 | 0.6 | 0.2–1 | Bank | <1 | 1 | 0.2–10 |
| | Shortspine thornyhead | 1 | 3 | 0.3–12 | Rosethorn | <1 | 1 | 0.2–6 |
| | Sharphcin | 2 | 2 | 2 | Half-banded | <1 | 1 | 0.3–5 |
| | Stripetail | 2 | 2 | 0.9–4 | Stripetail | <1 | 2 | 0.2–30 |
| | Bank | 3 | 4 | 0.5–8 | Pygmy | <1 | 2 | 0.4–30 |
| | | | | | Flag | 0.2 | 0.2 | 0.2 |
| | | | | | Tiger | 0.7 | 0.7 | 0.7 |
| | | | | | Swordspine | 0.8 | 0.8 | 0.6–0.9 |
| | | | | | Zaniolepis | 1.5 | 2 | 0.9–3 |
| | | | | | Rosy | 2 | 1 | 0.6–3 |
| | | | | | Shortspine thornyhead | 3 | 5 | 0.3–14 |
| | Total | 0.5 | 2 | 0.1–12 | Total | 0.1 | 1 | 0.1–30 |



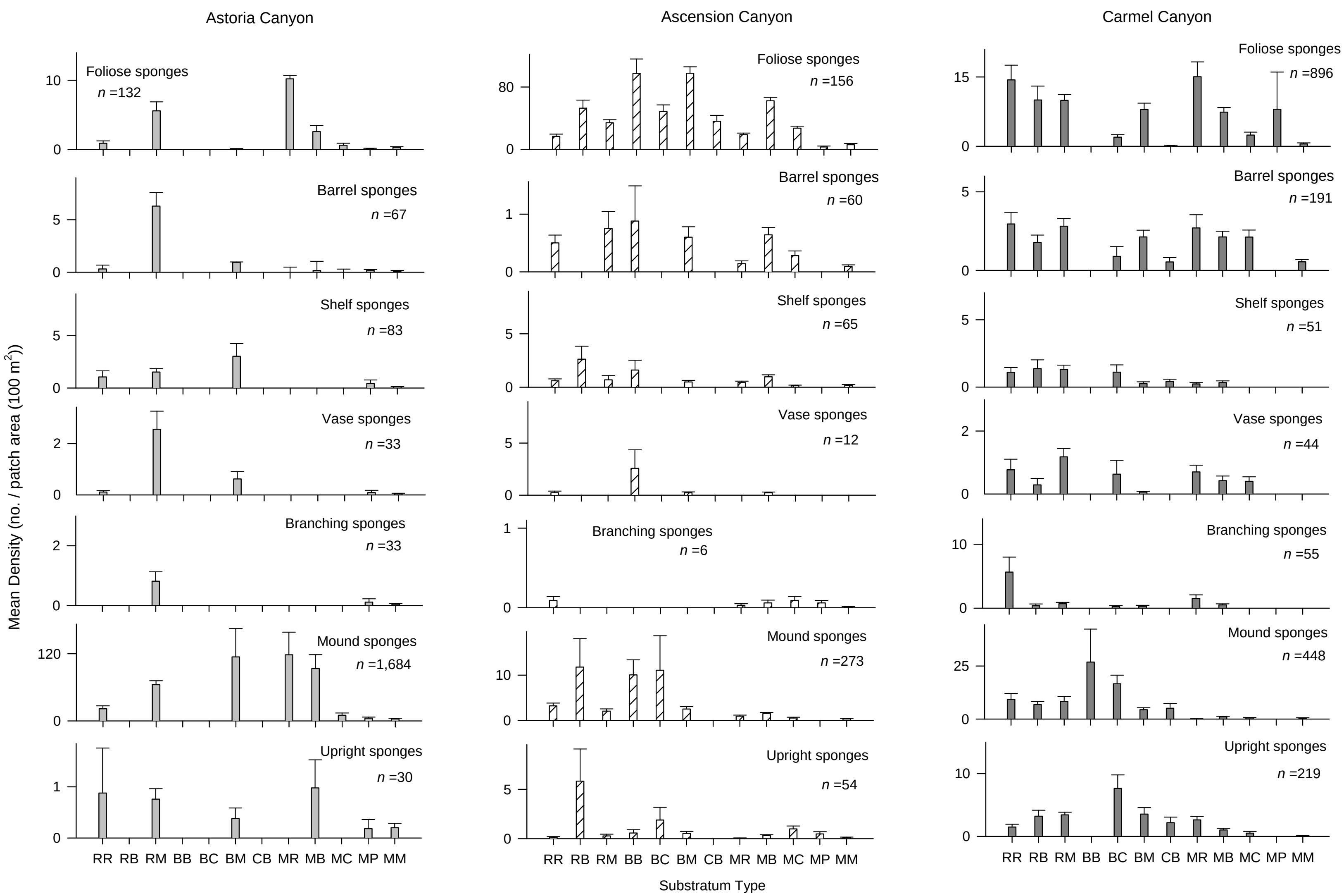

Appendix N. Astoria Canyon dives.



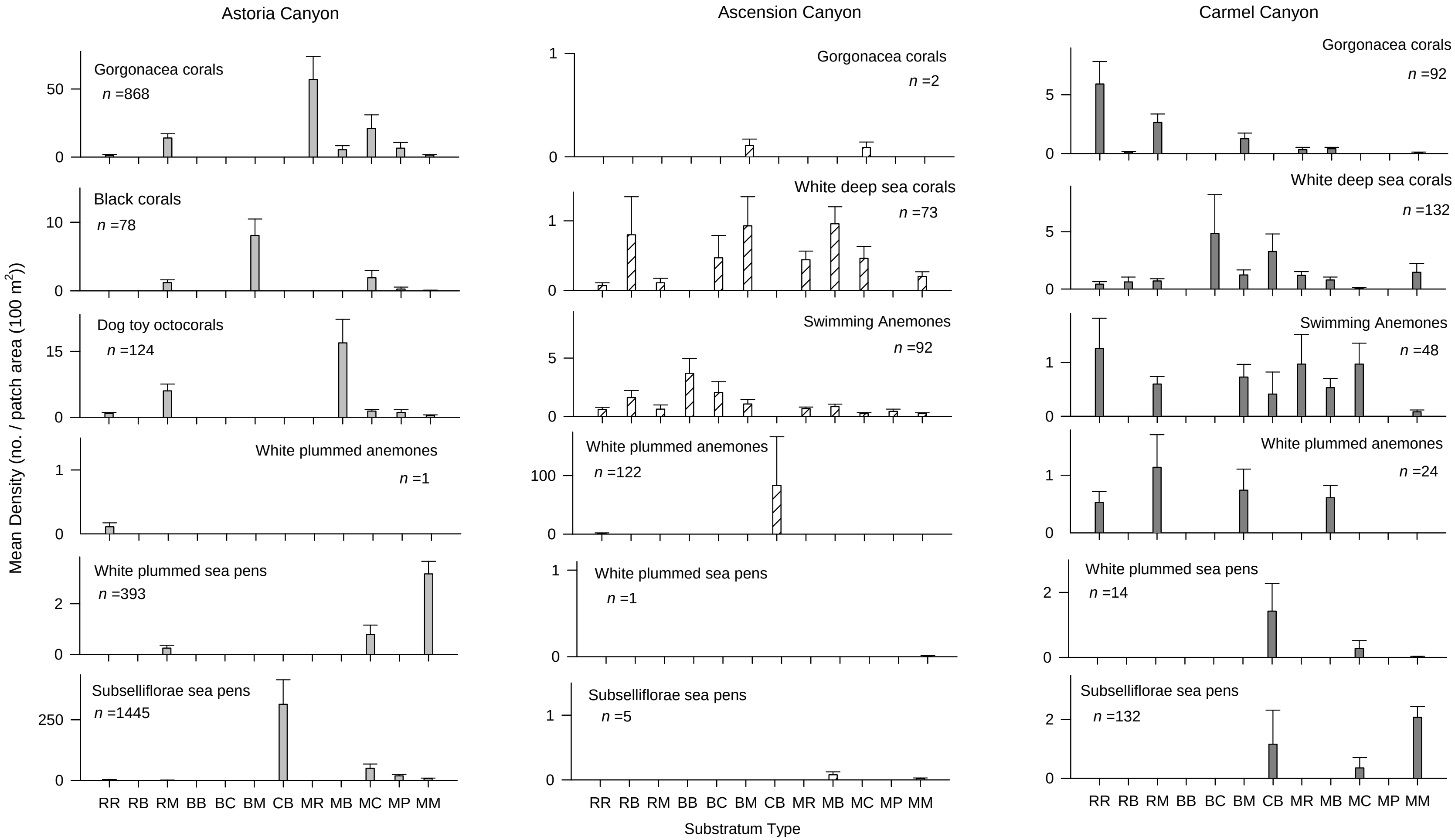

Appendix O. Ascension Canyon dives.




Appendix P. Carmel Canyon dives.




Appendix Q. Mean density (no. of individuals/ patch area (100 $m^2$)) of sponges distributed across substratum type.




Appendix R. Mean density (no. of individuals/ patch area (100 $m^2$)) of cnidarians distributed across substratum type.