

GIMME SHELTER: THE IMPORTANCE OF CREVICES TO SOME FISH SPECIES INHABITING A DEEPER-WATER ROCKY OUTCROP IN SOUTHERN CALIFORNIA

MILTON S. LOVE

Marine Science Institute
University of California
Santa Barbara, California 93106-6150
love@lifesci.ucsb.edu

DONNA M. SCHROEDER

Marine Science Institute
University of California
Santa Barbara, California 93106-6150

BILL LENARZ

P. O. Box 251
Kentfield, California 94914

GUY R. COCHRANE

USGS Pacific Science Center
400 Natural Bridges Drive
Santa Cruz, California 95060

ABSTRACT

Federal law governing fisheries management recognizes the role habitat plays in structuring fish assemblages and achieving sustainable fisheries. However, in most instances it is not known which aspects of habitat are important to the lives of fish species. In 2004, we examined the importance of sheltering sites (crevices) to fishes living along low ledges in deeper waters off Anacapa Island, southern California. We found that patterns of fish-habitat relationships varied among the eight most abundant species. Three species, bocaccio (*Sebastes paucispinis*), vermilion (*S. miniatus*), and flag (*S. rubrivinctus*) rockfishes, had densities one to three orders of magnitude greater in the deep crevice habitat compared to low relief rock or shallow crevice habitats. Density and mean size of the two most abundant fishes, halfbanded (*S. semicinctus*) and squarespot (*S. hopkinsi*) rockfishes, generally increased as complexity of rock habitat increased. Not all species had the highest densities in deep crevice habitat. Greenspotted rockfish (*S. chlorostictus*) and blackeye goby (*Rhinogobiops nicholsii*) showed no significant difference in density among rock habitats. Pink seaperch (*Zalembius rosaceus*) were absent in the deep crevice habitat and abundant only in low relief rock habitats. Our study implies that it is not sufficient to distinguish only between soft and hard bottom types when using habitat to guide fisheries management strategies. Finer-scale investigations of fish-habitat relationships, paired with habitat mapping and groundtruthing, aid in the design and positioning of Marine Park Areas (MPAs) and are necessary to facilitate understanding of how a particular MPA may contribute to fisheries management.

INTRODUCTION

In recent years, studies have begun to illustrate the role that habitats play in structuring fish assemblages. Much of the impetus for this research derives from the Sustainable Fisheries Act of 1996, which reauthorized and amended the Magnuson-Stevens Fishery Management and Conservation Act. The amended Magnuson-Stevens Act made habitat characterization and conservation central tenets and created the concept

of Essential Fish Habitat (EFH) and Habitats of Particular Concern (HAPCs). In addition, the establishment of Marine Protected Areas (MPAs), as a tool of fishery management (e.g., the Pacific Coast Rockfish Conservation Areas created by the Pacific Fishery Management Council, www.pcouncil.org/reserves/reservesback.html) and a protector of ecosystem function and structure (e.g., as delineated in the California Marine Life Protection Act, <http://www.dfg.ca.gov/mrd/mlpa/>), has demonstrated that understanding habitat preferences of fish species is crucial if we are to protect various life stages. However, as noted by Lindeman et al. (2000), in most instances it is not known which of the “finer scale, structural habitat types” are important to the lives of fish species and “characterizing structural and water-quality attributes influencing behavior of settlement-competent stages is fundamental to identifying primary nurseries and EFH-HAPCs.”

In general, the habitat preferences of deeper-water (below scuba-diving depth) fishes along the Pacific Coast have been characterized at the megahabitat (e.g., sediment-covered seafloor) and mesohabitat (e.g., rock outcrops, boulders, and cobble fields, *sensu* Greene et al. 1999) levels (Stein et al. 1992; Yoklavich et al. 2000; Nasby-Lucas et al. 2002). One issue is that, while within many larger habitats fishes may associate with smaller macro- and microhabitats (e.g., cracks, crevices, and substrate-forming invertebrates), these relationships are often difficult to discern in complex habitats, particularly in waters below scuba-diver depth where experimentally altering habitat (e.g., Matthews 1990) is problematic.

In 2004, surveys conducted using a manned submersible allowed us to examine the importance of sheltering sites, one aspect of complex habitats, to fishes living along low ledges in deeper waters off Anacapa Island, southern California. Although limited in scope, our surveys indicate that finer-scale investigations of fish-habitat relationships, paired with habitat mapping and groundtruthing, aid the design and positioning of Marine Park Areas (MPAs) and facilitate understanding of how a particular MPA may contribute to fisheries management.

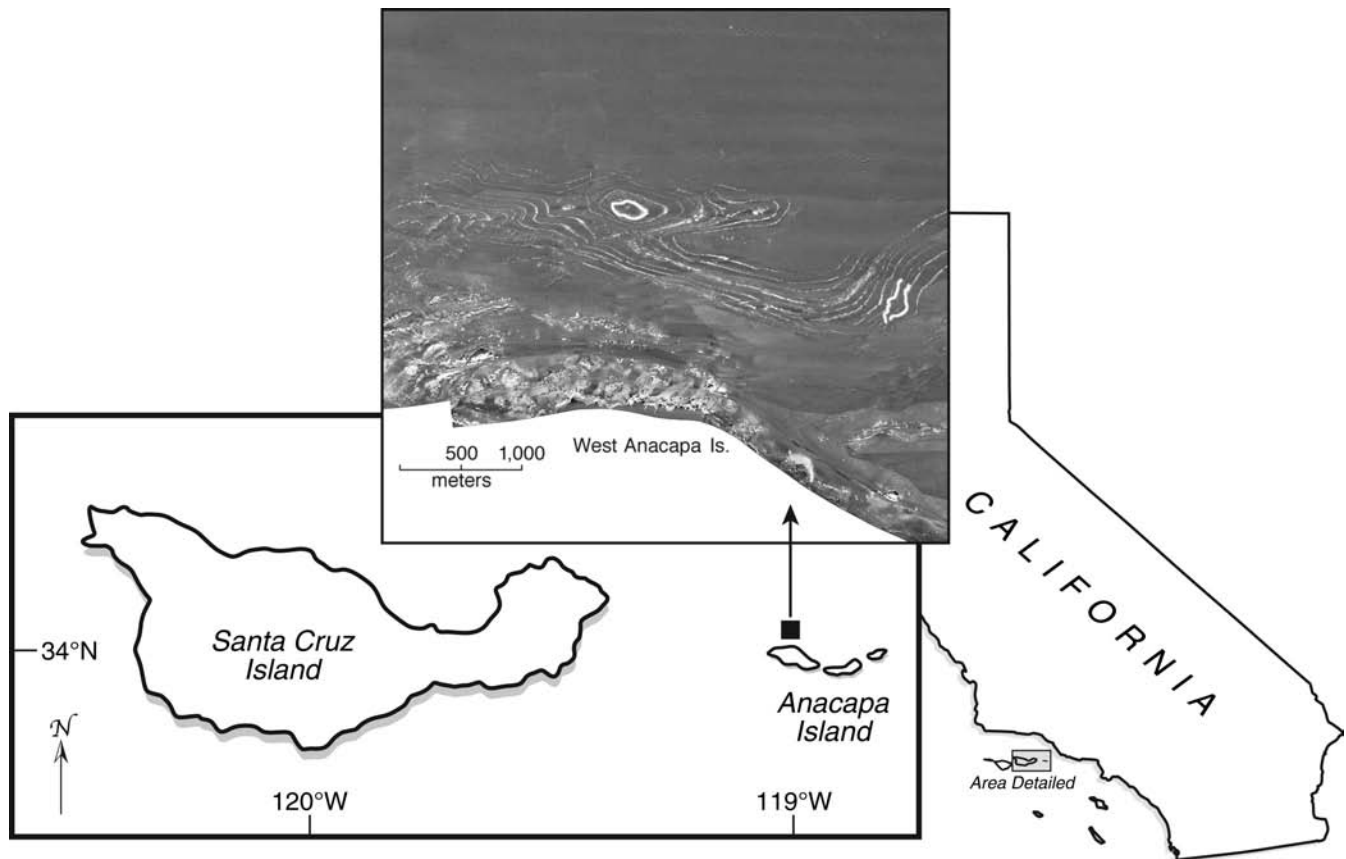


Figure 1. Location of the two sites (white tracks) surveyed for this study on 3 October 2004. Sonar backscatter intensity image from Cochrane et al. (2003) shows harder bottom as lighter gray in color. Numerical classification of the sonar image (Cochrane et al. 2003) suggests, and submersible observations confirm, that rock outcrops are relatively sparse and that much of the habitat detailed in this image is actually thinly covered with sediment.

METHODS

We conducted the surveys on 3 October 2004 on the north side of Anacapa Island (fig. 1) on local outcrops and on the sediments surrounding the outcrops. These surveys lay within the Anacapa Island State Marine Conservation Area, where all fishing is prohibited, except for pelagic fishes and lobster. Lithology of rocky outcrops consists of two forms. In depths less than about 70 m, volcanic rocks outcrop to form exposed surfaces up to 2 m in height, and broken small rocks lie scattered in the area. Occasional pinnacles rise to approximately 2–4 m in height. Cobble, shell hash, and coarse sand lay in the channels that separate outcrops at these shallow depths (Cochrane et al. 2003).

In contrast, folded sedimentary strata become the dominant rock form deeper than about 70 m. Ledges approximately 1 m high are composed of sedimentary rock that emerges from fine sediments along the north shelf of the island. The sedimentary layers were originally flat; tectonic forces folded and uplifted them, and this was followed by wave erosion at a lower sea-level stand. Resistance to erosion varies vertically and laterally in the sedimentary rocks due to changes in sediment grain size and degree of cementation. Thus, while much

of these outcrops are uneroded and show a featureless vertical face, some areas are undercut and these openings form horizontal crevices.

We surveyed two outcroppings of this formation, sites that were close together (about 3.6 km apart) and in similar depths (75–79 m). Because the features were part of the same formation, were in the same water depths, and were only a short distance apart, the major variable in that reef habitat was the absence or presence of the undercut, and the size of that crevice. This allowed for a comparison of “shelterless” and “sheltered” reef habitats (Hixon and Beets 1989).

We surveyed fish assemblages using the *Delta* submersible, a 4.6 m, two-person vessel, operated by Delta Oceanographics of Oxnard, California. Aboard the *Delta*, we conducted belt transects about 2 m from the substrata, while the submersible maintained a speed of about 0.5 knots. The two surveys were conducted during daylight hours within two hours of each other. During each transect, observations were taken from one viewing port on the starboard side of the submersible. An externally mounted hi-8 mm or digital video camera with associated lights filmed the same viewing fields as seen by the observers. The observer identified, counted, and esti-

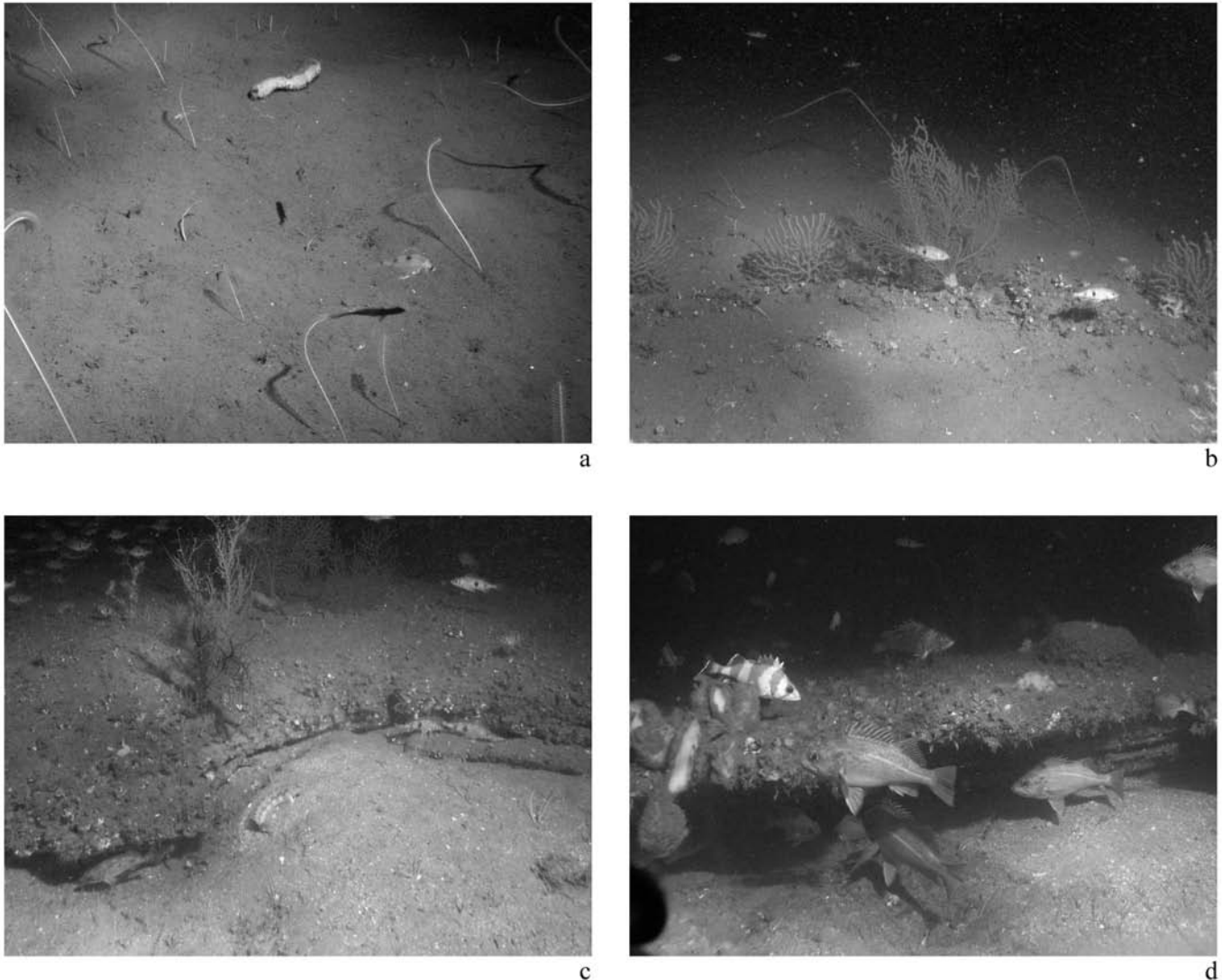


Figure 2. Examples of the four habitat types discussed in this study: A) Type 0 = no rock showing, B) Type 1 = rock exposed, but not undercut, C) Type 2 = rock undercut but the undercut not large enough to shelter a 20 cm fish, and D) Type 3 = rock with a large ledge or cave, large enough to shelter a 20 cm fish.

mated the lengths of all fishes and verbally recorded those data on the video. All fishes within 2 m of the submarine were counted and, thus, densities were calculated as fish per m^2 . Lengths of all fishes were estimated to the nearest 5 cm using a pair of parallel lasers mounted on either side of the external video camera. The projected reference points were 20 cm apart and were visible both to the observer and the video camera. An environmental monitoring system aboard the submarine continuously recorded date and time, depth, and altitude of the vessel above the sea floor. The environmental data were overlaid on the original videotape upon completion of each survey.

Many years of experience along the Pacific Coast have shown that if the *Delta* is moving at a constant and slow rate of speed, as in these surveys, there is very little obvious effect on demersal fishes (Love and York 2005).

In this study, we noted no movement from such benthic and solitary species as copper (*Sebastes caurinus*), flag (*S. rubrivinctus*), and vermilion (*S. miniatus*) rockfishes or bocaccio (*S. paucispinis*) as the research submersible passed by. In a few instances, individuals of schooling species, such as halfbanded rockfish (*S. semicinctus*), increased their swimming speed but did not appreciably change course.

Transect videos were reviewed in the laboratory. Field observations were transcribed into a database. For each fish, we recorded the following information: species (if known), its estimated total length, the habitat it occupied (i.e., soft substratum or rock), and the amount the rock habitat was undercut, forming crevices and caves. Habitat was scaled from 0 to 3: in Type 0, no rock was showing; in Type 1, rock was exposed, but not undercut; in Type 2, rock was undercut but the undercut was not large enough for a 20 cm fish to shelter in; and in

Type 3, rock had a large ledge or cave, large enough to shelter a 20 cm fish (fig. 2).

We treated each dive segment, defined as an uninterrupted part of a dive within a habitat type, as an observation. Since survey estimates of fish densities often are not normally distributed and sample sizes varied among habitat types, we used non-parametric statistical methods to analyze the data. We used the Kruskal-Wallis one-way analysis of variance test for hypotheses that median densities were the same in each of the four habitat types. While the main emphasis of the study was to compare the four habitat types, we thought that readers would also be interested in comparisons of densities in the soft bottom habitat to densities in the combined three rocky habitats. We used the Wilcoxon rank sum test for these comparisons. We compared length compositions among habitat types for the two most abundant fish species; there were insufficient data to examine size-habitat relationships for the other species. Because we estimated the size of every fish in each observed habitat, we assumed that the size compositions were known without sampling error and did not make statistical tests. We were not able to estimate measurement error.

RESULTS

We surveyed a total of 1,432 m of habitat (including both rock and soft substrata), encompassing an area of 2,863 m² of which 2,231 m² was rocky reef. The amount of each hard habitat type surveyed varied from a maximum of 1,240 m² of Type 1 (rock exposed, but not undercut) to a minimum of 298 m² of Type 3 (rock with the largest crevices) (tab. 1). We observed a minimum of 17 fish species (assuming the unidentified ronquils and *Citharichthys* comprised only one species) comprising 6,570 individuals (tab. 2). Rockfishes dominated this assemblage, comprising 97.5% of all fishes surveyed. The diminutive halfbanded rockfish was particularly abundant, comprising 84.8% of all fishes observed. There were seven other relatively abundant species; these were squarespot (*S. hopkinsi*), vermilion, flag, and greenspotted (*S. chlorostictus*) rockfishes, bocaccio, pink seaperch (*Zalembeus rosaceus*), and blackeye goby (*Rhinogobiops nicholsii*). Based on estimated fish lengths, we observed both juveniles and adults of all of the eight most abundant species (fig. 3). However, it is probable that most flag, halfbanded, and greenspotted rockfishes and pink seaperch were juveniles, while most bocaccio and blackeye goby were adults.

Patterns of fish-habitat relationships varied among the eight most abundant species (tabs. 3 and 4). Halfbanded rockfish was the most common species in every type of habitat, including sand. The density and mean size of halfbanded rockfish generally increased as the complexity of rock habitat increased, although the two non-

TABLE 1
Lengths and areas of each habitat type surveyed. Habitat was scaled from 0 to 3: Type 0 = no rock showing, Type 1 = rock exposed, but not undercut, Type 2 = rock undercut but the undercut not large enough for a 20 cm fish to shelter in, and Type 3 = rock with a large ledge or cave, large enough to shelter a 20 cm fish.

Habitat Type	Distance (m)	Area (m ²)
0	316	632
1	620	1,240
2	346	693
3	149	298
Total	1,432	2,863

TABLE 2
Numbers and densities of all fish species observed on two natural reefs in 75–79 m of water at Anacapa Island, 3 October 2004.

Common Name	Scientific Name	Number Observed	Density (no./100 m ²)
Halfbanded rockfish	<i>Sebastes semicinctus</i>	5,577	194.7
Squarespot rockfish	<i>Sebastes hopkinsi</i>	587	20.4
Pink seaperch	<i>Zalembeus rosaceus</i>	69	2.4
Vermilion rockfish	<i>Sebastes miniatus</i>	58	2.0
Bocaccio	<i>Sebastes paucispinis</i>	55	1.9
Blackeye goby	<i>Rhinogobiops nicholsii</i>	54	1.9
Flag rockfish	<i>Sebastes rubrivinctus</i>	43	1.5
Greenspotted rockfish	<i>Sebastes chlorostictus</i>	32	1.1
Copper rockfish	<i>Sebastes caurinus</i>	24	0.8
Unident. <i>Sebastes</i> ^a		19	0.7
Shortspine combfish	<i>Zaniolepis frenata</i>	17	0.6
Unident. ronquils ^b	<i>Rathbunella</i> spp.	12	0.4
Spotfin sculpin	<i>Icelinus tenuis</i>	5	0.2
Lingcod	<i>Ophiodon elongatus</i>	5	0.2
Starry rockfish	<i>Sebastes constellatus</i>	3	0.1
Unident. rockfish	<i>Sebastes</i> spp.	3	<0.1
Deepwater blenny	<i>Cryptotrema corallinum</i>	2	<0.1
Unident. flatfish		2	<0.1
Unident. sanddab	<i>Citharichthys</i> spp.	2	<0.1
Cowcod	<i>Sebastes levis</i>	1	<0.1
Total		6,570	

^aGreenspotted, rosy (*Sebastes rosaceus*) or swordspine (*Sebastes ensifer*) rockfishes.

^bMost of these were bluebanded ronquils (*Rathbunella hypoplecta*), but a few could have been stripefin ronquils (*Rathbunella alleni*).

parametric tests did not significantly discriminate density differences among habitat types (tab. 4, fig. 4). The second most abundant fish, squarespot rockfish, was completely absent from sand habitat, but otherwise showed increased mean size and density with increased rock complexity (fig. 4).

Three species, vermilion and flag rockfishes and bocaccio, had densities one to three orders of magnitude greater in the deep crevice habitat (habitat Type 3) compared to low relief rock habitat (Types 1 and 2) (tab. 3). These three species were not found over the sand. Not all species had the highest densities in deep crevice habitat. Greenspotted rockfish showed no significant difference in density among habitat types. Pink seaperch were absent in the deep crevice habitat and most abundant in

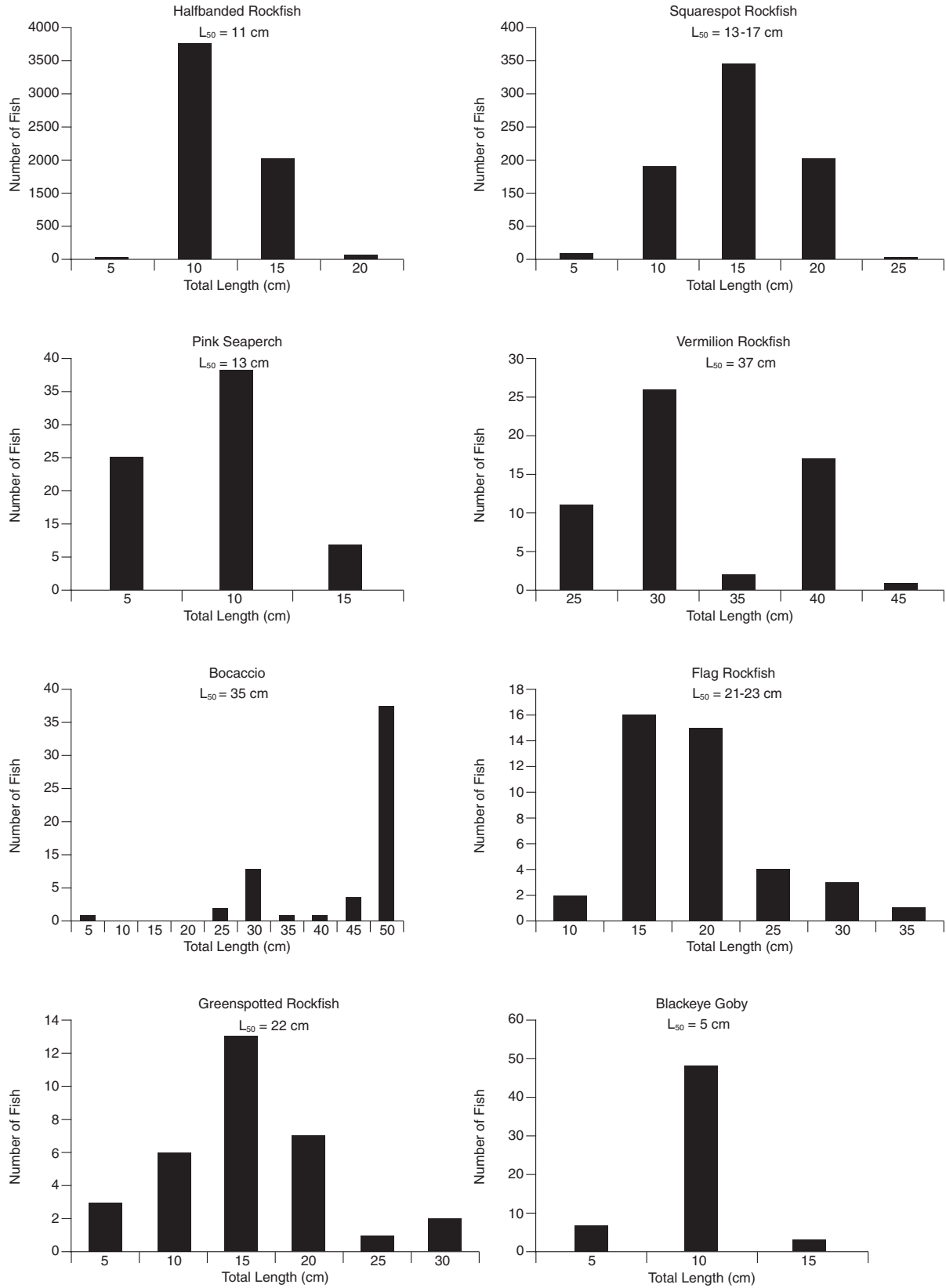


Figure 3. Size-frequency histograms of the eight most abundant species in this survey. Included are lengths at 50% maturity (L_{50}). Rockfish values are from Love et al. (2002), blackeye goby (*Rhinogobiops nicholsii*) from Wiley (1970), and pink seaperch (*Zalembeius rosaceus*) from M. Love (unpubl. data). Note that numbers of fish observed (y-axis) may differ by several orders of magnitude among species.

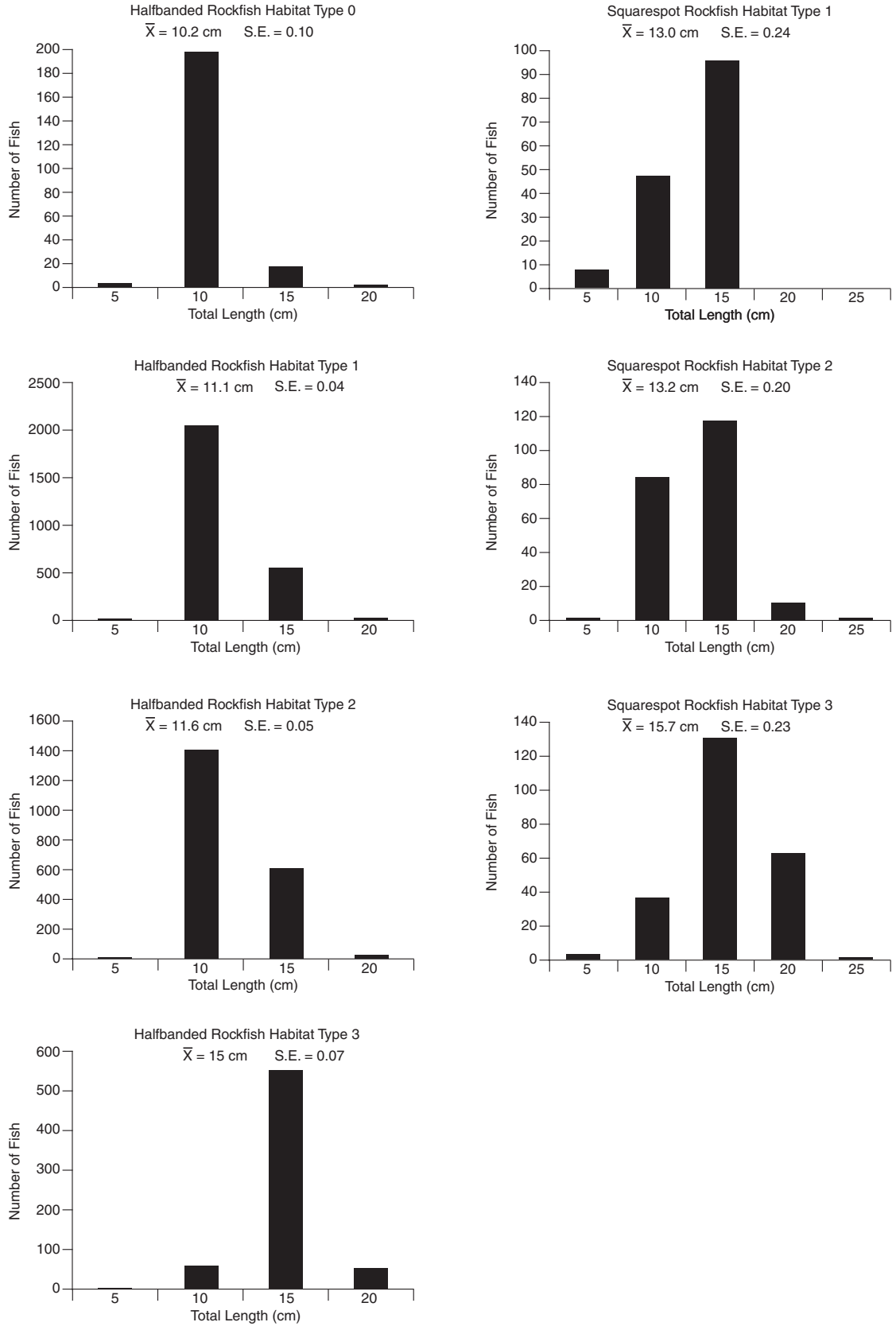


Figure 4. Size-frequency histograms of squarespot (*Sebastes hopkinsi*) and halfbanded (*Sebastes semicinctus*) rockfishes within the four habitat types. Note that numbers of fish observed (y -axis) may differ by several orders of magnitude among habitat types.

TABLE 3
 Habitat codes, number of transect segments, and number of positive transect segments
 (those that contain at least one individual) for the eight most abundant species in the study.

Number of Positive Segments									
Habitat Type	Number of Segments	Blackeye goby	Bocaccio	Flag rockfish	Greenspotted rockfish	Halfbanded rockfish	Squarespot rockfish	Vermilion rockfish	Pink seaperch
0	5	2	0	0	2	5	0	0	2
1	5	5	1	4	4	5	4	1	4
2	4	4	2	4	3	4	4	2	4
3	3	3	3	3	1	3	3	3	0

TABLE 4
 Comparing habitat preferences of the eight most abundant fish species observed on 3 October 2004 in 74 to 79 m of water along the northern edge of Anacapa Island, using the Kruskal-Wallis one-way analysis of variance test and Wilcoxon rank sum test. Values under each species and within each habitat type are densities (fish/m²).

Kruskal-Wallis									
Density (count/m ²)									
Habitat Type	Number of Segments	Blackeye goby	Bocaccio	Flag rockfish	Greenspotted rockfish	Halfbanded rockfish	Squarespot rockfish	Vermilion rockfish	Pink seaperch
0	5	0.0052	0.0000	0.0000	0.0069	1.2009	0.0000	0.0000	0.0100
1	5	0.0278	0.0005	0.0055	0.0173	1.5175	0.0770	0.0005	0.0230
2	4	0.0254	0.0020	0.0158	0.0179	2.3896	0.3406	0.0038	0.0415
3	3	0.0228	0.1441	0.0932	0.0024	2.7873	0.6991	0.1425	0.0000
Kruskal-Wallis H		5.49	8.26	13.35	3.46	2.46	12.25	8.26	7.84
Nominal Significance		ns	0.05	0.005	ns	ns	0.01	0.05	0.05
Wilcoxon									
Soft	5	0.0052	0.0000	0.0000	0.0069	1.2009	0.0000	0.0000	0.0100
Rocky	12	0.0257	0.0369	0.0309	0.0138	2.1256	0.3210	0.0371	0.0234
T (sum of ranks soft bottom)		23.00	30.00	17.50	35.00	33.00	17.50	30.00	35.00
Significance		0.02	ns	0.01	ns	ns	0.01	ns	ns

low relief rock. Both greenspotted rockfish and pink sea perch were occasionally found over the sand. When habitat was plainly classified as either soft or hard, the fish-habitat relationship for pink seaperch disappeared. Conversely, the simple soft-hard classification resulted in significant differences in blackeye goby density, whereas the finer-scale classification did not result in significant differences.

DISCUSSION

Our data are limited both spatially and temporally. Our surveys consisted of two adjacent dives covering a total of 2.863 km² on the north side of Anacapa Island, made on 3 October 2004, between the hours of 1330 and 1550. Thus, we are able to make only limited generalizations. However, when studying the habitat utilization patterns of fishes, our study results imply that it is not sufficient to distinguish only between soft and hard bottoms. This is clearly demonstrated by our observations that some deeper-water and rock-dwelling species off California (e.g., flag, squarespot, vermilion rockfishes and bocaccio) are members of a "sheltering habitat" guild. These are fishes that are most abundant around a

hard structure that contains crevices and other openings. It is likely that a suite of other rockfishes, including quillback, tiger, and yelloweye rockfishes and cowcod, also belong to this guild (Richards 1986; O'Connell and Carlile 1993; Yoklavich et al. 2000).

Sheltering guild fishes display a wide range of sizes. In our study, for instance, squarespot rockfish are dwarf fishes and rarely attain 25 cm in length, while bocaccio up to 50 cm long were also strongly associated with crevices (fig. 3). At the extreme, both cowcod and yelloweye rockfish, two species that are almost always associated with shelter, reach lengths of 100 cm and 91.4 cm, respectively (Love et al. 2002). Fish morphology and associated behavior also varies widely within this guild. For instance, squarespot rockfish are relatively oval, have small spines, and form large schools, while flag rockfish are generally squat, spiny, and solitary.

Our research (and that of Richards 1986; O'Connell and Carlile 1993; Yoklavich et al. 2000) demonstrates that at least some Pacific Coast reef fish species are found within specific habitat types. This has several implications for both MPA siting and monitoring. First, our data imply that subtle differences in habitats, such as the

number and size of sheltering sites, can have a profound effect on fish assemblages (as was noted in tropical waters by Hixon and Beets 1989). A better understanding of these subtleties could lead to more optimal MPA sitings. This is particularly true because many MPAs have been created "on the basis of social factors" rather than on underlying biological principles (Sala et al. 2002). Arguments have been made that despite an often less-than-rigorous approach to MPA siting, creating MPAs almost always yields positive benefits in increases in fish biomass and overall diversity (Roberts 2000). While this may be true for assemblages as a whole, our study reinforces the concept that a more precise understanding of the habitat needs of target species is necessary when reserves are created as fishery tools (i.e., to increase biomass of particular taxa, to test various hypotheses, or to study population trends).

Our research also has implications for designing the size and assessing the habitat content of an MPA. As an example, deeply undercut ledge habitat (occupied by bocaccio and other sheltering guild species) is relatively scarce in our study area. Given the paucity of this optimal habitat on the north side of Anacapa Island, an MPA designed to protect bocaccio would require a larger reserve than might have been predicted if it had been assumed that all rock was of equal importance. Certainly, if an MPA covered a very extensive area, it might be expected that all habitat types would be protected and an understanding of fish habitat guilds would be less important. However, where MPA siting is controversial (as in California) and support for protecting extensive amounts of sea floor problematic, effective siting (based on an understanding of fish habitat requirements) is important.

Lastly, it is clear that understanding the habitat requirements of species of interest is essential for an accurate assessment of the effects of an MPA. Monitoring the effectiveness of an MPA involves surveying the densities of fishes both inside and outside the reserve. Our research shows that for a number of species, all rocky habitat is not the same. This illustrates the need to 1) carefully define the habitat needs of target species; and 2) assure that essential habitat is present and monitored both inside a reserve and at reference sites.

ACKNOWLEDGMENTS

This work was funded by the Channel Islands National Marine Sanctuary through the Channel Islands

Marine Sanctuary Foundation. The authors wish to thank Sarah Fangman for supporting this research and Linda Snook for managing the survey data. We thank the pilots of the submersible *Delta*, Chris Ijames, Joe Lily, and Dave Slater and the crew of the R/V *Velero IV* for their very professional handling of the technical aspects of this survey. We thank Mary Yoklavich for improving this paper's title.

LITERATURE CITED

- Cochrane, G. R., N. M. Nasby, J. A. Reid, B. Waltenberger, and K. M. Lee. 2003. Nearshore Benthic Habitat GIS for the Channel Islands National Marine Sanctuary and Southern California State Fisheries Reserves Volume 1, U.S. Geological Survey Open-file Report 03-85, <<http://geopubs.wr.usgs.gov/open-file/of03-85/>><http://geopubs.wr.usgs.gov/open-file/of03-85/>.
- Greene, H. G., M. M. Yoklavich, R. M. Starr, V. M. O'Connell, W. W. Wakefield, D. E. Sullivan, J. E. McRea Jr., and G. M. Cailliet. 1999. A classification scheme for deep seafloor habitats. *Oceanologica Acta*. 22:663-678.
- Hixon, M. A. and J. P. Beets. 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull. Mar. Sci.* 44:666-680.
- Lindeman, K. C., R. Pugliese, G. T. Waugh, and J. S. Ault. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. *Bull. Mar. Sci.* 66:929-956.
- Love, M. S. and A. York. 2005. A comparison of the fish assemblages associated with an oil/gas pipeline and adjacent seafloor in the Santa Barbara Channel, Southern California Bight. *Bull. Mar. Sci.* 77:101-177.
- Love, M. S., M. Yoklavich, and L. Thorsteinson. 2002. The rockfishes of the Northeast Pacific. Berkeley, Calif.: University of California Press, 405 pp.
- Matthews, K. R. 1990. An experimental study of the habitat preferences and movement patterns of copper, quillback, and brown rockfishes (*Sebastes* spp.). *Env. Biol. Fish.* 29:161-178.
- Nasby-Lucas, N. B., W. Embley, M. A. Hixon, S. G. Merle, B. N. Tissot, and D. N. Wright. 2002. Integration of submersible transect data and high-resolution multibeam sonar imagery for a habitat-based groundfish assessment of Heceta Bank, Oregon. *Fish. Bull., U.S.* 100:739-751.
- O'Connell, V. M. and D. W. Carlile. 1993. Habitat-specific density of adult yelloweye rockfish *Sebastes ruberrimus* in the eastern Gulf of Alaska. *Fish. Bull., U.S.* 91:304-309.
- Richards, L. J. 1986. Depth and habitat distributions of three species of rockfish (*Sebastes*) in British Columbia: observations from the submersible PISCES IV. *Env. Biol. Fish.* 17:13-21.
- Roberts, C. M. 2000. Selecting marine reserve locations: optimality versus opportunism. *Bull. Mar. Sci.* 66:581-592.
- Sala, E., O. Aburto-Oropeza, G. Paredes, I. Parra, J. C. Barrera, and P. K. Dayton. 2002. A general model for designing networks of marine reserves. *Science*. 298:1991-1993.
- Stein, D. L., B. N. Tissot, M. A. Hixon, and W. Bars. 1992. Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. *Fish. Bull., U.S.* 90:540-551.
- Wiley, J. W. 1970. The life history of the bluespot goby (*Coryphopterus nicholsii*). Master's thesis, California State University, Fullerton, 72 pp.
- Yoklavich, M. M., H. G. Greene, G. M. Cailliet, D. E. Sullivan, R. N. Lea, and M. S. Love. 2000. Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. *Fish. Bull., U.S.* 98:625-641.