A CHARACTERIZATION OF THE FISH ASSEMBLAGE OF DEEP PHOTIC ZONE ROCK OUTCROPS IN THE ANACAPA PASSAGE, SOUTHERN CALIFORNIA, 1995 TO 2004, WITH EVIDENCE OF A REGIME SHIFT

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ABSTRACT

During 1995, 1999, and 2001–04, using a manned research submersible, we surveyed the fish assemblage on rocky outcrops (situated at depths of 45–50 m) in the Anacapa Passage, southern California. We observed 40,132 fish and a minimum of 32 fish species. Rockfishes (*Sebastes* spp.) dominated the assemblage both in diversity and abundance. Squarespot rockfish (*Sebastes hopkinsi*), a schooling small-sized species, was the most abundant taxa, while blue rockfish (*S. mystinus*), blackeye goby (*Rhinogobiops nicholsii*), blacksmith (*Chromis punctipinnis*), halfbanded rockfish (*S. semicinctus*), vermilion rockfish (*S. miniatus*), rosy rockfish (*S. rosaceus*), senorita (*Oxyjulis californica*), lingcod (*Ophiodon elongatus*), and sharpnose/white seaperches (*Phanerodon atripes* and *P. furcatus*) were also characteristic species. The species assemblage on these outcrops represented a transition between that of the nearshore kelp beds and those more typical of deeper-water sites. The fish assemblage changed over time, due primarily to the addition of some species and increases in densities of many taxa. This occurred during a period where the oceanographic regime shifted from low productivity and warm water to high productivity and cool conditions.

INTRODUCTION

The fish assemblages of several benthic marine habitats in southern California have been well described. Trawl surveys (e.g., Allen et al. 2002) have characterized soft sea floor assemblages and considerable attention has been given to the hard bottom fish assemblages in the shallow photic zone (30 m and less) (North and Hubbs 1968; Ebeling et al. 1980; Stephens et al. 1984). However, the fish assemblages of rocky outcrops below 30 m remain very poorly described. With the exception of a semi-quantitative survey of some rocky outcrop fishes on Tanner and Cortes banks (Lissner and Dorsey 1986), there have been no published accounts, based on underwater observations, of the fish communities that inhabit rocky outcrops in waters below about 30 m in the Southern California Bight.

Since 1995 we have conducted surveys of the fish assemblages of oil platforms and natural reefs in 30 to 360 m of water in southern California using a manned submersible. Usually, reefs were surveyed once or twice over this period. In contrast, a rocky area in the deep photic zone (45–50 m of water) in the Anacapa Passage (between Anacapa and Santa Cruz islands) was surveyed during six of the nine years. Our repeated visits to the

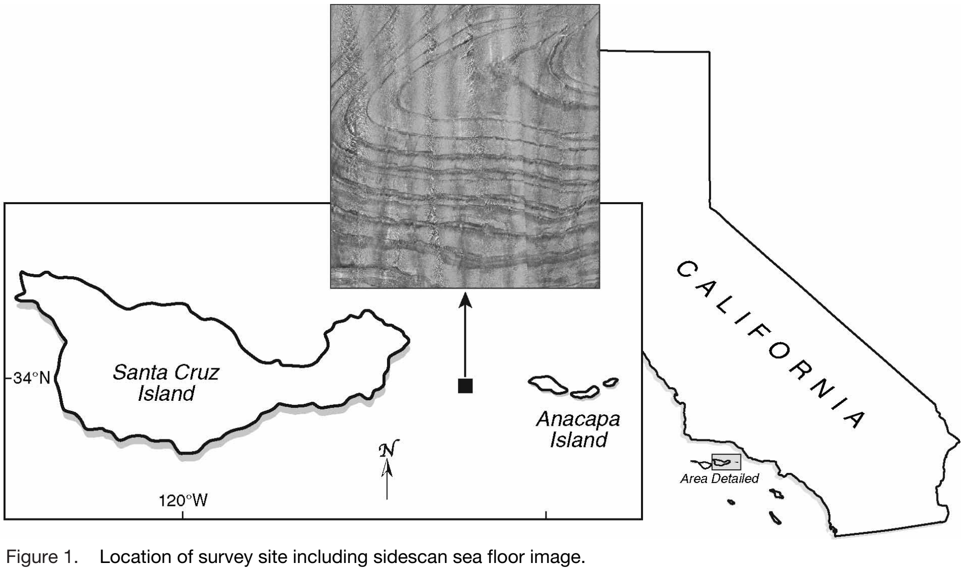

Figure 1. Location of survey site including sidescan sea floor image.

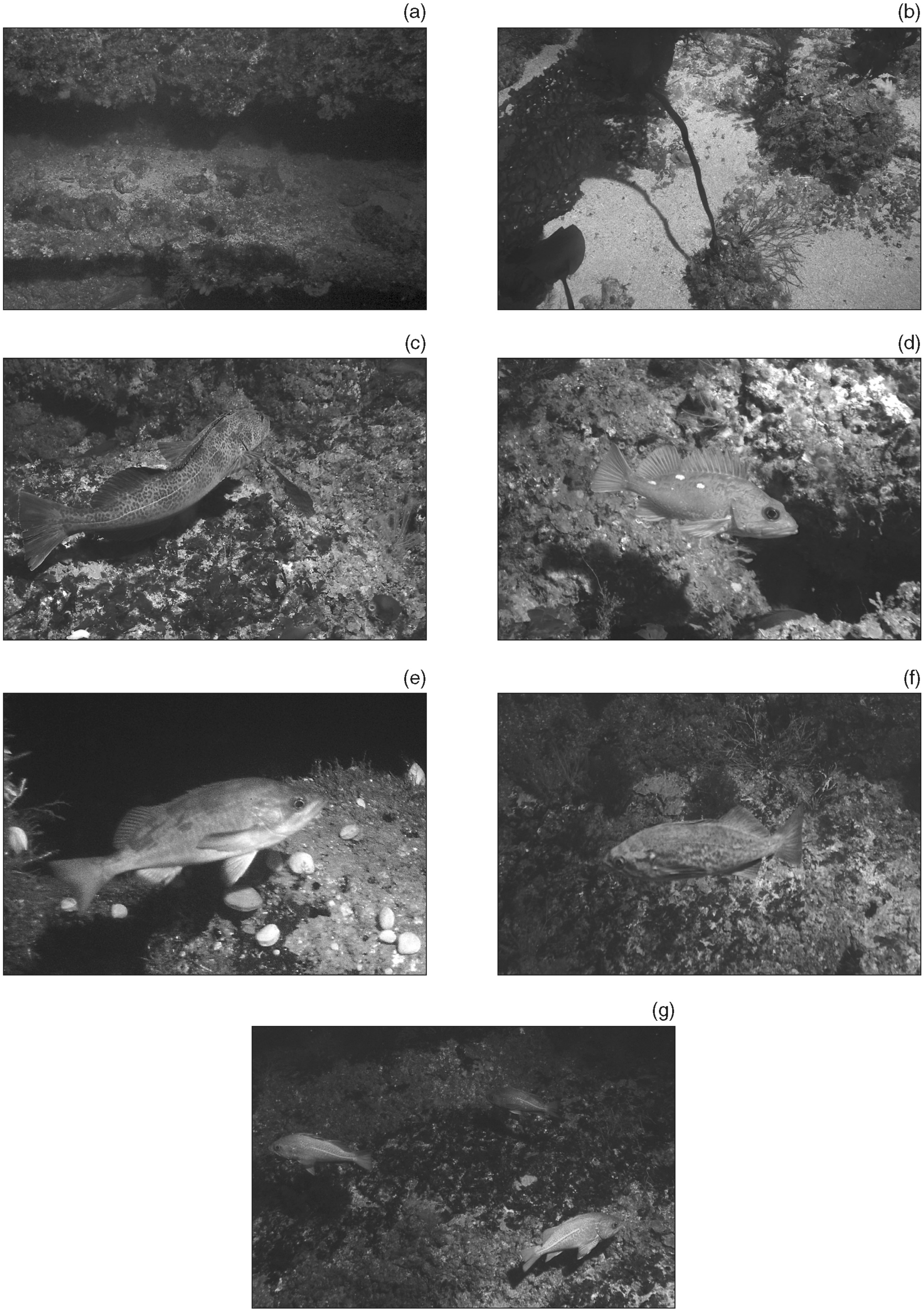

Figure 2. Typical habitat and fishes of the study site: (A) boulder and ledge habitat, (B) small boulders and sand with brown algae, (C) juvenile lingcod (*Ophiodon elongatus*), (D) rosy rockfish (*Sebastes rosaceus*), (E) squarespot rockfish (*S. hopkinsi*), (F) blue rockfish (*S. mystinus*), and (G) juvenile vermilion rockfish (*S. miniatus*).

Anacapa Passage site have provided us with an opportunity to both characterize this previously little-known fish community and to observe how that community changed over the study period; it is that which we explore in this study.

METHODS

Study area: The study area is located at approximately 33°59.9'N, 119°28.6'W (fig. 1). The outcrops lie at depths of 45–50 m and some extend more or less unbroken for at least 1,500 m. The features are sedimentary rock that extends 1–2 m above the sandy sea floor forming ledges with shelter holes and overhangs. The rock has been differentially eroded with some layers sticking up through thin sediment, forming long, linear ridges (fig. 1). The layers that are most easily eroded form low areas filled with coarse sediments (Cochrane et al. 2003). Some of the outermost sections of exposed strata have collapsed, adding boulders to the ledge habitat (fig. 2). Cobble surrounds some of these features. The outcrops support locally high densities of brown algae (including *Laminaria farlowii*), foliose red algae (*Plocamium cartilagineum*), articulate coralline algae (*Bossiella californica*), branching coralline algae (probably *Calliarthron tuberculosum*), and encrusting coralline algae. Sponges, red urchins, gorgonians, and bryozoans also dot the outcrops.

Field sampling: We surveyed fish assemblages using the *Delta* research submersible, a 4.6 m, two-person vessel, operated by Delta Oceanographics of Oxnard, California. Aboard the *Delta*, we conducted 15-minute-long (10 minute 1995) belt transects about 2 m from the substrata, while the submarine maintained a speed of about 0.5 knots. We conducted surveys in 1995, 1999, and 2001–04. Four transects were conducted in every year except 1999 and 2001, when three transects were made. Within the study area, we selected ridges more or less randomly and transects were run parallel to these structures. In every year except 2002, surveys were conducted in October; in 2002 surveys occurred in November. Late fall is the optimal time to conduct surveys because of generally good weather and water clarity. In addition, many fish species have completed their seasonal juvenile recruitment by this time.

In each year, submersible surveys were conducted during daylight hours between 1400 and 1700. The same observer (D.S.) conducted all of the transects during all years. During each transect, the researcher made observations from a viewing port on the starboard side of the submersible. An externally mounted hi-8 mm video camera with associated lights filmed the same viewing fields as seen by the observer. The observer identified, counted, and estimated the lengths of all fishes and verbally recorded those data onto the video tape. All fishes in a volume 2 m from the seafloor upwards and from the submarine outwards were counted. Fish lengths were estimated 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 to both the observer and the video camera. Transect lengths were computed by counting the number of 20 cm laser segments in 15 second subsamples (one per minute) throughout the transect, calculating speed based on those counts and averaging it over the whole transect, and multiplying that average speed by the transect duration.

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 was overlaid on the original videotape upon completion of each survey. Transect videos were reviewed aboard the research vessel or in the laboratory and observations transcribed into a database. For each fish, we recorded species and estimated its total length in 5 cm increments. All individuals were identified to species. The common and scientific names of all species observed are listed in Table 1.

Statistical analyses: Interannual relationships in the Anacapa Passage fish assemblage were investigated using

TABLE 1
Common and scientific names of species observed in this study.

Common Name	Scientific Name
Blackeye goby	*Rhinogobiops nicholsii*
Black perch	*Embiotoca jacksoni*
Blacksmith	*Chromis punctipinnis*
Blue rockfish	*Sebastes mystinus*
Bocaccio	*Sebastes paucispinis*
California scorpionfish	*Scorpaena guttata*
California sheephead	*Semicossyphus pulcher*
Copper rockfish	*Sebastes caurinus*
Deepwater blenny	*Cryptotrema corallinum*
Flag rockfish	*Sebastes rubrivinctus*
Gopher rockfish	*Sebastes carnatus*
Halfbanded rockfish	*Sebastes semicinctus*
Honeycomb rockfish	*Sebastes umbrosus*
Kelp rockfish	*Sebastes atrovirens*
Lingcod	*Ophiodon elongatus*
Olive rockfish	*Sebastes serranoides*
Painted greenling	*Oxylebius pictus*
Pile perch	*Rhachochilus vacca*
Pink seaperch	*Zalembius rosaceus*
Pygmy rockfish	*Sebastes wilsoni*
Rainbow seaperch	*Hypsurus caryi*
Rosy rockfish	*Sebastes rosaceus*
Rubberlip seaperch	*Rhachochilus toxotes*
Senorita	*Oxyjulis californica*
Sharpnose seaperch	*Phanerodon atripes*
Squarespot rockfish	*Sebastes hopkinsi*
Starry rockfish	*Sebastes constellatus*
Treefish	*Sebastes serriceps*
Unidentified ronquil	
Unidentified seaperches[1]	*Phanerodon* sp.
Vermilion rockfish	*Sebastes miniatus*
White seaperch	*Phanerodon furcatus*
Wolf-eel	*Anarrhichthys ocellatus*

[1] Probably both sharpnose and white seaperches.

hierarchical cluster analysis and non-metric multidimensional scaling (MDS) plots. We fourth-root transformed fish densities (the full species set was used) to reduce the impact of extremely abundant species, and then constructed a triangular similarity matrix among year-pairs using the Bray-Curtis index (Bray and Curtis 1957). The Bray-Curtis index is useful in ecological analyses because joint absences of species between sample pairs are not used in similarity calculations (joint absences being difficult to interpret biologically). Of further benefit, the Bray-Curtis index is robust to non-linear species responses (Faith et al. 1987). Using this similarity matrix, we constructed a dendrogram of all transects using a hierarchical agglomerative procedure, with group-average linking (McCune and Grace 2002), to determine if transects grouped randomly or were nested within years. Next, we displayed similarities using MDS plots to illustrate relationships among all transects and among years (using the mean of either three or four transects surveyed during each year) in two dimensions. The usefulness of the two-dimensional display is represented by the stress statistic, where stress values <0.1 are reliable depictions of relationships, and stress values >0.2 are unreliable depictions of relationships (Clarke 1993). Both MDS plots show the minimum stress calculated from 1,000 random starts.

We tested the significance of among-year similarities in the structure of the Anacapa Passage fish assemblage by using a one-way analysis of similarity (ANOSIM; Clarke and Warwick 1994). We further investigated among-year differences in density and size structure of the most abundant fish species observed during the study. Density analyses used either a fixed-factor, one-way analysis of variance (ANOVA), or its nonparametric equivalent, the Kruskal-Wallis ANOVA, to test for significant differences in density among years. Density data were transformed when appropriate to meet ANOVA assumptions of normality and heterogeneity.

The PRIMER statistical package was used to calculate similarities, generate the dendrogram and MDS ordination plots, and to calculate ANOSIMs. The software program SPSS was used to conduct ANOVA and Kruskal-Wallis tests.

RESULTS

Over the course of the study, we observed 40,132 fish representing a minimum of 32 fish species (tab. 2). Rockfishes, genus *Sebastes*, dominated the assemblage (fig. 2), comprising almost half (15 of 32) of all species observed. Rockfishes made up 91.2% of all fishes surveyed. Over all years, squarespot rockfish, a schooling dwarf species, was by far the most abundant; it comprised a minimum of 78.4% of all fishes seen. Even when squarespot rockfish were subtracted from the observations, rockfishes still comprised 59.4% of all fishes. Other particularly abundant species included blue rockfish, blackeye goby, blacksmith, and halfbanded rockfish. Vermilion and rosy rockfishes, senorita, lingcod, and sharpnose/white seaperches comprised the remaining top ten species or species complexes.

Many of the species we observed recruited as young-of-the-year (YOY) to the study reefs (we defined recruited fish as those less than 10 cm long, except for 5 cm for blackeye gobies). Of the most abundant fishes, species that at least occasionally recruited as YOYs included blue, halfbanded, rosy, and squarespot rockfishes, blackeye goby, blacksmith, and sharpnose/white seaperch (not figured) (fig. 3). Of the less abundant species, we also observed some recruitment of flag, pygmy, rosy, and starry rockfishes, treefish, pink seaperch, painted greenling, and deepwater blennies. Recruitment from the plankton was sporadic among years and some species, such as blacksmith, recruited in only one year. Among the more abundant species, we did not observe YOY recruitment of lingcod, vermilion rockfish, and senorita.

Assemblages of fishes on transects exhibited consistent temporal patterns as indicated in both cluster and MDS plots (figs. 4A, B). The ANOSIM showed that the Anacapa Passage fish assemblage changed significantly over the course of the study, though, not surprisingly, pairwise comparisons revealed that years close together in time were similar (tab. 3). Through 2004, the fish assemblage continued to diverge, becoming increasingly unlike that of the earlier years (fig. 4C). Many of the changes we observed were caused by an increase both in the overall number of species living on the reefs and in the density of many species (tab. 2). In particular, the densities of blue (*Sebastes mystinus*), halfbanded (*S. semicinctus*), rosy (*S. rosaceus*), squarespot (*S. hopkinsi*), starry (*S. constellatus*), and vermilion (*S. miniatus*) rockfishes, blackeye goby (*Rhinogobiops nicholsii*), blacksmith (*Chromis punctipinnis*), lingcod (*Ophiodon elongatus*), painted greenling (*Oxylebius pictus*), and treefish (*S. serriceps*) all increased over time.

Of the eleven species with the highest mean density over all years, eight species varied significantly through time (tab. 4), and this variability was generally on the order of one magnitude (tab. 2). For species that had significant changes, we used density information along with size distributions to infer potential sources of density variability.

For squarespot rockfish, the dominant species in the Anacapa Passage assemblage, inspection of size distributions showed that years with the highest densities (2001, 2003, 2004) were characterized by strong YOY classes (tab. 2, fig. 3A). Due to the diminutive maximum size of squarespots, size classes were too coarse to follow pulses of YOY recruitment through time. The year of

TABLE 2
Numbers, densities, and mean total lengths (standard deviations in parentheses) of the species observed in the Anacapa Passage, 1995, 1999, 2001–04. Species ordered by overall abundances. Unidentified species are listed at the end of the table.

Common Name		1995	1999	2001	2002	2003	2004
Squarespot rockfish	Total	1313	3231	868	255	12,609	13,177
	Density	50.48 (64.4)	121.90 (84.9)	28.89 (33.8)	13.22 (4.3)	236.00 (204.3)	351.99 (332.5)
	TL	14.94 (3.3)	10.45 (1.7)	11.29 (4.5)	13.25 (3.6)	5.17 (1.2)	12.41 (4.4)
Blue rockfish		75	218	182	444	1275	127
		2.95 (2.1)	8.45 (3.8)	5.93 (4.2)	23.30 (10.7)	23.18 (17.3)	3.29 (1.4)
		24.77 (4.3)	17.80 (9.0)	22.80 (4.4)	23.20 (5.0)	23.50 (3.0)	22.26 (3.6)
Blackeye goby		8	64	73	273	95	692
		0.33 (0.3)	2.42 (1.2)	2.37 (1.4)	14.05 (10.9)	1.60 (1.7)	18.74 (9.3)
		12.13 (3.2)	10.23 (1.1)	11.30 (2.8)	10.53 (2.6)	11.32 (3.3)	10.03 (1.4)
Halfbanded rockfish		—	5	—	—	810	266
		—	0.19 (0.2)	—	—	15.27 (16.1)	6.86 (5.8)
		—	10.00 (0.0)	—	—	5.00 (0.0)	10.08 (1.1)
Blacksmith		—	—	294	213	554	41
		—	—	9.40 (8.1)	11.28 (12.6)	8.63 (7.5)	1.11 (0.8)
		—	—	18.18 (2.9)	19.91 (2.1)	17.05 (5.9)	19.39 (2.3)
Senorita		202	13	23	—	27	2
		7.98 (15.7)	0.49 (0.7)	0.65 (0.9)	—	0.47 (0.7)	0.05 (0.1)
		20.00 (0.0)	10.77 (2.8)	18.48 (3.2)	—	20.00 (0.0)	20.00 (0.0)
Sharpnose/White seaperch		21	38	98	3	4	76
		0.94 (1.8)	1.50 (2.1)	2.64 (5.1)	0.16 (0.1)	0.07 (0.1)	2.03 (2.2)
		10.00 (5.5)	11.18 (5.8)	5.10 (1.0)	6.67 (1.7)	10.00 (5.8)	10.13 (4.8)
Rosy rockfish		6	44	42	66	65	111
		0.25 (0.2)	1.66 (1.4)	1.36 (1.0)	3.41 (1.6)	1.11 (0.8)	3.01 (1.5)
		19.17 (3.8)	19.32 (4.0)	18.81 (2.7)	18.94 (2.7)	18.98 (2.7)	18.83 (2.8)
Vermilion rockfish		15	34	21	98	175	50
		0.60 (0.2)	1.30 (0.5)	0.69 (0.7)	5.09 (1.8)	3.06 (1.1)	1.35 (0.6)
		38.00 (5.6)	34.26 (6.6)	30.71 (5.1)	26.73 (4.8)	28.24 (6.1)	28.90 (6.2)
Lingcod		18	8	49	64	78	50
		0.73 (0.1)	0.31 (0.1)	1.58 (0.9)	3.34 (0.2)	1.40 (0.7)	1.35 (0.4)
		52.50 (17.8)	38.75 (9.5)	38.85 (11.0)	41.75 (9.0)	44.49 (7.6)	38.67 (11.9)
California sheephead		8	16	15	16	61	11
		0.34 (0.2)	0.62 (0.5)	0.46 (0.2)	0.83 (0.2)	1.12 (0.8)	0.29 (0.2)
		29.38 (10.2)	24.69 (12.0)	21.67 (5.6)	28.75 (7.6)	28.81 (8.4)	22.27 (2.6)
Treefish		—	—	35	24	4	26
		—	—	1.15 (0.9)	1.26 (0.4)	0.07 (0.1)	0.71 (0.3)
		—	—	24.29 (3.2)	22.92 (4.2)	22.50 (5.0)	22.12 (2.9)
Starry rockfish		—	2	10	14	5	50
		—	0.08 (0.1)	0.33 (0.3)	0.73 (0.3)	0.08 (0.1)	1.36 (0.7)
		—	15.00 (7.1)	25.00 (4.7)	26.07 (6.6)	22.00 (2.7)	15.80 (9.0)
Painted greenling		1	8	10	9	21	22
		0.04 (0.1)	0.30 (0.2)	0.31 (0.3)	0.47 (0.3)	0.37 (0.1)	0.61 (0.4)
		15.00 (0.0)	13.13 (3.7)	16.00 (2.1)	14.44 (1.7)	14.52 (3.1)	15.23 (3.3)
Copper rockfish		5	7	3	15	13	9
		0.22 (0.3)	0.27 (0.1)	0.10 (0.1)	0.78 (0.4)	0.22 (0.1)	0.23 (0.2)
		26.00 (8.9)	28.57 (3.8)	18.33 (2.9)	23.33 (4.1)	24.62 (3.2)	20.00 (5.6)
Gopher rockfish		1	11	8	15	7	6
		0.04 (0.8)	0.41 (0.5)	0.25 (0.2)	0.78 (0.0)	0.11 (0.1)	0.17 (0.2)
		—	24.55 (5.7)	19.38 (4.2)	23.00 (2.5)	22.86 (2.7)	21.67 (2.6)
Rubberlip seaperch		1	—	3	14	26	4
		0.04 (0.1)	—	0.10 (0.1)	0.74 (0.6)	0.47 (0.7)	0.11 (0.2)
		40.00 (0.0)	—	31.67 (2.9)	31.43 (3.1)	26.15 (5.5)	32.50 (2.9)
Olive rockfish		8	2	2	8	5	7
		0.32 (0.2)	0.08 (0.1)	0.05 (0.1)	0.41 (0.5)	0.08 (0.1)	0.19 (0.1)
		38.13 (7.0)	40.00 (0.0)	27.50 (3.5)	27.5 (4.6)	29.00 (8.2)	27.86 (2.7)
Pile perch		12	—	1	4	2	—
		0.47 (0.4)	—	0.03 (0.1)	0.21 (0.1)	0.04 (0.0)	—
		25.50 (7.3)	—	30.00 (0 .0)	31.25 (7.5)	27.50 (3.5)	—
Black perch		8	—	—	—	—	—
		0.31 (0.2)	—	—	—	—	—
		23.75 (2.3)	—	—	—	—	—
Pygmy rockfish		—	12	—	—	—	—
		—	0.45 (0.8)	—	—	—	—
		—	10.00 (0.0)	—	—	—	—

TABLE 2 (continued)

Numbers, densities, and mean total lengths (standard deviations in parentheses) of the species observed in the Anacapa Passage, 1995, 1999, 2001–04. Species ordered by overall abundances. Unidentified species are listed at the end of table.

Common Name	1995	1999	2001	2002	2003	2004
California scorpionfish	—	—	1	—	5	7
	—	—	0.03 (0.1)	—	0.08 (0.0)	0.19 (0.1)
	—	—	30.00 (0.0)	—	27.00 (2.7)	24.29 (1.9)
Flag rockfish	1	—	2	—	6	1
	0.04 (0.1)	—	0.06 (0.1)	—	0.12 (0.2)	0.03 (0.1)
	10.00 (0.0)	—	15.00 (0.0)	—	21.00 (9.6)	20.00 (0.0)
Deepwater blenny	—	—	2	—	3	1
	—	—	0.06 (0.1)	—	0.04 (0.1)	0.03 (0.1)
	—	—	15.00 (0.0)	—	15.00 (0.0)	10.00 (0.0)
Kelp rockfish	—	—	1	—	—	1
	—	—	0.03 (0.1)	—	—	0.03 (0.1)
	—	—	25.00 (0.0)	—	—	25.00 (0.0)
Honeycomb rockfish	1	—	1	—	—	1
	0.04 (0.1)	—	0.04 (0.1)	—	—	0.03 (0.1)
	20.00 (0.0)	—	15.00 (0.0)	—	—	20.00 (0.0)
Rainbow seaperch	—	—	—	—	—	—
	—	—	—	—	—	—
	—	—	—	—	—	—
Wolf-eel	—	—	—	—	—	—
	—	—	—	—	—	—
	—	—	—	—	—	—
Pink seaperch	1	—	1	—	—	—
	0.04 (0.1)	—	0.03 (0.1)	—	—	—
	15.00 (0.0)	—	5.00 (0.0)	—	—	—
Bocaccio	1	—	—	—	—	1
	0.04 (0.1)	—	—	—	—	0.02 (0.1)
	100.00 (0.0)	—	—	—	—	25.00 (0.0)
Unidentified young-of-year rockfishes	—	11	—	—	386	162
	—	0.42 (0.3)	—	—	6.95 (6.9)	4.25 (4.9)
	—	5.00 (0.0)	—	—	5.00 (0.0)	5.00 (0.0)
Unidentified rockfishes	—	18	3	4	36	14
	—	0.68 (0.5)	0.09 (0.1)	0.21 (0.2)	0.57 (0.4)	0.38 (0.2)
	—	10.00 (0.0)	20.00 (10.0)	15.00 (8.7)	15.59 (5.0)	16.15 (5.5)
Unidentified fishes	—	6	1	1	28	10
	—	0.23 (0.2)	0.04 (0.1)	0.05 (0.1)	0.47 (0.3)	0.27 (0.3)
	—	16.67 (19.2)	15.00 (0.0)	—	7.14 (5.0)	6.00 (2.1)
Unidentified seaperches	59	57	1	1	11	1
	2.37 (4.4)	2.28(3.9)	0.03 (0.1)	0.05 (0.1)	0.19 (0.1)	0.03 (0.1)
	5.42 (1.4)	10.35 (2.7)	5.00 (0.0)	20.00 (0.0)	10.91 (5.8)	15.00 (0.0)
Unidentified ronquils	1	1	—	—	—	5
	0.04 (0.1)	0.04 (0.1)	—	—	—	0.14 (0.1)
	20.00 (0.0)	25.00 (0.0)	—	—	—	16.00 (5.5)
Unidentified sculpins	24	—	—	—	—	3
	1.00 (1.6)	—	—	—	—	0.08 (0.2)
	5.83 (3.2)	—	—	—	—	6.67 (2.9)

lowest squarespot rockfish density (2002; tab. 2) coincided with the year of greatest density of piscivorous species (lingcod and various large rockfishes). However, it is not clear if this inverse relationship is due to a reduction of individuals through predation, behavioral shifts by squarespots to areas of lower predator density, or some other reason.

A suite of five species (blackeye goby, lingcod, and blue, rosy, and vermilion rockfishes) generally increased in density during the study, with 2002 the strongest year for all species. In particular, we can see effects of the 1999 oceanographic conditions, which have been noted as a good year for survival for lingcod and blue and vermilion rockfish juveniles in the Southern California Bight

TABLE 3

Multivariate analysis of similarity (ANOSIM) to detect differences in fish assemblage structure among years. Bars beneath pairwise comparisons between years show levels of significance greater than $P = 0.05$.

Factor	Sample Statistic (Global *R*)	Number of Permutations[a]		Significance Level (*P*)	
Year	0.567	0/1000		0.001	
1995	1999	2001	2002	2003	2004

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[a] The number of permuted statistics ≥ to the sample statistic out of a random sample from a large number of possible permutations.

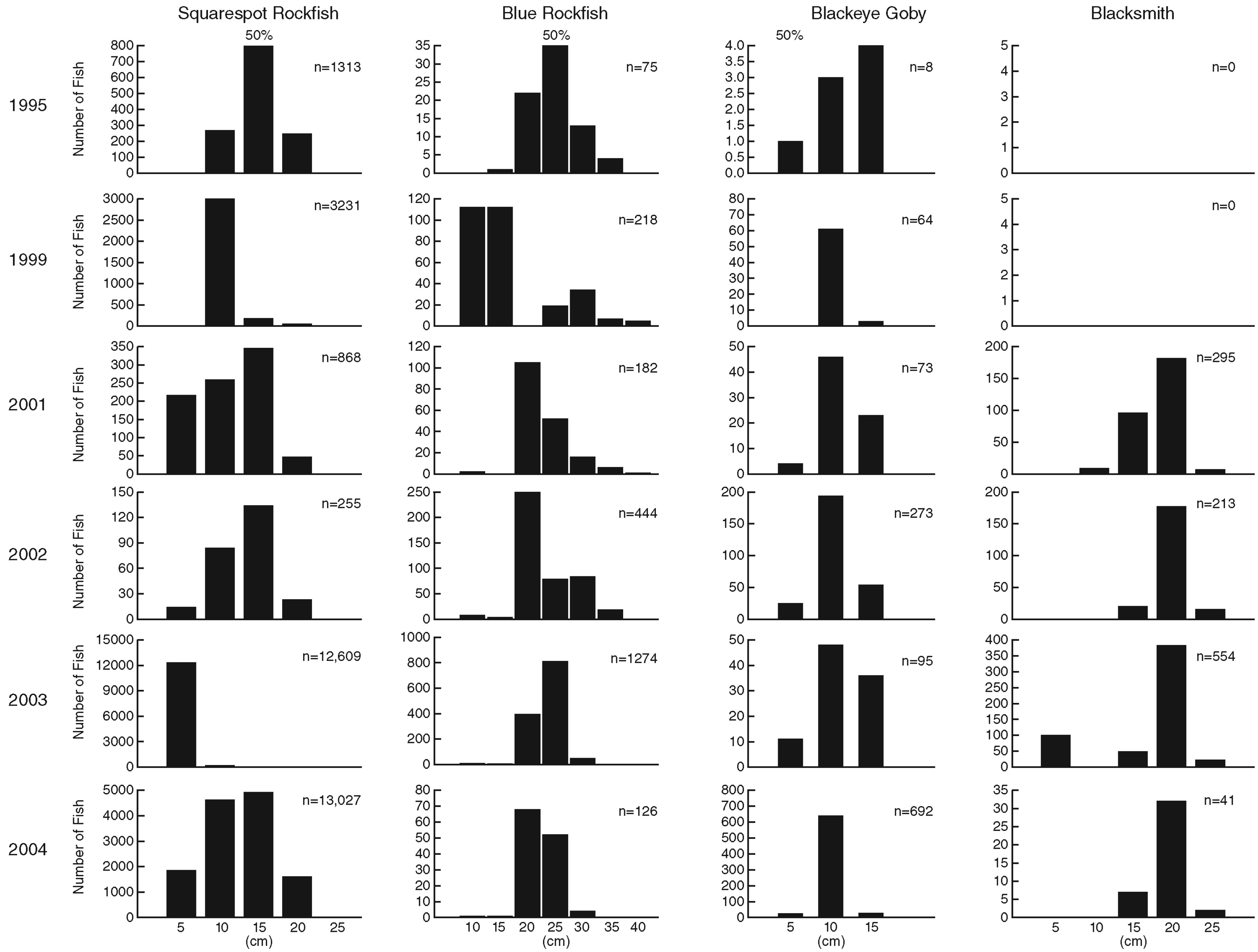
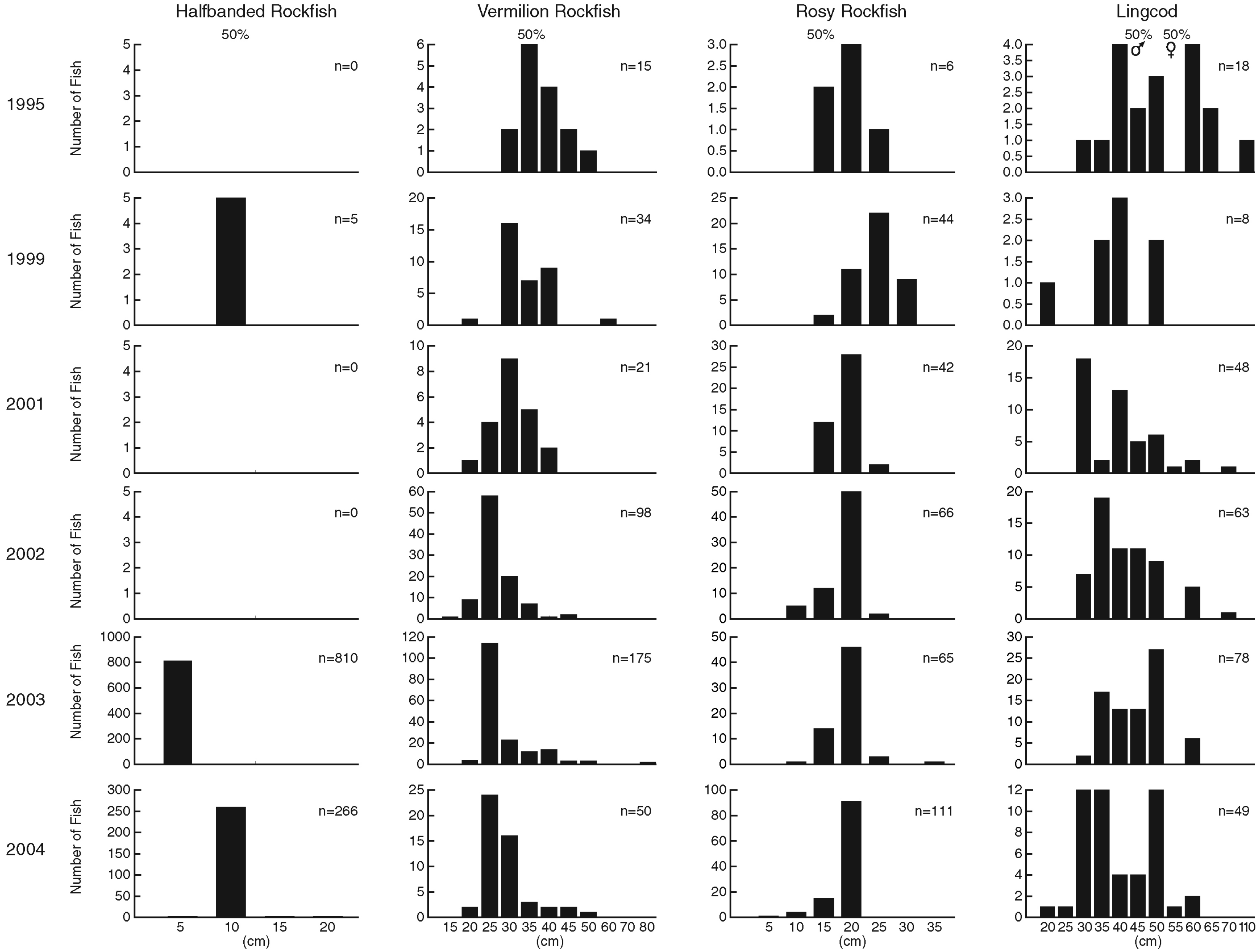


Figure 3. Size-frequency histograms of some major species observed in this study. Individuals 10 cm or less were assumed to be young-of-the-year for all species except blackeye goby (*Rhinogobiops nicholsii*) (young-of-the-year were 5 cm long). Also noted are the sizes at 50% maturity (data for halfbanded (*Sebastes semicinctus*), rosy (*S. rosaceus*), squarespot (*S. hopkinsi*), and vermilion (*S. miniatus*) rockfishes are from Love et al. (2002); blue rockfish (*S. mystinus*) from Miller and Geibel (1973); blackeye goby from Wiley (1970); lingcod (*Ophiodon elongatus*) from Silverberg et al. (2001); and blacksmith (*Chromis punctipinnis*) from Limbaugh (1955)).



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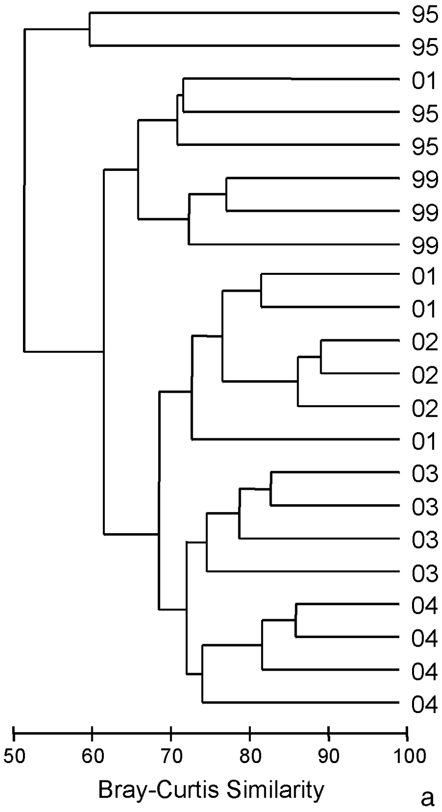

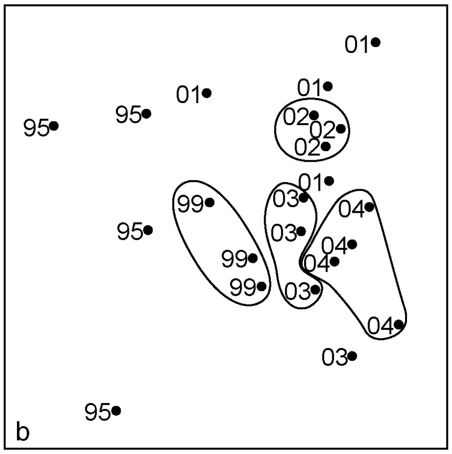

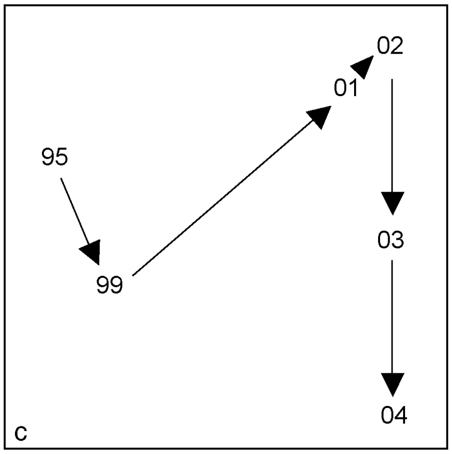

Figure 4A. Dendrogram from standard hierarchical cluster analysis using Bray-Curtis similarities on fourth-root transformed fish densities for all transects.
Figure 4B. MDS ordination of Bray-Curtis similarities showing fish assemblage relationships among all transects. Stress = 0.15.
Figure 4C. MDS ordination showing fish assemblage relationships among years. Arrows indicate shifts of assemblage in hyperspace through time. Stress = 0.0.

TABLE 4

Summary of results from analyses of variance (ANOVA and Kruskal-Wallis ANOVA) testing interannual significance on density of selected species in the Anacapa Passage fish assemblage. P values in bold are significant at the <0.05 level.

Common Name	Mean no. fish/ 100m^2 (all years)	Data transformation	Test	*F* or chi-square	*P*
Squarespot rockfish	133.7	log(*x*+1)	ANOVA	3.765	0.019
Blue rockfish	11.2	log(*x*+1)	ANOVA	6.091	0.002
Blackeye goby	6.6	log(*x*+1)	ANOVA	14.832	0.000
Halfbanded rockfish	7.4		Kruskal-Wallis	18.096	0.003
Blacksmith	7.6		Kruskal-Wallis	14.935	0.011
Senorita	1.9		Kruskal-Wallis	5.682	0.338
Sharpnose/White seaperch	1.2		Kruskal-Wallis	2.702	0.764
Rosy rockfish	1.8	none	ANOVA	4.147	0.013
Vermilion rockfish	2.0		Kruskal-Wallis	16.366	0.006
Lingcod	1.5		Kruskal-Wallis	14.427	0.013
California sheephead	0.6	none	ANOVA	2.497	0.075
Treefish	0.8		Kruskal-Wallis	17.326	0.004
Starry rockfish	0.5	log(*x*+1)	ANOVA	14.306	0.000
Painted greenling	0.4	log(*x*+1)	ANOVA	2.631	0.064
Copper rockfish	0.3	log(*x*+1)	ANOVA	3.274	0.032
Gopher rockfish	0.3		Kruskal-Wallis	9.585	0.088
Rubberlip seaperch	0.3		Kruskal-Wallis	5.995	0.307
Pile perch	0.2		Kruskal-Wallis	17.539	0.004
Black perch	0.3		Kruskal-Wallis	14.826	0.011
California scorpionfish	0.1		Kruskal-Wallis	16.515	0.006

(Love et al. 2002, 2003; Jagielo and Wallace 2005; MacCall 2005). Blackeye goby and rosy rockfish did not show any pattern between density and size structure, perhaps because the size classes were too coarse to detect patterns.

Blue rockfish YOY recruited strongly to the Anacapa Passage in 1999. In 2001 and 2002, 20 cm fish dominated the size distribution, with 25 cm showing strongly in 2003. This pulse of blue rockfish sizes corresponds to sizes we might expect from fish recruiting in the 1999 year class. Densities of 20 cm and 25 cm fish are greater than the original density of YOY fish, suggesting that fish which recruited as juveniles to other habitats (perhaps nearby kelp beds) immigrated to deeper reefs as they matured. A few blue rockfish YOY were observed in 2001, 2003, and 2004.

For vermilion rockfish, high density years were dominated by 25 cm fish, which is in the size range that we would expect from fish recruiting in 1999. As we observed in blue rockfish, it appears that vermilion rockfish recruit as juveniles to other and shallower habitats, and immigrate to deeper reefs as they grow larger. There are low densities of adult vermilion rockfish, perhaps suggesting that the majority of larger fish seek out even deeper reefs.

Blacksmith were completely absent in 1995 and 1999, but then showed a spike in 2001. Densities of blacksmith then declined over the final years within the study. Halfbanded rockfish density varied sporadically across years, which may reflect the amount of sandy habitat in transects, and not reflect real population trends in time. The senorita and sharpnose/white seaperch complex showed no significance among years, probably due to its patchy spatial distribution. Finally, we note that sheephead did not show significant differences among years.

DISCUSSION

The fish assemblage living on the Anacapa Passage reefs represents a transition between that found in southern California kelp beds and nearshore outcrops and that of deeper-water features. Of the relatively abundant species in our study, blackeye goby, blacksmith, blue and gopher rockfishes, senorita, California sheephead, painted greenling, and rubberlip seaperch are also abundant in shallower waters. On the other hand, rosy, squarespot, starry, and post-YOY vermilion rockfishes rarely inhabit shallower waters in southern California and all have ranges that extend much deeper than our survey sites. Two species, blacksmith and kelp rockfish, were near their maximum depth ranges on these outcrops and our observations of both rainbow seaperch and rubberlip seaperch comprised new maximum depth records (Love et al. 2005). A number of species that commonly occur on shallow hard features at Anacapa and Santa Cruz islands, such as black-and-yellow rockfish (*Sebastes chrysomelas*), garibaldi (*Hypsypops rubicunda*), kelp bass (*Paralabrax clathratus*), opaleye (*Girella nigricans*), and rock wrasse (*Halichoeres semicinctus*) (Ebeling et al. 1980; Kushner et al. 2001) were absent from these outcrops. Similarly, several species (i.e., greenspotted, *S. chlorostictus*, and swordspine, *S. ensifer*, rockfishes) typical of nearby outcrops in 80–100 m of water did not occur at our study site.

The Anacapa Passage assemblage was structured both by species that recruit as YOY to the study reefs and by somewhat older individuals that recruit elsewhere and immigrated to these reefs. Most or all of some species, such as halfbanded and squarespot rockfishes and blackeye goby, originated as YOY recruits to the study reefs. Pelagic juveniles of both halfbanded and squarespot rockfishes rarely settle in to shallower waters. On the other hand, some species (e.g., blacksmith and blue rockfish) rarely recruit into these relatively deep waters and the occurrence of very young fishes was relatively uncommon. All members of some species, such as vermilion rockfish (which are known to recruit to shallower waters, Love et al. 2002) and lingcod (which recruit to a wide range of depths but usually to low relief, Miller and Geibel 1973) settled elsewhere and immigrated to the reefs. We did not observe species that likely settled deeper and then swam into shallower waters. Thus, the species assemblage of our study site reflects recruitment success both on our study outcrops and at other, mostly shallower, sites. Clearly there is connectivity between the relatively deep reefs we studied and those that are shallower, as the densities of some species that live on the Anacapa Passage outcrops are dependent on more shallow-water productivity. On the other hand, it can be argued that the year-class success of some species that recruit to nearshore waters, such as vermilion rockfish, may be dependent on larvae from adults living on deeper reefs.

Most of the changes in the assemblage represented increasing densities of a number of species, probably reflecting increased productivity in nearshore waters, rather than a turnover in species composition. It is likely that at least some of the alteration in fish assemblages was linked to recent changes in oceanographic conditions that were conducive to increased larval survivorship. Bograd et al. (2000) noted that between 1997 and 1999 oceanographic conditions off southern California “shifted dramatically off southern California” from low productivity and warm water to high productivity and cool conditions. During 1999, we made extensive scuba and submersible fish assemblage surveys throughout the Santa Barbara Channel, northern Channel Islands, and off Points Conception and Arguello around both oil platforms and over natural outcrops. During these surveys we noted higher young-of-the-year densities of a number of species compared to what we had seen between 1995 and

1998 (Love et al. 2001; Schroeder 2001). Species that recruited more heavily in that year included blue, flag, halfbanded, olive, vermilion, and widow (*S. entomelas*) rockfishes, cowcod (*S. levis*), bocaccio (*S. paucispinis*), lingcod, and kelp greenling (*Hexagrammos decagrammus*). During that same year, relatively high recruitment of blue, olive, and vermilion rockfishes and treefish was also noted around some of the northern Channel Islands (Kushner et al. 2001).

The fate of the present fish assemblage, which reflects the highly productive and cooler waters that began in 1999, is unclear. Regarding much of the California Current, Peterson et al. (2006) stated that the "dramatic shift to cold ocean conditions that lasted for a period of four years (1999–2002)" was followed by a "more subtle but persistent return to warm ocean conditions initiated in October 2002." If these warm conditions, which led to reduced fish recruitment in many areas, persist, we might expect overall fish densities to decline and perhaps a return to the assemblages of earlier years.

Diminutive fishes dominated our study reefs. Dwarf species, such as squarespot and halfbanded rockfishes, or blackeye goby, were very abundant and comprised most of the assemblage. Among species that grow to substantial sizes, such as lingcod and vermilion rockfish, we observed relatively few large individuals. In southern California, larger vermilion rockfish and lingcod are only rarely found in nearshore waters. On our study reefs, it is likely that at least some of the larger adults of these species migrate into deeper waters. However, we believe that at least part of this phenomenon is due to substantial fishing pressure acting on local fish populations. The Anacapa Passage is located close to four mainland harbors and is usually protected from prevailing winds. For many decades these outcrops have been heavily fished by commercial passenger fishing vessels, private vessel recreational anglers, and, to a lesser extent, by commercial fishermen (Love et al. 1985; Schroeder and Love 2002). On our study reefs, fishing may not alter the species composition of the assemblage (i.e., removing the last member of a species). Rather it may crop and thus reduce the abundance of larger individuals and allow for increased densities of smaller fishes. However, this pattern is not limited to outcrops in the Anacapa Passage; many reefs off California are dominated by small fishes, reflecting intense fishing pressure (Yoklavich et al. 2000; Love and Yoklavich 2006).

ACKNOWLEDGEMENTS

We would like to thank Lyman Thorsteinson for his unflagging support of this research. This research was funded by the Biological Resources Division, U. S. Geological Survey (National Offshore Environmental Studies Program 1445-CA-0995-0386) based on an information need identified by the Minerals Management Service's Pacific OCS Region, as well as by the Minerals Management Service and the California Artificial Reef Enhancement Program (CARE).

We thank the pilots of the submersible *Delta*, Chris James, Joe Lily, and Dave Slater, for their very professional handling of the technical aspects of that survey, as well as the crews of the R/V *Cavalier*, R/V *McGaw* and R/V *Velero IV*. Linda Snook managed the survey data. Thanks also to Dan Reed who identified some of the algae living on the survey site and to Guy Cochrane for providing details and the sidescan image of the rocky outcrops.

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