Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge

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Abstract.—A multidisciplinary assessment of benthic rockfishes (genus *Sebastes*) and associated habitats in deep water was conducted in Soquel Submarine Canyon, Monterey Bay, California. Rock habitats at depths to 300 m were identified by using bathymetric and side-scan sonar imaging, verified by visual observations from a manned submersible, mapped and quantified. Species composition, abundance, size, and habitat specificity of fishes were determined by using a video camera and parallel laser system along transects made by a submersible.

We counted 6208 nonschooling fishes representing at least 52 species from 83 10-min strip transects that covered an estimated 33,754 m^2. Rockfishes represented 77% of the total number of individuals, and included a minimum of 24 species. Six distinct habitat guilds of fishes were manifest from habitat-based clustering analysis: small species were associated with mud and cobble substrata of low relief, and larger species of rockfishes were associated with high-relief structures such as vertical rock walls, ridges, and boulder fields. There was remarkable concordance between some of the guilds identified in Soquel Canyon and the results of other habitat-specific assessments of fishes along the west coast of the United States from central California to Alaska. These generalities are valuable in predicting community structure and evaluating changes to that structure, as well as in applying small-scale species-habitat relationships to broader-scale fishery resource surveys. Additionally, establishment of these groups is critical when incorporating the concept of essential fish habitat (EFH), and negative impacts to it, into the management of fisheries in relatively deep water, as required by the Sustainable Fisheries Act of 1996.

High numbers of large rockfishes (e.g. *Sebastes chlorostictus*, *S. levis*, *S. rosenblatti,* and *S. ruberrimus*) were locally associated with rock ledges, caves, and overhangs at sites having little or no evidence of fishing activity. Abundance and size of several species were lower at fished than at unfished sites. We suggest that rock outcrops of high relief interspersed with mud in deep water of narrow submarine canyons are less accessible to fishing activities and thereby can provide natural refuge for economically important fishes, as exemplified in Soquel Canyon.

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Rockfishes (*Sebastes* spp.) are quite speciose, dominate coastal benthic fish assemblages on the west coast of the United States, and are among the most valuable fisheries in California. They have been harvested commercially in California as early as 1875 (Phillips, 1957). About 85% of the 57 or more rockfish species in California have some economic value, and landings have increased dramatically over the last 40 years (Lea, 1992). During the past decade (1988–97), commercial fishermen have landed an average of nearly 10,000 metric tons of rockfish at California ports per year, with an average exvessel value of $11.4 million per year (Thomson, 1999). During this period, recreational anglers on commercial passenger fishing vessels caught an additional 1.8 million individual rockfish per year (Thomson, 1999), at a value that far exceeds that of the commercial catch.

Many species of rockfishes are slow-growing, long-lived, and relatively old at maturity, making them particularly vulnerable to overfishing. Historically, rockfish landings have been especially high in Monterey (Phillips, 1939), and there are recent indications that numbers and sizes are decreasing for some species (Pearson and Ralston, 1990; Mason, 1995, 1998; Ralston, 1998). As with many coastal fisheries, the Monterey fleets have expanded their range to deeper and more remote areas as local stocks have become depleted in shallow water (Deimling and Liss, 1994; Karpov et al., 1995; Mason, 1995).

As increased fishing effort is applied to populations in deep coastal waters, it becomes critical to identify and protect areas of natural refuge for larger, older individuals of valuable rockfish species. There is little information on the distribution, abundance, and habitat characteristics of mature rockfishes associated with deep-water benthic marine habitats off California. This type of habitat is below scuba depths (<30 m), and the rocky heterogeneous substrata inhabited by many rockfish species prohibit accurate estimates of fish abundance with conventional trawl surveys. Diversity, quality, and extent of habitat likely are among the most significant environmental determinants of distribution, abundance, and species richness of adult rockfishes (Larson, 1980; Richards, 1986; Pearcy et al., 1989; Carr, 1991; Stein et al., 1992). Characterizing and quantifying elements of suitable habitat, such as substratum type, texture, and relief, are therefore critical for evaluating the effectiveness of refugia, both natural and designated protected areas, to maintain regional marine resources.

Eight submarine canyons cut into the continental shelf off central California, placing deep-water habitats in close proximity to shore. We hypothesized that isolated rock outcrops in deep water along the steep walls of these canyons could serve as natural harvest refugia and allow certain rockfish species locally to attain large sizes and high abundances. Subsequent distribution of offspring from these mature fishes could help maintain viable populations and species diversity in adjacent areas of greater fishing activity.

Our general goal in this study was to characterize rockfish assemblages and their relationship to specific benthic habitats within submarine canyons by combining geophysical and *in situ* submersible surveys. Because temperate benthic habitats are often defined by geologic attributes, geophysical techniques are critical in determining habitat structure, depth, and lithology.

Within our general goal, this study had four specific objectives. Our first objective was to characterize the geomorphology of our study site in Soquel Canyon using bathymetric mapping and side-scan sonar imaging (i.e. sonographs) to classify the substrata and to locate rock outcrops on a spatial scale of 100s of meters to kilometers. Our second objective was to map and quantify the amount of exposed hard substrata at depths suitable to rockfishes within our study site. Third, using a manned submersible, we set out to verify our interpretations of the remotely sensed images of habitat on a smaller scale (i.e. 1 meter to 10s of meters) and determine frequency of occurrence, distribution and type of habitat that support assemblages of adult benthic rockfishes in Soquel Canyon. Our fourth objective was to estimate and compare species composition, abundance, size, and diversity of fishes among habitat types, depth zones, and locations that have been subject to various amounts of fishing activity within the canyon.

Materials and methods

Study site

Soquel Canyon (ca. 36°49′N, 121°59′W) is a submarine canyon of inactive sediment that cuts into the continental shelf in Monterey Bay nine miles south of Santa Cruz, at a water depth of 80 m. This canyon trends southwest for 10 km, at which point it intersects the larger Monterey Canyon at a depth of 915 m (Fig. 1A). Soquel Canyon is eroded from the generally flat-lying beds of the Pliocene Purisima Formation, a shallow-water marine deposit comprising interlayers of sandstone, mudstone, and shell hash (coquina). Previous undercutting of the canyon walls has caused extensive landslides and slumping; resultant rock exposures were the targets of our survey of rockfishes and their associated habitats.

Our study area covered about 17 km^2 of the headward part of the canyon, between 80 and 360 m water depth. This represents about two-thirds (6.7 km) of the length of the canyon's axis; at 6.7 km along the axis, the canyon is 3.5 km wide and 650 m deep.

Geophysical surveys

Side-scan sonar is a suitable method for distinguishing blocks of hard substrata from surrounding soft sediment by differences in intensity of reflected sound (Able et al., 1987; Greene et al., 1995; Yoklavich et al., 1997). Our sonographs of seafloor morphology resemble a black and white photographic negative. Topographic features such as ledges, vertical walls, and boulders produce dark and light images on the records, depending on the orientation and hardness of the feature. A strong signal or reflector (dark) is received from the side of a relatively hard feature facing the transducer, whereas a weak signal or shadow (light) is received from the side sloping away from the transducer.

We conducted a side scan sonar survey along 110 km of track lines using a 100 kHz acoustic signal with a swath width of 600 m (300 m per side). The sonographs along each track line were positioned precisely with navigational data from a differential global positioning system (GPS) to form a mosaic of rock type and texture within the canyon. Because of steep relief, only one side of the transducer received usable signals and 200% coverage was necessary to produce a complete mosaic.

We used the mosaic to quantify the amount of hard substrata at depths suitable to rockfishes. Our interpretations of the sonographs were verified by direct observations made by marine geologists (HGG and DS) during nine dives in the *Delta* submersible. Type, relief, and size and depth range of features were described; these field descriptions assisted the marine biologists in planning dives at each site and in assessment of habitat after the cruise.

We conducted a bathymetric survey of Soquel Canyon using a 3.5-kHz precision depth recorder integrated with Loran and GPS navigational data. The resultant high-resolution map (20-m intervals) was used to identify areas of high relief and potential slumps.

Fish and habitat surveys

We used the *Delta* submersible to assess benthic fish assemblages and associated habitat in Soquel Canyon in August 1992 and October 1993. The *Delta* is a small (4.75-m) submersible, accommodates one scientific observer and a pilot, has a maximum operating depth of 365 m, and a cruising speed of 1.5 knots. An acoustic track-point

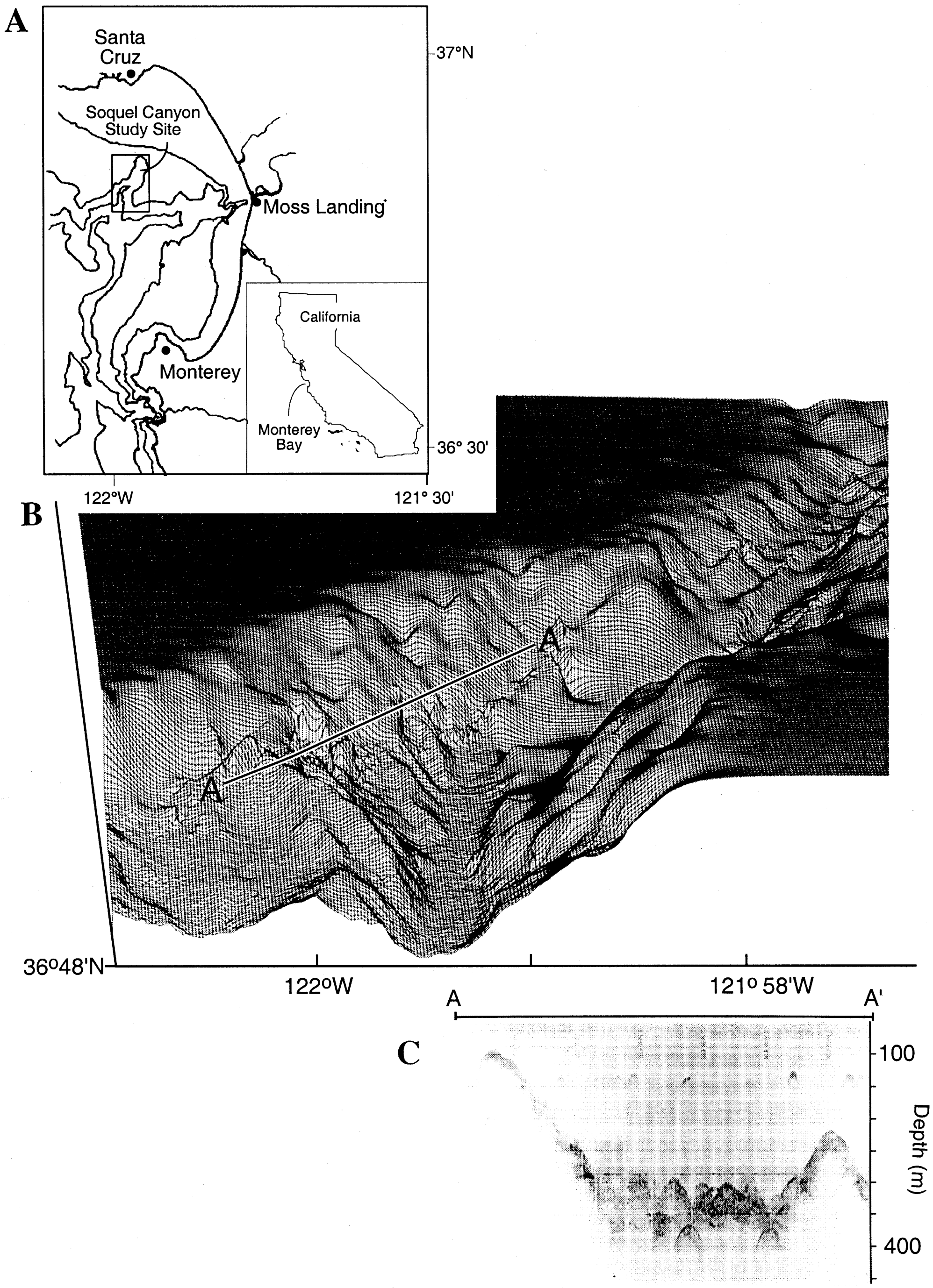


Figure 1

(**A**) Study area in Soquel Canyon, the northernmost tributary to the Monterey Submarine Canyon System. (**B**) A physiographic map of Soquel Canyon, produced from 3.5-kHz echo-sounding data. Transect A–A' is at the location of the seafloor profile (**C**), and displays the hummocky nature of slump deposits on the west wall of the Canyon.

system and differential GPS were used on board the support vessel to record the underwater location of the submersible. All dives were made during daylight to avoid potential bias due to diel activity patterns of some species (Hixon[1]; Yoklavich, pers. obs.)

To quantify fish abundance and habitat use, strip transects of 10-min duration were conducted 1–2 m off the

[1] Hixon, M. 1992. Personal commun. Department of Zoology, Oregon State University, Corvallis, OR 97331-2914.

bottom at 0.4–0.9 knots. Transects were purposely of short duration to maintain constant depth within the rock habitat at each station. Each transect was documented continuously with a high 8-mm video camera and associated lights that were externally mounted on the starboard side of the submersible. The scientific observer verbally annotated each videotape, identifying, counting, and estimating size of all fishes in front of the starboard viewing port. A hand-held dive sonar was aimed at objects (e.g. large fish and boulders) along the transects from inside the submersible to estimate distance from the observer to the object; this procedure helped us to estimate the width of the transect. After each dive, divers transcribed observations on fishes and habitat from video tapes into a computerized database on board the support vessel.

Two parallel lasers were mounted on either side of the external video camera at the fixed distance of 39.5 or 20.0 cm apart, in association with different laser systems each year. The laser spots were projected onto the seafloor habitats. They were visible to the observer, recorded onto the video tape, and were critical in accurately estimating the size of fishes, distance traveled along a transect and area of habitat patches. We made measurements by comparing the size of a fish or habitat feature to the known spacing of the two bright laser spots when the object was perpendicular to the camera and lasers (Tusting and Davis, 1993). We estimated the length of each transect, independent of submersible speed and bottom currents and type, by counting the number of laser-spot intervals as they moved along the substrata in the video transect (much like using a yardstick, end-over-end along the transect).

Microhabitat of each fish within the transect was characterized from the video tapes. Various combinations of substratum type, including mud, pebble, cobble, boulders, and rock ridge (see Greene et al., 1999, for definitions), were categorized according to primary (at least 50% of the area viewed) and secondary (>20% of the area viewed) microhabitat (conforming to Stein et al., 1992). Relief was categorized as flat (0–5°), low (5–30°), and high (>30°). Each surface area of uniform habitat (i.e. a patch) along the quantitative transect was measured to the nearest 0.1 m^2. Species-specific abundance was standardized per area of associated habitat patch. The habitat patch was used as our sample unit.

Data analyses

Similarity of assemblages of nonschooling fishes among the different combinations of substrata was evaluated with cluster analysis on the basis of abundance of each species standardized by area of associated bottom type in each patch. Only species representing ≥1% of the total abundance in each bottom type category and only bottom types representing ≥1% of the total area surveyed were used in this analysis. Only nonschooling (i.e. nonpolarized aggregations or solitary individuals) benthic fishes were included in our analyses because schooling fishes commonly were more abundant in midwater above our field of view and therefore could not be accurately enumerated. Clustering was performed with the average linkage method and with Euclidean distance as a measure of dissimilarity (SYSTAT, 1992). Dissimilarity among clusters ≥50% of the maximum overall distance was considered a major division and used to define distinct habitat guilds of fishes (*sensu* Root, 1967).

Further analyses were focused on nonschooling fish species that dominated the rock habitat guild, as defined by the cluster analysis. These are some of the species important in commercial and recreational catches (Weinberg, 1994; Mason, 1995, 1998). We used the incidence of fishing gear and associated debris, observed on the seafloor during the quantitative fish transects, as a relative index of fishing activity throughout our study area. Statistical differences in abundance (number of fish per 100 m^2 of habitat patch) of those species in the rock habitat guild were analyzed among five sites of varying fishing activity by using analysis of variance (ANOVA) with equal sample variances and otherwise by resampling statistics (Bruce et al., 1995). We used Cochran's test for homogeneity of variance (Winer, 1971).

Differences in size of selected dominant species were tested among two arbitrarily chosen 100-m depth categories (i.e. shallow [75–175 m] and deep [176–275 m]) and the five sites were tested by using two-factor ANOVA (with homogeneity of sample variances) where appropriate.

Overall species diversity was calculated as

$$H' = \sum_{i=1}^{s} [p_i][\ln p_i],$$

where s = number of species; and
p_i = proportional abundance of species i.

Richness (number of species), and evenness ($J' = H'/H'_{MAX}$), as well as species diversity, were evaluated for all habitat types (see Krebs, 1989) and then among sites just within the rock habitat guild in shallow and deep water. Sufficiency in the number of samples necessary to reliably characterize overall diversity for each habitat type was examined by plotting cumulative numbers of species against the sample unit (both for number of patches and area of habitat surveyed). These plots indicated that the number of samples was sufficient to yield a reliable estimate of diversity for comparisons among all habitats and for comparisons among sites in shallow and deep rock habitat (i.e. the number of samples evaluated for diversity always surpassed the number comprising 95% of the species; see data on Figs. 8 and 9).

Results

Geophysical mapping of habitats

A physiographic representation of the relatively high-resolution bathymetric data (Fig. 1B; production assisted by the U.S. Geological Survey, Menlo Park, CA) helped us to visualize canyon morphology, to identify areas of high relief and potential slumping, and to select submersible dive sites for fish and habitat surveys. The bathymetry indicated that Soquel Canyon is steeper and more rugged than previously interpreted from NOAA's Seabeam data. From the 3.5-kHz bottom profiles we identified large slumps along both walls and in the axis of the canyon. These areas had a hummocky surface with little or no sediment cover and were bounded by sharp relief on either side (e.g. Fig. 1C); these characteristics indicated likely rockfish habitat.

Five study sites were defined (Fig. 2) on the basis of a series of side-scan images identified along the canyon walls. These images were interpreted as rock outcrops representing approximately 35 ha of the total area surveyed in Soquel Canyon. Area of rock outcrop in the five study sites ranged from 1.4 ha of isolated rocks in about 200 m water depth at site 5 to 19.6 ha of extensive rock in 90–350 m water depth at site 3. We considered these estimates to accurately represent the amount of exposed outcroppings within our study area.

From submersible observations we verified our interpretation of these reflectors as well-bedded rock outcrops of various resistance, lithologies, and bottom morphology (e.g., Fig. 3, A and B). Crescent-shaped slump scarps were imaged along the upper walls of the canyon, and extensive rockfalls comprising large (meters in diameter) angular to sub-rounded (having rounded corners but not spherical) blocks and smaller boulders (0.25–1.0 m diameter) were concentrated at the base and in the axis. Well-layered, friable sedimentary rocks were differentially eroded into overhangs (>90°), crevices, and caves. These rocks occurred as isolated outcrops (Fig. 3A), and as more extensive rock exposures (Fig. 3C) interspersed with soft mud along very steep walls from at least 150 to 330 m water depth.

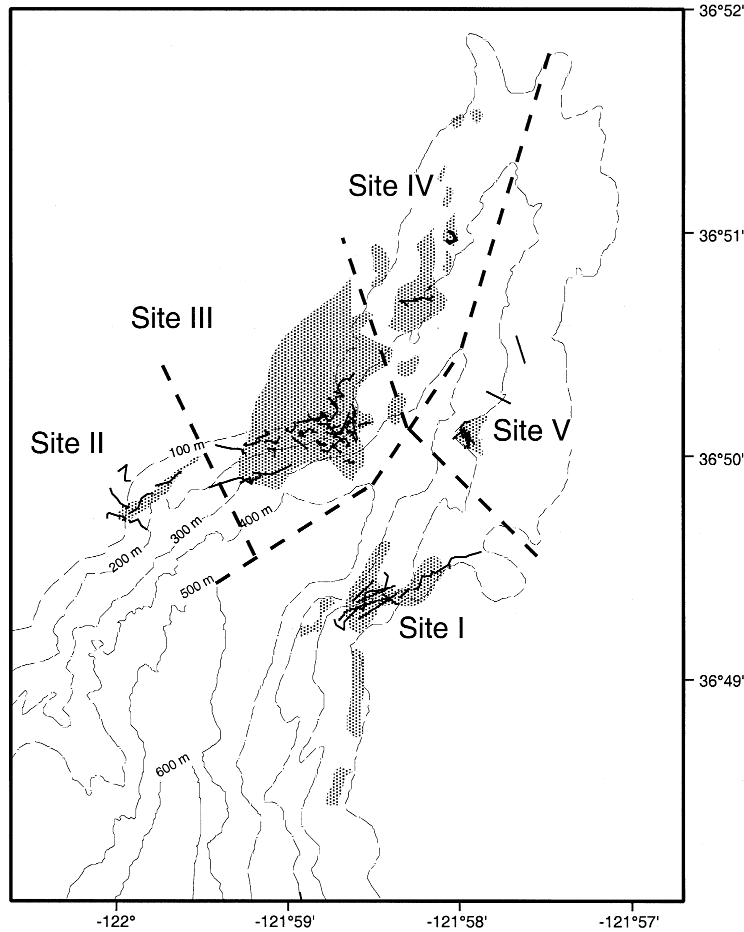


Figure 2

Schematic map constructed from interpretations of side-scan sonographs of rock outcrops (stippled areas) in Soquel Canyon. Submersible track lines during quantitative transects are mapped (lines), and the five main study sites are labeled.

Fish and habitat associations

Thirty-three submersible dives were made at five sites to assess rockfish assemblages and habitat associations in Soquel Canyon. We counted 6208 nonschooling fishes, representing at least 52 species (see Table 1 for both scientific and common names), from 83 10-min strip transects that covered an estimated 33,754 m^2. Rockfishes represented 77% of the total number of individuals, and included a minimum of 24 species. The 20 most abundant taxa (90% of total abundance) included 4540 individual rockfishes representing at least 12 species. Nonrockfish species were represented primarily by six species, which comprised 17.2% of the total abundance: *Microstomus pacificus*, *Ophiodon elongatus*, *Sebastolobus alascanus*, *Eptatretus stouti*, *Merluccius productus*, and an unidentified species (or possibly a complex of species) in the family Agonidae (most likely *Xeneretmus* spp.).

Major rockfish habitat types in Soquel Canyon included vertical cliffs with joints, fractures, and overhangs, small and large ledges, talus slopes, cobble, and boulder fields of exposed sandstone and mudstone interspersed with soft mud. Most rockfishes of all sizes were associated with some structure, including invertebrates such as crinoids, sea anemones and sponges, debris, and simple shallow depressions in the mud.

Cluster analysis (Fig. 4), which grouped standardized abundance of each fish species (number per 100 m^2) by bottom type, resulted in six habitat guilds. Most distinct were guild I, having small species found on uniformly mud bottom of flat or low relief, dominated by *S. saxicola* (42%) and to a lesser degree by *M. pacificus*, Agonidae, and *S. alascanus*, and guild VI, a rock-boulder habitat of low-to-high relief largely at 75–175 m depth, dominated by *S. wilsoni* (42%), and with less representation by *S. paucispinis*, *S. pinniger*, and *S. chlorostictus*.

The remaining four habitat guilds (guilds II, III, IV, and V; Fig. 4) were grouped two each into two clusters at Euclidian distances 0.058 and 0.063. Guilds II and III were characterized by combinations of mud and large-grain cobbles and pebbles that were of mostly flat or low relief (72% occurrence). These assemblages were relatively diverse, evenly distributed (see results of diversity analysis that follows), and included mostly small species (i.e. *S. semicinctus*, *S. wilsoni*, and *S. elongatus*) and small members of a large species (*S. chlorostictus*). Most (88–95%) of habitat guild II occurred at shallow depth (75–175 m); about one-half of guild III occurred in water <175 m. Guilds IV and V represented habitats of large structure, high relief (78% occurrence), and both shallow and deep (>175 m) water. Although they both had similar top-ranked species, guild IV (boulder-mud) was much less diverse and was dominated by a single species (*S. helvomaculatus*). Economically valuable rockfish species made up most (52–77%) of guild V (rock habitat). The rock habitat guild, in particular, contained high numbers of large species up to 1 m in total length, such as *S. levis* (12% of total fish abundance in this habitat) and *S. ruberrimus* (5% total abundance). These fishes were closely associated with ledges, caves, crevices, and overhangs.

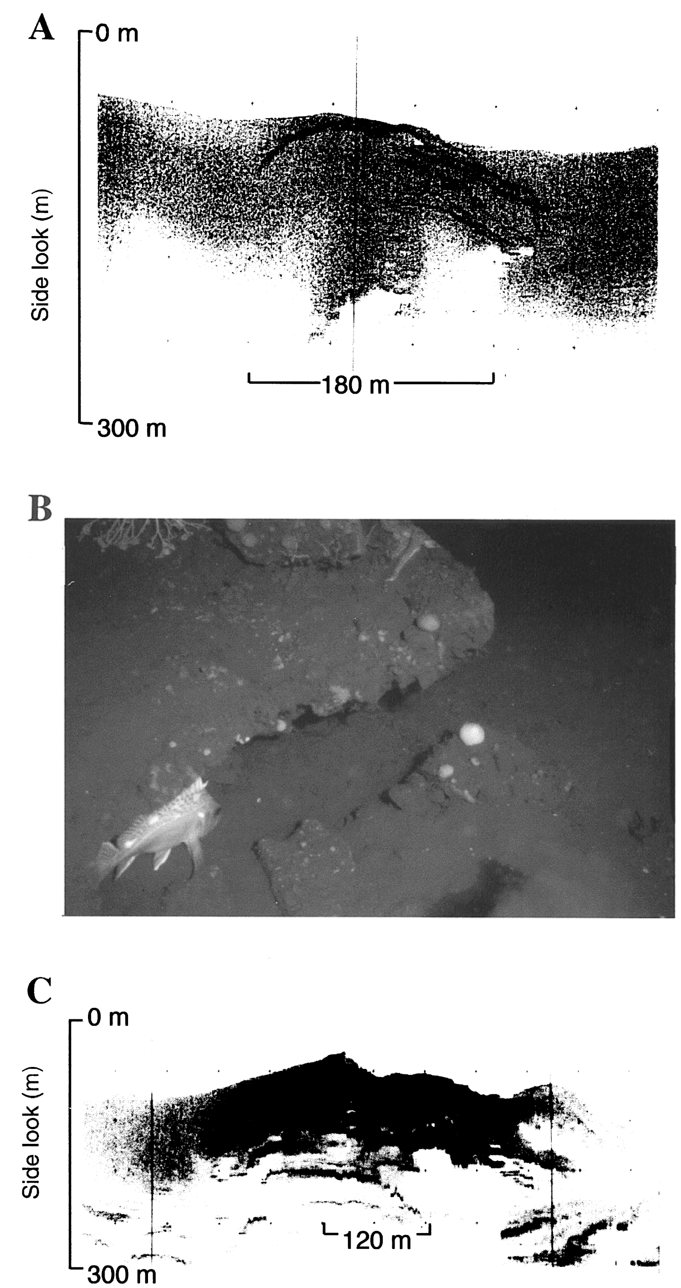


Figure 3

(**A**) Side-scan sonograph of isolated rock outcrop on steep wall of Soquel Canyon. Strong acoustic reflectors (dark areas) are from exposed bedding faces, white areas are shadows behind faces, and gray areas are nonreflective mud. (**B**) These eroded mudstone beds comprise habitat for benthic fishes, such as this adult greenspotted rockfish (*Sebastes chlorostictus*). (**C**) Side-scan sonograph of steep, well-bedded rock walls on southeast side of canyon from 150 to 330 m.

Fishes and habitat by site

In general, our study area in Soquel Canyon comprised five sites of exposed rock ridge, boulder, cobble, pebble, and mud bottom types (Fig. 5). From the mosaic of side scan sonographs, total area of outcrops ranged from 1.4 ha (site 5) to 19.6 ha (site 3), and the sampling effort (i.e. number of dives, transects) in these sites tended to vary accordingly. We quantitatively surveyed fish and habitat in 1025 sample patches (average area of a habitat patch was 34.0 m^2; SE=1.9 m^2), representing from 1285 to 13,626 m^2 per site. From analysis of 83 transects, 74–94% of the bottom types at these sites were characterized by mud, rock ridge, and combinations of both. Not surprisingly, nearly 50% of our survey was in areas of high relief, and almost all (97%) rock ridge was high relief. Mud habitats were largely (78%) of flat and low relief.

Site 1, located on the east canyon wall at a water depth from 98 to 305 m, was characterized as rock outcrop with moderate vertical fracturing, stepped rock ridges of 1–6 m height (habitat guild V), mud-cobble and mud-boulder fields (habitat guilds II and III), and mud terraces (habitat guild I). Directly opposite on the west wall, site 2 included a series of rock ledges, mud terraces, and vertical walls extending from 263 to 148 m depth; this site is heavily fished (see later criteria). Site 3 comprised small ledges interspersed with mud, boulder, cobble, and pebble slopes of low relief at 94–150 m, high-relief rock ledges with fractures cutting the bedding planes and massive vertical mudstone walls (150–250 m), and scattered boulder-mud fields at the base of the wall. Sites 4 and 5 were largely isolated outcrops of rock ridges surrounded by fields of mud at 152–226 m depth.

Rockfishes of various species ranked first in abundance at all of the five study sites (Table 1); over all habitat types and depth, at least three of the top five species were rockfishes (4–5 of 5 at most sites). Average abundance was highest at site 5 (42.4 fish per 100 m^2), 96% of which comprised economically valuable species (e.g. in rank order of abundance, *S. pau-*

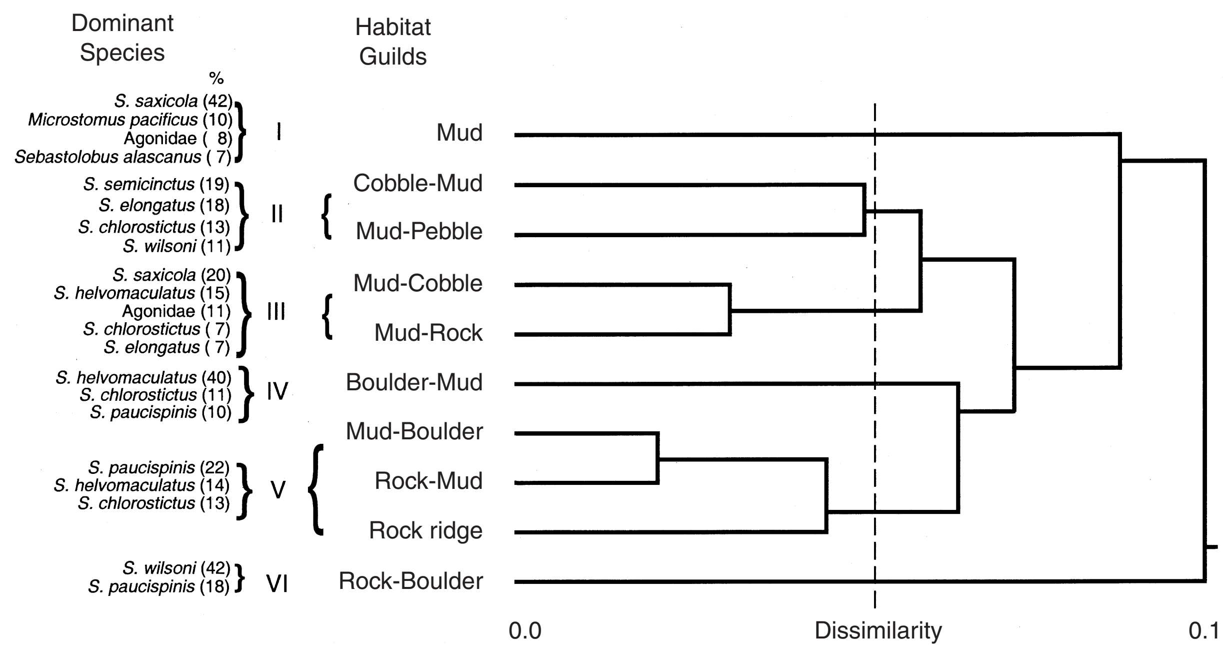


Figure 4

Cluster dendogram that groups standardized abundance (number per 100 m^2) of nonschooling benthic fish species in Soquel Canyon, based on associated type of bottom substrata. Dominant species (percent relative abundance in parentheses) of the six main habitat guilds are indicated. See Figure 8 for number of habitat patches sampled in each habitat.

cispinis, *O. elongatus, S. levis, S. rosenblatti, S. chlorostictus, S. ruberrimus*). These sedentary fishes were primarily sheltered under ledges, in crevices, and among large sea anemones (*Metridium giganteum*) on this isolated rock outcrop.

One objective of our study was to compare species composition, abundance, size, and diversity of fishes among sites receiving varying amounts of fishing pressure within the canyon. Seventy-five lines (polypropylene and monofilament; n=67) and cables (n=8) were observed on 83 transects during 13.5 h; no mesh nets, pots, or trawl tracks were found. Eighty-five percent of these sightings occurred at site 2, with 26.7 observations of gear made per hour of survey (or 0.9 sightings per 100 m^2). Observations of 1.5 and 0.7 per hour were made at sites 3 and 1, respectively. No evidence of fishing gear or activity was found at sites 4 and 5. These observations are supported by California Department of Fish and Game (CDFG) records of site-specific activities of commercial passenger fishing vessels (Reilly[2]).

From the cluster analysis, economically important rockfishes are largely represented by the rock habitat guild (V). After limiting statistical comparisons among sites to those species occurring on mud-boulder, rock-mud, and rock ridge bottom types (i.e. habitat guild V), we found abundance of each of the top eight species in this guild (Fig. 6) varied significantly among sites (ANOVA or randomization test; P<0.01). Large solitary and sedentary species, such as *S. chlorostictus, S. ruberrimus, and S. levis*, were most abundant at sites 1, 3, 4, and 5, which received minimal to no fishing pressure. Abundances of these three species were statistically less at site 2, the area of highest fishing activity.

Sebastes paucispinis, one of the most important species in commercial and recreational fisheries of Monterey Bay, occurred in high numbers at all sites but was significantly more abundant at site 5 (Fig. 6; randomization test, P<0.01). Although we limited our study to nonschooling individuals, *S. paucispinis* can be semipelagic and we sometimes encountered this species in loose groups of 50 or more fishes above rock outcrops. These groups were not included in our analysis but indicate that this species is more active and broad ranging than the solitary benthic rockfishes.

Interestingly, the most abundant species at the site most heavily fished (site 2) was *S. helvomaculatus*, a relatively small species and historically of minor interest to either commercial or recreational fisheries. This species also was significantly more abundant at this site than at any of the other four sites (Fig. 6; resampling test, P<0.01). *Sebastes crameri* and *S. rufus*, relatively important rockfish species in the commercial trawl fishery but rarely taken by hook and line, were abundant only at site 2 (ranking second and fifth, respectively). *Sebastes elongatus*, a relatively small species that was most abundant in the cobble-mud guild, was moderately abundant in the rock guild but only at sites 1–3.

Size of most of these species differed by site and depth category (shallow=75–174 m; deep=175–275 m; Fig. 7). Significantly smaller individuals of *S. chlorostictus*, *S. helvomaculatus*, *S. elongatus*, and *S. paucispinis* occurred

[2] Reilly, P. 1997. Personal commun. CDFG, 20 Lower Ragsdale Dr., Monterey, CA 93940.

Table 1

Abundance (mean number/100 m^2), total number and percentage, and mean total length of nonschooling fishes counted during 83 transects at five sites in Soquel Canyon. SE = standard error. Species names follow Robins et al. (1991).

		Site 1		Site 2		Site 3		Site 4		Site 5		Total		Length (cm)	
Species	Common name	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	No.	%	Mean	SE
Sebastes saxicola[1]	stripetail rockfish	3.6	0.6	2.7	0.7	3.7	0.7	0.2	0.2	0.3	0.2	1005	16.2	16.4	0.2
Sebastes paucispinis	bocaccio	2.5	0.8	2.5	0.6	0.7	0.3	1.9	1.2	18.2	5.6	712	11.5	55.3	0.5
Sebastes helvomaculatus	rosethorn rockfish	2.9	0.5	5.5	1.0	1.3	0.3	<0.1	<0.1	0.3	0.2	542	8.7	22.1	0.3
Sebastes chlorostictus	greenspotted rockfish	2.0	0.4	0.6	0.2	5.6	0.9	4.0	1.2	2.3	0.6	426	6.9	32.5	0.6
Sebastes spp	unidentified rockfishes	0.7	0.2	3.6	0.6	1.4	0.6	1.0	0.6	0.3	0.1	349	5.6	21.1	0.8
Agonidae	poachers	1.5	0.4	1.2	0.2	2.4	0.4	0.4	0.2	0.1	0.1	324	5.2	16.8	0.3
Sebastes elongatus	greenstriped rockfish	0.9	0.3	1.9	0.5	1.4	0.2	<0.1	<0.1	<0.1	<0.1	289	4.7	25.7	0.5
Sebastes crameri	darkblotched rockfish	—	—	4.7	0.8	<0.1	<0.1	0.4	0.4	—	—	259	4.2	21.3	0.3
Sebastes semicinctus	halfbanded rockfish	1.1	0.5	—	—	0.8	0.2	—	—	—	—	230	3.7	12.7	0.2
Sebastes levis	cowcod	0.6	0.4	0.1	0.1	0.2	0.1	0.4	0.4	5.1	1.1	202	3.3	58.6	1.1
Sebastes wilsoni	pygmy rockfish	1.9	1.4	0.2	0.1	0.7	0.3	—	—	—	—	201	3.2	16.2	0.3
Microstomus pacificus	Dover sole	0.7	0.3	0.1	<0.1	0.6	0.2	0.1	<0.1	0.3	0.2	199	3.2	24.5	0.7
Ophiodon elongatus	lingcod	<0.1	<0.1	0.3	0.1	1.4	0.4	0.3	0.2	6.4	1.8	171	2.8	57.8	1.5
Sebastolobus alascanus	shortspine thornyhead	0.6	0.3	<0.1	<0.1	1.3	0.3	—	—	<0.1	<0.1	171	2.8	19.8	0.6
Eptatretus stouti	Pacific hagfish	0.5	0.2	<0.1	<0.1	0.8	0.3	0.2	0.2	0.4	0.2	115	1.9	23.6	0.7
Sebastes ruberrimus	yelloweye rockfish	0.3	0.1	0.1	0.1	0.3	0.1	0.5	0.5	1.7	0.6	104	1.7	56.1	1.9
Merluccius productus	Pacific hake	0.2	0.1	0.1	0.1	0.1	<0.1	1.7	1.0	0.1	0.1	83	1.3	18.4	0.6
Sebastomus complex[2]	unidentified rockfishes	<0.1	<0.1	0.4	0.1	0.2	0.1	0.1	0.1	—	—	83	1.3	24.8	1.5
Sebastes pinniger	canary rockfish	—	—	—	—	0.5	0.2	—	—	—	—	73	1.2	37.5	0.5
Sebastes rosenblatti	greenblotched rockfish	0.1	<0.1	0.3	0.1	0.1	<0.1	0.9	0.3	5.0	3.3	65	1.0	42.7	1.4
Pisces	unidentified fish	0.2	0.1	0.3	0.1	0.3	0.2	—	—	<0.1	<0.1	56	0.9	17.6	2.6
Pleuronectiformes	unidentified flatfishes	0.3	0.2	0.3	0.1	0.1	<0.1	—	—	—	—	53	0.9	22.1	1.3
Sebastes rufus	bank rockfish	—	—	0.7	0.2	—	—	—	—	—	—	48	0.8	28.6	1.7
Sebastes entomelas	widow rockfish	—	—	0.1	0.1	—	—	—	—	1.4	0.6	45	0.7	45	1.8
Sebastes flavidus	yellowtail rockfish	—	—	—	—	0.4	0.1	—	—	—	—	36	0.6	40.3	1.2
Zaniolepis frenata	shortspine combfish	0.1	<0.1	0.1	<0.1	0.1	<0.1	—	—	—	—	31	0.5	21.6	0.7
Zalembius rosaceus	pink seaperch	0.1	<0.1	—	—	0.1	<0.1	—	—	—	—	30	0.5	15.9	0.6
Hydrolagus colliei	spotted ratfish	0.1	0.1	0.1	0.1	0.3	0.3	0.1	0.1	—	—	29	0.5	32.9	1.8
Sebastes chlorostictus and *S. rosenblatti*	greenspotted and greenblotched rockfish	<0.1	<0.1	—	—	0.2	0.1	—	—	0.2	0.1	29	0.5	41.3	1.1
Sebastes babcocki	redbanded rockfish	—	—	0.1	<0.1	<0.1	<0.1	—	—	0.3	0.1	24	0.4	39.3	3.5
Zoarcidae	unidentified eelpouts	0.1	0.1	0.1	0.1	<0.1	<0.1	—	—	<0.1	<0.1	24	0.4	24.4	1.6
Sebastes diploproa	splitnose rockfish	<0.1	<0.1	0.1	0.1	<0.1	<0.1	—	—	<0.1	<0.1	20	0.3	25.5	4.1
Lycodes cortezianus	bigfin eelpout	0.1	0.1	<0.1	<0.1	<0.1	<0.1	0.1	0.1	<0.1	<0.1	18	0.3	29.7	1.9
Zaniolepis spp	unidentified combfish	—	—	0.1	<0.1	<0.1	<0.1	—	—	—	—	17	0.3	22	2

continued

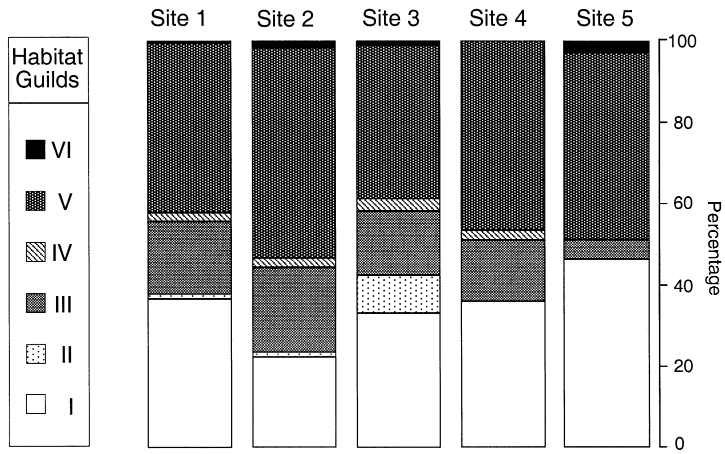
Table 1 (continued)

Species	Common name	Site 1		Site 2		Site 3		Site 4		Site 5		Total		Length (cm)	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	No.	%	Mean	SE
Errex zachirus	rex sole	<0.1	<0.1	—	—	<0.1	<0.1	<0.1	<0.1	—	—	15	0.2	21	0.8
Pleuronectes vetulus	English sole	—	—	<0.1	<0.1	0.1	<0.1	<0.1	<0.1	—	—	12	0.2	26.3	1.7
Icelinus filamentosus	threadfin sculpin	0.1	0.1	<0.1	<0.1	<0.1	<0.1	—	—	—	—	11	0.2	14.3	1.9
Eopsetta exilis	slender sole	—	—	0.1	<0.1	—	—	0.1	0.1	—	—	11	0.2	20	4.5
Sebastes miniatus	vermilion rockfish	0.1	0.1	—	—	—	—	—	—	0.1	<0.1	11	0.2	47	3.4
Sebastes ensifer	swordspine rockfish	—	—	0.2	0.1	—	—	—	—	—	—	9	0.1	22.9	2
Cottidae[3]	unidentified sculpins	—	—	0.1	<0.1	<0.1	<0.1	—	—	—	—	9	0.1	13.3	3.3
Chilara taylori	spotted cusk-eel	<0.1	<0.1	—	—	<0.1	<0.1	—	—	—	—	8	0.1	20	
Plectobranchus evides	bluebarred prickleback	<0.1	<0.1	—	—	0.2	0.2	—	—	—	—	7	0.1	10.8	1.4
Synodus lucioceps	California lizardfish	—	—	—	—	<0.1	<0.1	0.2	0.2	—	—	6	0.1	32.5	5.9
Anoplopoma fimbria	sablefish	<0.1	<0.1	—	—	—	—	—	—	<0.1	<0.1	5	0.1	32	3.6
Bathymasteridae	unidentified ronquil	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	—	—	—	—	5	0.1	11	2.1
Coryphopterus nicholsi	blackeye goby	—	—	—	—	<0.1	<0.1	—	—	—	—	5	0.1	9	0.9
Raja rhina	longnose skate	<0.1	<0.1	—	—	<0.1	<0.1	—	—	<0.1	<0.1	5	0.1	42	7.5
Porichthys notatus	plainfin midshipman	<0.1	<0.1	—	—	—	—	—	—	—	—	4	0.1		
Sebastes goodei	chilipepper	—	—	—	—	<0.1	<0.1	—	—	—	—	4	0.1	28.3	6.7
Zaniolepis latipinnis	longspine combfish	—	—	<0.1	<0.1	<0.1	<0.1	—	—	—	—	4	0.1	20	
Sebastes ovalis	speckled rockfish	—	—	—	—	<0.1	<0.1	—	—	—	—	3	<0.1	40	
Argentina sialis	Pacific argentine	—	—	<0.1	<0.1	—	—	—	—	—	—	2	<0.1	25	
Raja spp	unidentified skates	<0.1	<0.1	—	—	—	—	—	—	<0.1	<0.1	2	<0.1	30	10
Sebastes rubrivinctus	flag rockfish	—	—	<0.1	<0.1	—	—	—	—	—	—	2	<0.1	10	
Eopsetta jordani	petrale sole	—	—	0.1	0.1	—	—	—	—	—	—	1	<0.1	60	
Hexanchus griseus	sixgill shark	<0.1	<0.1	—	—	—	—	—	—	—	—	1	<0.1	200	
Sebastes hopkinsi	squarespot rockfish	—	—	—	—	<0.1	<0.1	—	—	—	—	1	<0.1	15	
Sebastes jordani	shortbelly rockfish	—	—	<0.1	<0.1	—	—	—	—	—	—	1	<0.1		
Torpedo californica	Pacific electric ray	—	—	—	—	—	—	—	—	<0.1	<0.1	1	<0.1	45	
Sum		21.3		26.8		25.7		12.8		42.4		6208			
Number of taxa		31		35		38		20		22		52			
Number rockfish species		12		17		18		9		12		24			

[1] Observations of this small species could include *Sebastes zacentrus*, a species with similar color patterns and body shape.

[2] Rockfishes within the *Sebastomus* complex comprise seven species off central CA, several of which are difficult to identify without close examination.

[3] Likely *Icelinus* spp.



	Site 1	Site 2	Site 3	Site 4	Site 5	Overall
Number Dives	5	6	13	3	6	33
Number Transects	13	14	39	4	13	83
Number Habitat Patches	207	185	515	52	66	1,025
Depth Range (m)	98-305	148-263	94-296	153-210	152-226	94-305
Time Surveyed (h)	2.7	2.4	6.0	0.6	1.7	13.4
Area Surveyed (m^2)	7,638	7,256	13,626	1,285	3,949	33,754
Total Area (ha)	6.9	1.5	19.6	5.8	1.4	35.2

Figure 5

Percent cover of bottom types in habitat guilds (see Fig. 4 for identifications) at five study sites in Soquel Canyon. Number of dives, transects, and habitat patches, depth range, time and area covered, and total area (as estimated from mosaic of side scan sonographs in geographic information system) are listed for each site.

at shallow depths (ANOVA, $P<0.01$). Within depth category, site 2 generally had smaller fishes, and site 5 consistently had the largest fishes. *S. levis* and *S. ruberrimus* were abundant only in the deep category, and were significantly bigger at site 5.

Patterns of species richness (S), diversity (H′), and evenness (J′) were evident among the species assemblages associated with different bottom types (Fig. 8). The two most distinct habitat guilds in the cluster analysis (i.e. mud [guild I] and rock-boulder [guild VI]) ranked among the lowest in both H′ and J′, with a single species clearly dominating each guild. Diversity also was low in the boulder-mud guild (IV), although with somewhat more even proportions among species. The most diverse and evenly distributed assemblages were those in the remaining three guilds (II, III, and V).

Considering just the rock habitat guild (V), diversity measures were examined among sites having different fishing activity in both shallow and deep depth categories (Fig. 9). No patterns in diversity among the three sites in the shallow rock habitat guild were evident (Fig. 9A), although differences in relative abundance of each species were clear. In deep water, a shift in relative abundance occurred from site 2 to site 5, with large species playing a larger role at the less fished sites. The deep rock habitat guild at the iso-

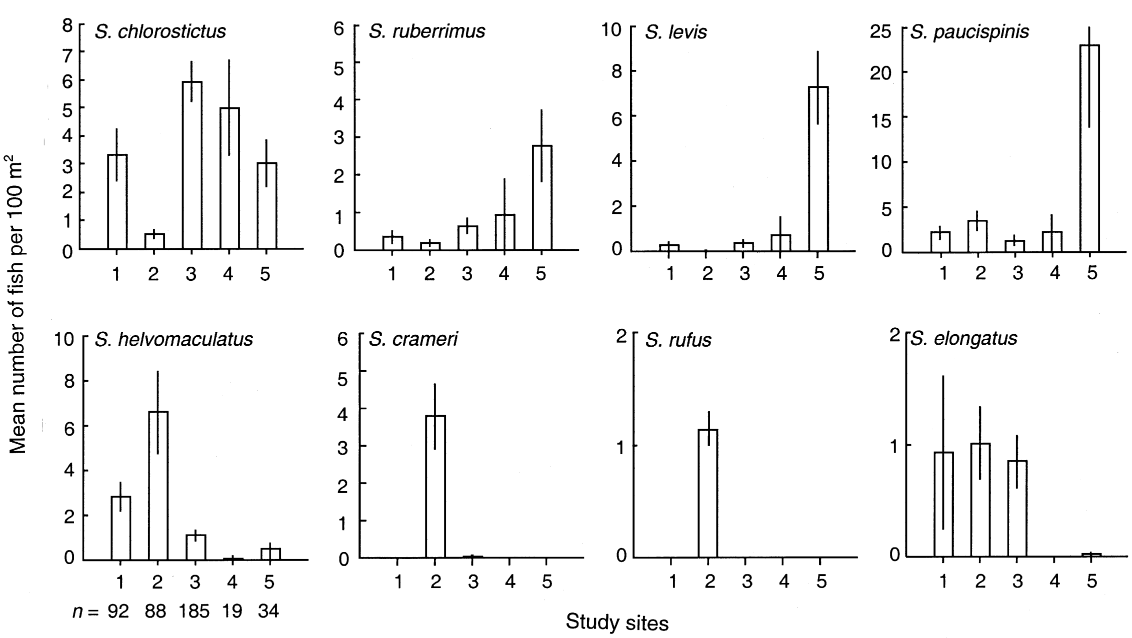


Figure 6

Index of abundance (mean number/100 m^2) of dominant species of nonschooling rockfishes in the rock habitat guild at five sites in Soquel Canyon. Vertical bars are 1 standard error; n = number of habitat patches at each site.

lated site 5 had the lowest diversity among all sites and depths, as measured by H′ and J′.

Discussion

Habitats

Several studies have described distinct fish-habitat associations for various species of benthic rockfishes during different stages of development (Carlson and Straty, 1981; Pearcy et al., 1989; Carr, 1991; Stein et al., 1992; O'Connell and Carlile, 1993). Although species composition may vary latitudinally, there is remarkable concordance between some of the habitat guilds identified in Soquel Canyon and the results of a habitat-based assessment of fishes using similar techniques and habitat characterizations on Heceta Bank off central Oregon (Stein et al., 1992). Mud, rock-boulder, and boulder habitats were most distinct in both studies and included the same dominant species; *M. pacificus*, *S. alascanus*, and Agonidae were abundant on mud, whereas *S. wilsoni* was the single most abundant species in the rock-boulder habitat of Soquel Canyon and the boulder habitat on Heceta Bank (Table 2). Fish assemblages in low relief, mixed habitats of mud, cobble, and pebble grouped together, and although dominant species were largely different (i.e. mud-cobble habitat dominated by *S. zacentrus* and *S. wilsoni* in Oregon and by *S. saxicola*, *S. helvomaculatus* and Agonidae in Soquel Canyon), the assemblages were made up of relatively small species in both studies. Several species common to both studies were characterized similarly in terms of habitats (e.g. associations of *S. pinniger* with rock-boulder combinations and *S. elongatus* with mud-cobble combinations).

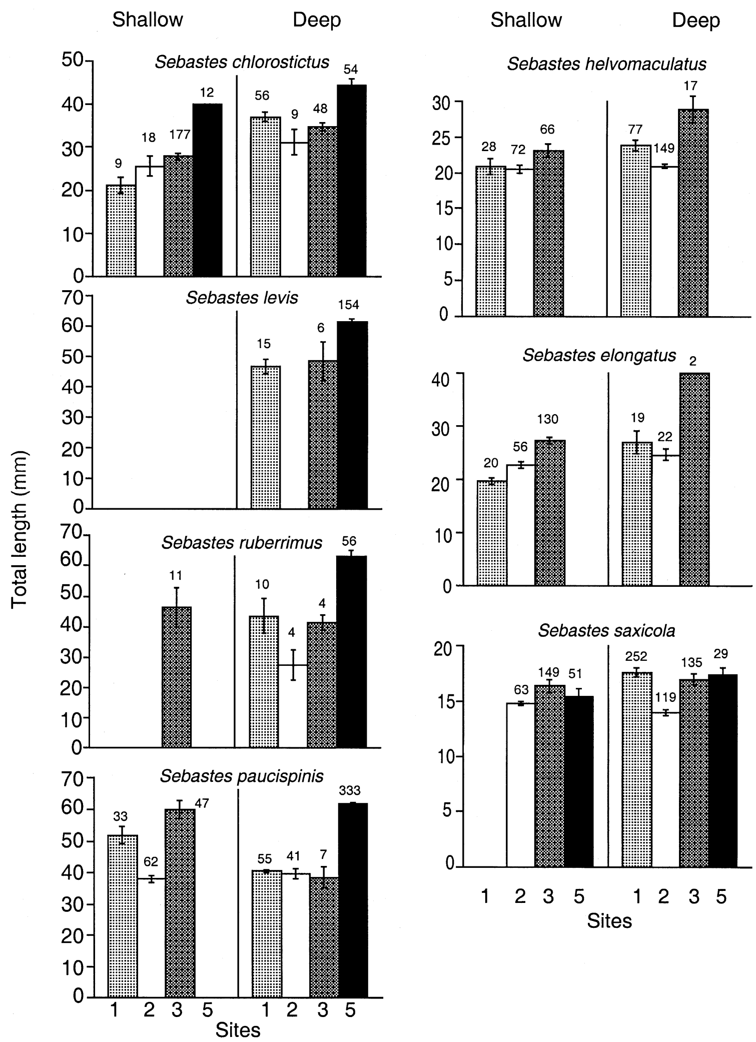


Figure 7

Mean size (vertical bars are 1 standard error) for dominant species in shallow and deep depth categories over all bottom types at study sites 1 to 3 and 5. Small numbers above bars are sample sizes.

Several of the species-habitat associations identified in Soquel Canyon also agreed with those described even farther north. From submersible observations off British Columbia, albeit made at shallower depths (21–150 m) and with less comprehensive habitat classifications than in Soquel Canyon or Heceta Bank, Murie et al. (1994) and Richards (1986) reported adult *S. ruberrimus* to be found exclusively on complex rock habitats, whereas *S. elongatus* was almost exclusively associated with sand-mud and mud-cobble substrata of low relief. In the eastern Gulf of Alaska, adult *S. ruberrimus* were found to be strongly associated with boulder fields, broken rock, overhangs, and crevices (O'Connell and Carlile, 1993), features similar to those of habitats described for this species in Soquel Canyon.

The generalities in habitat-specific associations, such as those described above for several rockfish species occurring along the entire west coast of the United States from central California to Alaska, can be valuable in predicting community structure and its response to perturbation. Identifying functional groups or habitat guilds that persist coastwide will be especially useful when applying these small-scale relationships between species and habitats to broader-scale resource surveys, potentially improving assessments of groundfish populations. Additionally, establishing these groups is critical to incorporating the concept of essential groundfish habitats, and negative impacts to them into the management of fisheries in relatively deep water, as required by the Sustainable Fisheries Act of 1996.

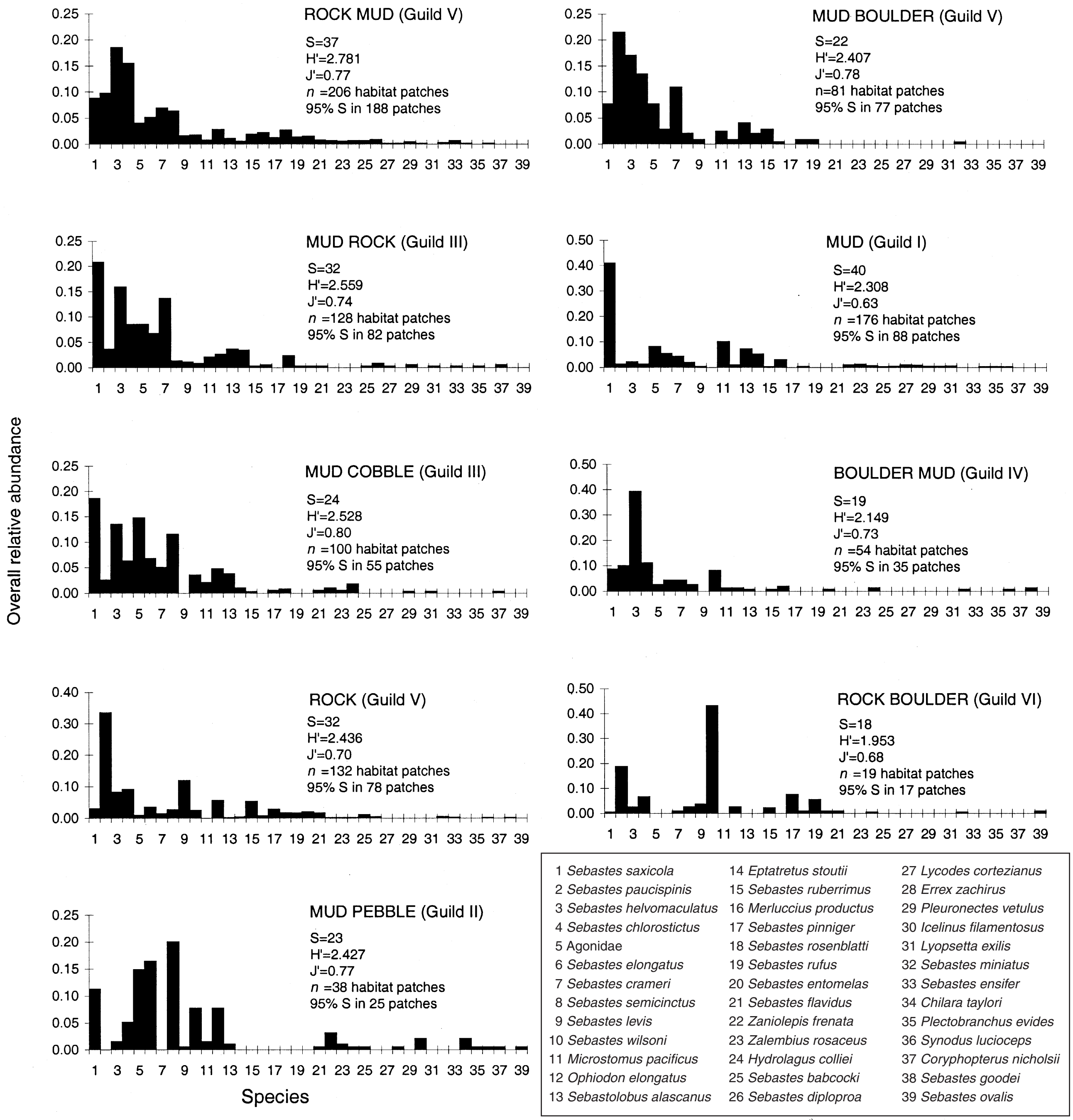


Figure 8

Overall relative abundance of each species associated with each type of habitat. Species richness (S), diversity (H′), and evenness (J′) were calculated for each habitat guild (see Fig. 4 for identifications). n = the number of habitat patches sampled in each habitat. The number of patch samples required to detect 95% of the species is indicated.

Refugia

The high abundances of adult rockfishes associated with rock habitats along the sides of Soquel Submarine Canyon indicate that this canyon may in part serve as a natural harvest refuge, especially for those species of economic value. A comparison of average number of fish per hectare of habitat for the most abundant taxa in Soquel Canyon with the results of the habitat-based study on Heceta Bank (Stein et al., 1992), a longtime area of fishing activ-

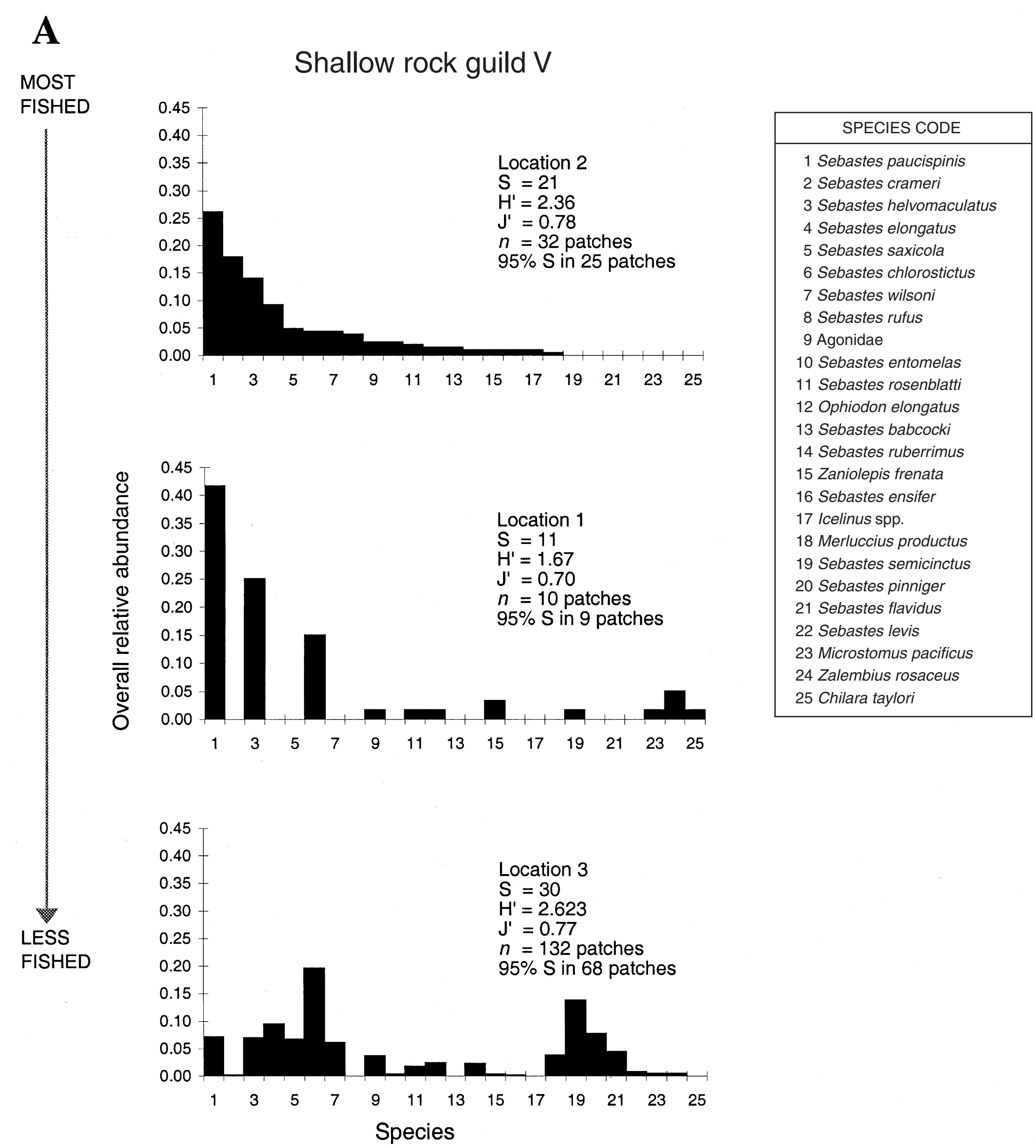


Figure 9

Overall relative abundance of each species in the rock habitat guild in (**A**) shallow (75–175 m) and (**B**) deep (176–275 m) water depths at locations with increasing relative levels of fishing activity in Soquel Canyon. Species richness (S), diversity (H′), and evenness (J′) were calculated for each location at each water depth. n = the number of habitat patches sampled in each habitat. The number of patch samples required to detect 95% of the species is indicated.

ities, supports this conclusion. For example, our study site had several abundant, economically important benthic species (e.g. *O. elongatus*, *S. chlorostictus*, *S. levis*, *S. rosenblatti*, *S. ruberrimus, S. paucispinis*, *S. crameri,* and *S. rufus*; Table 2). These species generally dominated the rock, boulder, mud combination habitats in Soquel Canyon. Comparable habitats in Oregon were dominated by less valuable, small benthic rockfish species (e.g. *S. zacentrus*, *S. wilsoni* and *S. helvomaculatus*). The benthic species of highest abundance in the Oregon study were all in mud-cobble-boulder combination habitats, and most of these were not economically important. Large species of benthic rockfishes and *O. elongatus* did not occur in high numbers on Heceta Bank, Oregon. Although neither study estimated the abundance of active, semipelagic rockfishes, which generally aggregated above the submersible, commercially valuable species such as *S. flavidus* and *S. entomelas* occurred occasionally in high numbers in Soquel Canyon and more commonly over Heceta Bank.

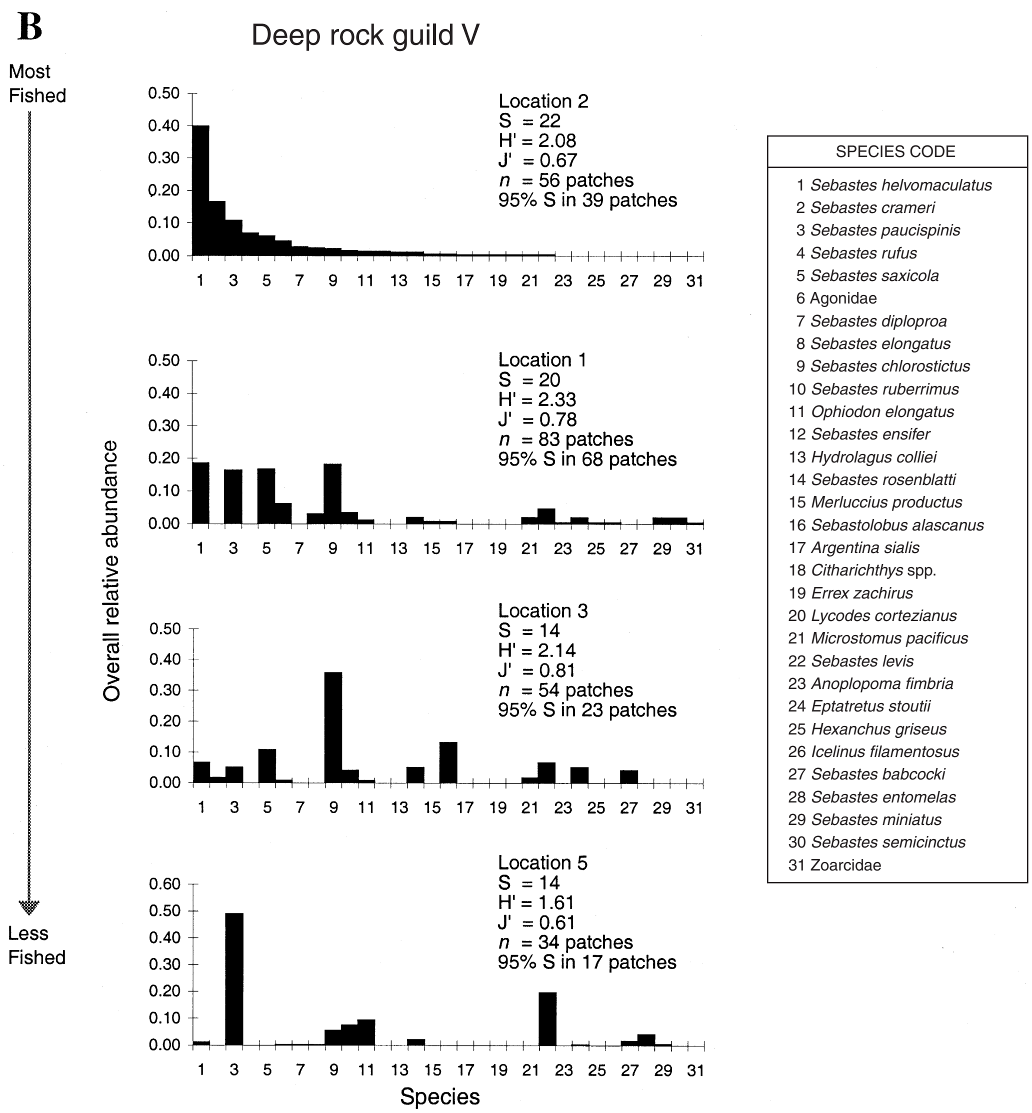


Figure 9 (continued)

The high abundances of large species of benthic rockfishes associated with complex habitats of rock, boulder, and mud combinations at several sites in Soquel Canyon are unique among other habitat-based groundfish assessments, lending further credibility to its designation as a natural harvest refuge. Other studies have reported relatively high numbers of various species of rockfishes associated with rock substrata (Richards, 1986; Stein et al., 1992; O'Connell and Carlile, 1993; Murie et al., 1994), but none have estimated abundances as high as those in Soquel Canyon. This is especially true when considering the extreme abundances of large fishes at site 5, an isolated outcrop on a steep section of the canyon wall surrounded by extensive fields of mud. For example, highest mean abundances of *S. ruberrimus* (number fish/100 m^2) on complex rock substrata were estimated to be about 0.3 off central Oregon (Stein et al., 1992), 0.9 in the Gulf of Alaska (O'Connell and Carlile, 1993), 1.4 off British Columbia (Richards, 1986), and 2.8 at site 5 in Soquel Canyon. Other economically valuable species (e.g. *S. paucispinis* and *O. elongatus*) had even higher abundances at some of the relatively unfished sites in the canyon (Table 1 and Fig. 6), but their abundances were not estimated in the other studies. Mean abundances of *S. elongatus*, a smaller species that is less frequently caught by anglers (Richards, 1986; Karpov et al., 1995), were similar off British Columbia, Oregon and in Soquel Canyon (about 1.5, 0.8, and 1.0 fish/100 m^2 of rock habitat, respectively).

The abundance of *Sebastes helvomaculatus*, another small species that is of minor value to regional fisheries, might be considered an indirect indicator of fishing activity. This benthic species was strongly associated with the same

Table 2

Average number of fish per hectare of habitat of most abundant taxa in Soquel Canyon study. Bold numbers are most common taxa in each habitat category. Number in brackets is abundance estimated in similar habitat off Oregon (Stein et al., 1992). Shading indicates economically valuable species that commonly occurred in relatively high abundance in Soquel Canyon but not off Oregon.

	Guild I	Guild II		Guild III		Guild IV	Guild V	Guild VI		
Species[1]	Mud	Cobble-mud	Mud-pebble	Mud-cobble	Mud-rock	Boulder-mud	Mud-boulder	Rock-mud	Rock-ridge	Rock-boulder
Agonidae	121 [186]	65 [-]	**228**	**251** [464]	110	53 [25]	147 [1122]	50 [-]	18 [18]	—
Eptatretus stouti	77	—	—	17	43	—	39	6	6	—
Merluccius productus	44	—	—	—	7	40	8	27	15	—
Microstomus pacificus	150 [499]	— [-]	24	34 [343]	27	26 [-]	46 [2295]	9 [-]	— [15]	—
Ophiodon elongatus	13 [-]	— [67]	118	81 [-]	33	26 [-]	15 [-]	35 [-]	117 [30]	123
S. chlorostictus and *S. rosenblatti*	5	—	—	—	3	13	15	11	18	20
Sebastes chlorostictus	19	**390**	78	106	110	237	**255**	**193**	**192**	328
Sebastes crameri	64	195	—	85	**176**	92	209	86	29	41
Sebastes elongatus	80 [64]	**325** [266]	**251**	115 [364]	87	92 [25]	54 [204]	64 [-]	74 [79]	—
Sebastes entomelas	1	—	—	—	3	13	—	18	42	41
Sebastes flavidus	— [-]	— [67]	8	8 [29]	3	— [176]	— [-]	9 [-]	34 [191]	41
Sebastes helvomaculatus	32 [26]	65 [933]	24	**229** [343]	**206**	**844** [161]	**325** [408]	**231** [474]	**172** [675]	123
Sebastes levis	5	—	8	—	13	—	15	20	**254**	184
Sebastes paucispinis	19	—	—	42	47	211	**410**	**122**	**714**	**922**
Sebastes pinniger	— [-]	— [-]	—	8 [14]	—	— [-]	— [102]	15 [158]	60 [82]	369
Sebastes rosenblatti	4	—	—	13	30	—	15	33	35	41
Sebastes ruberrimus	2 [-]	— [-]	—	4 [7]	3	13 [25]	54 [-]	23 [-]	111 [27]	102
Sebastes rufus	—	—	—	—	3	—	15	17	32	266
Sebastes saxicola[2]	**611** [60]	130 [133]	173	**314** [2930]	**270**	185 [-]	147 [2754]	109 [-]	62 [277]	20
Sebastes semicinctus	29	**325**	**306**	195	17	53	39	79	55	123
Sebastes wilsoni	1 [21]	260 [999]	118	59 [2129]	10	172 [2772]	— [8926]	21 [-]	51 [1785]	**2131**
Sebastolobus alascanus	108 [239]	— [-]	16	64 [443]	47	13 [-]	77 [2193]	14 [-]	2 [-]	—

[1] See Table 1 for common names.

[2] Comparison is made with *Sebastes zacentrus* in Stein et al. (1992) study.

complex rock habitats that harbor the larger, more valuable species, such as *S. ruberrimus*. *Sebastes helvomaculatus* ranked third in overall abundance both in Soquel Canyon and on Heceta Bank, Oregon (Stein et al., 1992). This was one of the dominant species in the complex rock habitats on Heceta Bank, as well as on site 2 (the area with the most fishing activity in Soquel Canyon). Interestingly, abundance of *S. helvomaculatus* was significantly lower in this same habitat at those sites having high numbers of larger species and less fishing activity in Soquel Canyon (i.e. sites 3–5; Fig. 6).

It is generally understood, especially in the broad literature on artificial and tropical reefs, that complex rock outcrops of high relief provide shelter and protection to reef fishes (Bohnsack, 1989; Potts and Hulbert, 1994, among others). O'Connell and Carlile (1993) noted that the occurrence of adult *S. ruberrimus* was higher in areas with more voids or refuge spaces, and that "extremely high" densities of this and other species were associated with isolated abrupt pinnacles comprising boulders and overhangs. This type of habitat, surrounded by fields of mud as is the case at Site 5 in Soquel Canyon, likely functions as a natural aggregating device for structure-oriented species such as many of the benthic rockfishes. Moreover, in seeking shelter near these rock outcrops in Soquel Canyon, large rockfishes may be excavating the semiconsolidated mudstone (Yoklavich, pers. obs.), thereby creating more of their own habitat (not unlike the construction of burrows in soft sediments by tilefish [*Lopholatilus chamaeleonticeps*; Able et al. 1982]). The extraordinary abundances estimated for several large species (*S. paucispinis, S. levis, S. rosenblatti, O. elongatus*) in a relatively small area of the canyon provide an insight into considerations of design and location when establishing protected areas as a management tool.

In addition to high abundances of valuable species on those rock outcrops in Soquel Canyon with little or no evidence of fishing activities, the large sizes of individual fishes further support the concept of a natural harvest refuge in these areas. Although overall mean length of many species was similar and in some cases smaller in Soquel Canyon when compared with those on Heceta Bank (Stein et al., 1992), sizes were substantially larger for the large benthic species in the canyon (i.e. *S. ruberrimus, S. paucispinis*, *S. babcocki,* and *O. elongatus*).

Aggregations of young rockfishes were absent at any depth during our surveys of Soquel Canyon, leading us to conclude that although the canyon is likely a refuge for adult rockfishes it does not serve as a nursery ground. In contrast, from submersible observations of dense schools of young-of-the-year rockfishes associated with the shallow (100 m) ridge tops of Heceta Bank, Pearcy et al. (1989) suggested that rocky portions of the bank function as a nursery for young rockfishes. Heceta Bank is topographically isolated and located about 55 km off the Oregon coast; it is likely that there are no suitable nursery areas for rockfishes nearby. Soquel Canyon, however, is about 15 km offshore in Monterey Bay, and in close proximity to shallow rock outcrops, cobble fields, and kelp forests that function as nursery areas for many rockfish species (Carr, 1991; Johnson, 1997).

Aside from changes in population numbers and sizes, marine fisheries have been identified as one of the most critical environmental threats to marine biodiversity (Sobel, 1993; Boehlert, 1996), and it has been suggested that harvest refugia may contribute to the preservation of individual species, genotypes, and habitats (Bohnsack and Ault, 1996). Overall, the benthic fish assemblages in the various habitats of Soquel Canyon are relatively diverse; total species richness in the canyon was 52 (20 species comprising 90% of the total abundance) compared with 38 species on Heceta Bank (where only 10 species contributed to 90% of the abundance; Stein et al., 1992). Species diversity, as measured by H' (Fig. 8), clearly varied among habitats; fish assemblages associated with complex habitats of rock, cobble, and mud maintained the highest diversity, whereas boulder habitats had lower diversity with a few dominant species. There was no clear influence of relative fishing activity on species diversity in the complex rock habitats of the canyon, but there was an influence on the relative abundance and sizes of the species themselves.

We conclude that some heterogeneous rocky habitats of high relief interspersed with soft mud in deep water of Soquel Submarine Canyon support high numbers of large adult rockfishes, in particular those species important to regional fisheries. These fishes are likely protected from excessive harvest because these habitat characteristics make them difficult to locate and target. These areas appear to function as a natural harvest refugium, potentially contributing new recruits to adjacent fished areas. We suspect that other such isolated high-relief rock habitat, as yet undetected or described, exists elsewhere in deep water on the continental shelf and slope of the west coast. The challenge now is to identify and characterize these habitats and associated fish assemblages, and to relate these small scale patterns to larger geographic areas relevant to benthic fishery stocks.

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