ANNUAL VARIABILITY OF REEF-FISH ASSEMBLAGES IN KELP FORESTS OFF SANTA BARBARA, CALIFORNIA

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ABSTRACT

Assemblages of kelp-bed fishes that live in and about the kelp canopy or over the reef bottom were censused by movie strips (cinetransects) every September from 1971 to 1974 at rock reefs off Santa Barbara, southern California. Cinetransects provided an adequate and efficient way to estimate species composition (order of relative or ranked species abundances), diversity, and numbers of fish for yearly comparisons between canopy and bottom habitats at mainland and Santa Cruz Island study sites. Canopy assemblages were simpler and more variable than bottom assemblages. They differed less in composition between sites. Between-site differences in fish assemblages reflected differences in structural habitat between mainland and island. Variation in species composition was less among years than between habitats or sites in the sense that site- and habitat-specific composition of assemblages persisted in the course of significant yearly changes in counts of fish and species per transect. Despite these changes, "annual variation," as measured by variance of year-to-year $\log_{10}$ ratios of numbers of 16 common species, was relatively small. Its size was characteristic of stable communities in predictable environments. As a group, planktivores, which form dense aggregations in midwater, fluctuated most in numbers. Perhaps fish responded directly to local changes in water clarity, temperature, currents, and density of giant kelp. However, coincident changes in fish counts at mainland and island sites indicated that these local environmental factors, which did not vary accordingly, were not the only causes of annual variability in fish abundance.

Off southern California, rocky reefs and beds of giant kelp, *Macrocystis pyrifera*, harbor more than 125 species of fish, almost 25% of the Californian marine total (Quast 1968b; Feder et al. 1974). Subtidal reef-fish assemblages have been extensively studied in the warm-temperate San Diegan Faunal Region to the south of Santa Barbara (Quast 1968b, c; Hobson and Chess 1976; Limbaugh[5]), and in the cool-temperate Montereyan Faunal Region to the north (Miller and Geibel 1973; Burge and Schultz[6]; Gotshall et al.[7]). Except

for scattered observations and species lists (Hewatt 1946; Quast 1968c; Clarke and Neushul 1967; Neushul et al. 1967; Alevizon 1976), however, virtually nothing is known of the structure and annual variability of such fish assemblages off Santa Barbara, which is at the northern end of the San Diegan Region as defined by Hubbs (1960).

Ebeling et al. (in press) analyzed Santa Barbaran assemblages of kelp-bed fishes sampled from a variety of habitats and localities along the mainland coast and across the Santa Barbara Channel at Santa Cruz Island. The fish community was assumed to comprise smaller groups of species that tend to segregate among habitat types. Photographic observations made throughout 1970 were used to resolve five such "habitat groups." A group of "kelp-rock species" (e.g., garibaldi, *Hypsypops rubicundus*, and California sheephead, *Pimelometopon pulchrum*) was most abundant in relatively clear water and dense kelp over high-relief rocky reef. "Canopy species" (e.g., kelp

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perch, *Brachyistius frenatus*, and señorita, *Oxyjulis californica*) usually aggregated within and just below the kelp canopy; "bottom species" (e.g., gopher rockfish, *Sebastes carnatus*) rested on the rocky reef surface far below; while "commuter species" (e.g., kelp bass, *Paralabrax clathratus*) swam about at all depths. "Inner-marginal species" (e.g., black perch, *Embiotoca jacksoni*) occurred abundantly over mixed rock and sand inshore as well as deeper reefs offshore. Members of different groups tended to mingle in areas of continuous reef and kelp where habitat types were close together. The more complex and extensive island reefs harbored the greatest numbers of "reef specialists" in the kelp-rock group.

The present study is an analysis of annual variability in species composition, diversity, and abundance of kelp-bed fishes in the faunistically transitional (Neushul et al. 1967; Hubbs 1974; Horn and Allen 1978) Santa Barbara Channel. There have been few long-term studies of stability and variability in reef-fish communities (Thomson and Lehner 1976; Sale 1978). Yet, understanding the scope and causes of variation in natural communities has both practical and theoretical importance (Larkin 1978; Wolda 1978). Our primary purposes, therefore, were to 1) document yearly changes in kelp-bed fish assemblages, which had previously impressed us as appearing relatively uniform in time, and 2) relate observed changes to environmental variables that we could readily observe. Secondarily, we assessed the use of underwater movies to census fishes in a complex environment. To these ends, we made annual censuses of fishes in and about the canopy of giant kelp and over the bottom in areas of continuous rock reef at sites off the Santa Barbara mainland and Santa Cruz Island.

METHODS

Study Sites

Sampling was conducted in areas of rocky reef and kelp on either side of the Santa Barbara Channel (Figure 1). Our mainland sampling site was Naples Reef, an isolated system of rocky outcrops and ledges located about 1.6 km offshore, 24
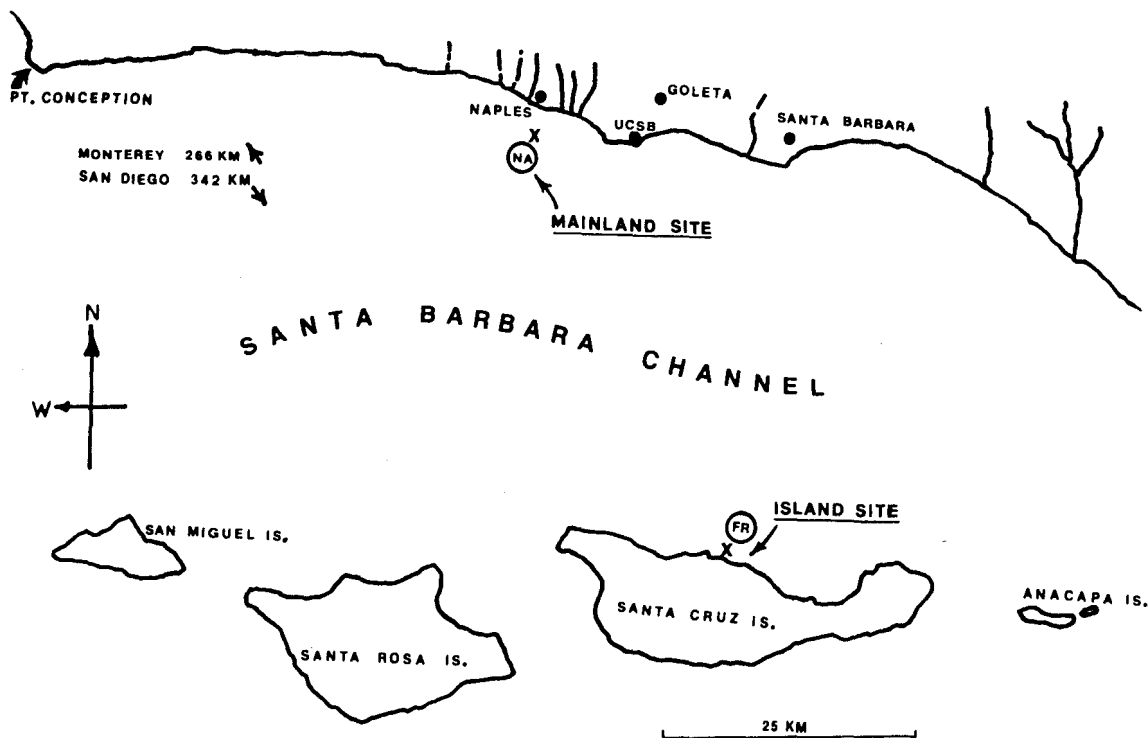

FIGURE 1.—Study sites for yearly sampling of fish assemblages in areas of reef and kelp off Santa Bárbara, southern California. Circled letters identify the mainland site, Naples Reef (NA), and the island site, Fry's Harbor and vicinity (FR).

km west of Santa Barbara, Calif. (lat. 34°25′ N, long. 119°57′ W). Measuring 275 × 80 m (2.2 ha), the reef surface averaged 8-12 m in depth, though some crests projected to within 5 m of the surface. The reef was surrounded by flat sand or cobble bottom, 16-20 m deep, with smaller rock outcrops. Above the reef, the kelp canopy usually proliferated during spring and summer, but thinned during late fall and winter.

Island observations were made at a site centered about Fry's Harbor on the north side of Santa Cruz Island (Figure 1). The subtidal substrates here were mostly rocky, with boulder areas, ledges, and caves interspersed occasionally with sand or flat-faced rock. The bottom sloped rather steeply to sand at depths of 15-25 m about 20-50 m from shore. Most sampling was conducted at depths of 3-15 m. Here, the kelp canopy extended a short distance seaward over greater depths and shore-ward to meet steep rock cliffs. In contrast with the mainland observations, therefore, most island observations were made within about 10-50 m of the shore, over an area of rapidly increasing bottom depth.

We saw anglers and divers at both sites. Yet, we rarely observed concentrated fishing effort, probably because of the erratic state of the Santa Barbara partyboat industry during the early 1970's (Love and Ebeling 1978). Fishermen in small boats were more frequently seen casting bait and lures near the surface at Naples Reef than at the island site. Hence, catches of kelp bass and other surface predators were probably substantial at Naples Reef only. Sport divers exploited both sites, albeit more sporadically than boat fishermen and seldom during the sampling periods. We suspect that catches of bottom fishes were not large and about the same at both sites.

We noted no kelp cutting and harvesting in the area of either site. About the island site, kelp beds are limited to a narrow band along the steep shore, and so are inaccessible and too small for harvest.[8] Kelp in the mainland area is harvested only in-shore of Naples Reef, which is left undisturbed.[9]

Cinetransects

We sampled fish and observed habitat charac-

teristics by means of "cinetransects." These were 2.5-min, Super-8 mm[10] movie films taken at 24 frames/s by scuba divers. The use of 50 ft (15.24 m) film cartridges standardized sampling time, and allowed rapid changing of film. High-speed color film yielded good photographs when water visibility exceeded 3 m. Starting from opportune points within the kelp-rock habitat, divers swam at relatively constant speeds, and, with the camera held level or pointed slightly downward (for bottom transects), steadily panned in about 10° arcs. Large aggregations of fish were photographed in one sweep of the camera; thereafter the camera was not pointed at the aggregation. This procedure allowed rapid and accurate enumeration of aggregations, and avoided redundant sampling of fish. During a given transect, a diver would keep to the same general depth and terrain, so that each transect could be classified by its habitat characteristics. For each transect, he measured depth of filming, depth of bottom, underwater visibility, temperature, and depth of thermocline. Films were taken in two general habitats: bottom and kelp canopy. Canopy transects were made at depths of 2-3 m, just below the mat of floating fronds. Bottom transects were taken from about a meter above the bottom, at depths ranging from about 3 to 15 m. All cinetransects were photographed during September of the years 1971-74. This was in the midst of the season of maximum thermal stratification, when water was predictably calm and clear (Brown 1974; Love and Ebeling 1978).

Two observers counted and tallied individuals per species from cinetransects projected at low speed and stop action. For each film, observers also scored bottom relief and algal density from 1 (low) to 5 (high). They often stopped, reversed, and reran the film to accurately count fish in dense clusters. When observers disagreed, they re-counted, and recorded the average of the two closest values. All species but two were tallied separately. The sibling rockfishes *Sebastes carnatus* and *S. chrysomelas*, which were identifiable by color only, were tallied as one, because subtle color differences were not always discernible in cinetransects filmed at greater depths or in more turbid water. Observers did not count small (young-of-year) juveniles, such as the reddish growth stage of blue rockfish, *S. mystinus*. Nor did

[8]Ron H. McPeak, Senior Marine Biologist, Kelco Corp., 2145 East Belt St., San Diego, CA 92113, pers. commun. October 1979.
[9]Bruce W. W. Harger, General Manager, Neushul Mariculture Corp., 275 Orange St., Goleta, CA 93017, pers. commun. October 1979.

[10]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

they count island seaperch, *Cymatogaster gracilis*, in 1971-73 samples. Island seaperch were observed only at Santa Cruz Island, sporadically in dense schools in the kelp canopy. To judge the effect of ignoring this species in 1971-73, we compared two 1974 samples, one with, the other without counts of island seaperch.

Bottom cinetransects were calibrated for area covered by estimating their length and width in the field. We estimated length experimentally by measuring distances swam during transects at Naples Reef. On each of five weekly tests, one diver photographed while a second followed with a tape measure. On 4 of 5 days, one transect went upcurrent, the other downcurrent; on the fifth day, three transects were measured in almost no current. Lengths of all 11 transects averaged 47.8 ± 2.78 m (95% confidence interval—CI). We estimated transect width by counting markers placed along a surveyed course. A tape measure marked the midline of a 50 m stretch of reef flat and rill, and pairs of red floats, anchored 2 m on either side of the tape at 5 m intervals, delimited a 4 m wide band. Four transects were photographed along the course, with divers panning the camera as usual. While viewing the projected films, we estimated widths of pans by taking 4 m (width of the marked band) and adding or subtracting estimated distances before or beyond each float seen at the extremes of the pans. Since widths of 43 pans averaged 4.41 ± 0.288 m (95% CI), the area covered by an average bottom transect was taken as 47.8 m (length) times 4.41 m (width) = 211 m^2.

Calibration of canopy transects was inherently less accurate. Photographers swam more circuitous routes at more variable speeds in midwater, where light fluctuated between dim and bright. The best we could do was roughly measure distance travelled by a photographer swimming unidirectionally under the canopy: an average length of 62.3 m in four trials both with and against the current. We estimated band width by counting kelp blades (which averaged 0.5 m long) passed during sweeps of the camera: counts usually varied from 8 to 10, translating to 4-5 m. Hence, we assumed band width of canopy transects to equal that for bottom transects (4.41 m), and estimated area covered by a canopy transect as 62.3 m (length) times 4.41 m (width) = 275 m^2.

Statistical Analyses

Samples were specific for habitat, site, and year.

For example, one sample was made up of fish counts from a set of 43 transects filmed in the canopy habitat at the mainland site during 1974.

Sample species diversity of yearly canopy or bottom samples of fish assemblages in mainland and island sites was measured by information-theoretical indices (H), combining species "richness" (total species) and "evenness" (distribution of individuals among species). We used Pielou's (1966) method to estimate population diversity from a set of cinetransects pooled incrementally in random order. Diversity (Brillouin's H) of successively larger subsamples (size k) first increases and then levels off, as the decrease in diversity from adding more individuals of common species balances the increase from adding rare species. Then increments of diversity per added individual (h_k) between adjacent subsample estimates $(H_{k-1}$ and $H_k)$ are independent, and the mean $(\bar{h})$ and variance of h_k's estimate the corresponding population parameters. Species richness (S) was the species count in a whole sample of size $k = n$. Species evenness (J) was the ratio $H_n/\ln S$, where H_n is sample diversity and $\ln S$ (natural log of species count) is the theoretically maximum value of H_n if the S species were equally abundant.

We compared species composition between sites and among years by proportionate similarity and rank correlation. Similarity (I) in species composition was measured as: $I = 1.0 - [0.5(\Sigma_{i=1}^{S}|p_{ij} - p_{ik}|)]$, where p_{ij} is the proportionate abundance of species i in sample j. Rank correlation (Kendall's tau) was measured between ranked species arrays (Johnson and Koo 1975). Clusters of similar samples were computed from matrices of I by the unweighted pair-group method using arithmetic averages (Sneath and Sokal 1973).

Mean counts of individuals and species per transect were compared between sites and among years (1971-74) by two-way analysis of variance (ANOVA) for unequal and disproportionate subclass sizes, and by one-way ANOVA for unequal sample sizes (Nie et al. 1975; Meeter and Livingston 1978). With variates transformed, sample distributions tended to normality (as indicated by nonsignificant Kolmogorov-Smirnov tests of goodness-of-fit) and sample variances equalized (as indicated by nonsignificant $F_{\max}$ tests of largest variance ratios) (Sokal and Rohlf 1969; Meeter and Livingston 1978). A posteriori contrasts among means were obtained by grouping means with nonsignificant ranges (Dunnett 1970; Nie et al. 1975).

Annual variability (AV) in numbers of fish per species was measured as variance in $\log_{10}$ ratios ($\log R$) of estimated numbers per hectare between consecutive years. For each species, we estimated number per hectare by summing mean counts per bottom and canopy cinetransects after correcting canopy means for greater area covered per transect, then multiplying by 47.39, the estimated number of bottom transects covering 1 ha (which approximates the average number per year, 44.12). According to Wolda (1978), $\log R = \log N_i - \log (N_{i-1})$, where N_i is number of individuals for 1 yr and N_{i-1} is that for the preceding year. The mean $\log R$ for an array of species indicates the average net change in species abundance, and the variance of the $\log R$'s (AV) measures the scope of change in species abundances. For example, a mean $\log R$ near zero indicates that about as many species increased as decreased in abundance between years, while a relatively low AV shows that increases and/or decreases were generally small; i.e., that annual variability was low. To increase the reliability of R, only species with at least 5 individuals/ha per year were included in the analysis (Wolda 1978). Although samples covered more than 2 yr, arrays must appear in calculations only once (Wolda 1978). Thus, we computed AV's for an array of 16 $\log R$'s for ratios of species abundances between 1972 and 1971, and for a similar array between 1974 and 1973 (separately for mainland and island study sites). Then, we computed overall AV between the years from the array of 32 $\log R$'s: those for 1972-71 plus those for 1974-73.

RESULTS

Yearly sampling yielded 297 and 331 cinetransects from mainland and island study sites, and recorded 46 fish species in 21 families, although only 31 species in 11 families were common enough to be analyzed (Table 1).[11] On the average, about 35 transects were needed to record 90% of 16

species that were filmed in the kelp-canopy habitat (the "canopy assemblage" of fishes), while 50 transects were needed to record 90% of 31 species that were filmed in the reef-bottom habitat (the "bottom assemblage").

Although our primary objective was to measure yearly variability, our analysis revealed significant differences in species composition, diversity, and abundance of fish assemblages between canopy and bottom habitats, and between mainland and island study sites. Therefore, we describe the observed spatial differences as a prelude to the account of yearly differences.

Spatial Differences

Differences in composition between assemblages in canopy and bottom habitats were obvious and easily demonstrated. For example, canopy and bottom arrays from all years and both sites were segregated in the cluster analysis based on proportionate species abundances (Figure 2). Canopy samples contained relatively more planktivores and kelp browsers like blacksmith, *Chromis punctipinnis*; kelp perch; blue rockfish; juvenile olive rockfish, *S. serranoides*; and señorita (Table 1). Bottom samples contained more bottom grazers and ambushers like pile perch, *Damalichthys vacca*; black perch; garibaldi; California sheephead; gopher rockfish; and black-and-yellow rockfish, *S. chrysomelas*.

The canopy assemblage was simpler than the bottom assemblage in the sense that more individuals of fewer species occurred in the canopy. All of our 31 common species were recorded in bottom cinetransects, but only 16 were filmed in the canopy (Table 1). Furthermore, while the median number of individuals (33—corrected for greater volume per transect) recorded in canopy transects significantly exceeded that (24) for bottom transects, the median species count (5) was significantly less than that (8) in bottom transects (Wilcoxon tests based on 275 canopy and 353 bottom counts, $P < 0.005$). These differences were reflected in the shapes of the abundance-diversity curves for the two habitats (Figure 3). Those from the canopy habitats sloped steeply, reflecting the fact that only a few species were relatively common there, while those from the bottom habitats had flatter tops, reflecting a more coequal commonness of several species.

In general, the composition of fish assemblages differed markedly between mainland and island

[11]Additional species that were rarely recorded include: *Heterodontus francisci* (Heterodontidae), *Cephaloscyllium ventriosum* (Scyliorhinidae), *Myliobatis californica* (Myliobatididae), *Torpedo californica* (Torpedinidae), *Syngnathus* spp. (Syngnathidae), *Atherinops affinis* (Atherinidae), *Cymatogaster gracilis* (Embiotocidae—sporadically common at island, see text), *Phanerodon atripes* (Embiotocidae), *Caulolatilus princeps* (Branchiostegidae), *Gibbonsia elegans* (Clinidae), *Coryphopterus nicholsi* (Gobiidae), *Scorpaena guttata* (Scorpaenidae), *Sebastes auriculatus* (Scorpaenidae), *Pleuronichthys coenosus* (Pleuronectidae), and *Mola mola* (Molidae).

TABLE 1.—Relative abundance of 31 species of kelp-bed fishes from canopy and bottom assemblages in yearly cinetransect samples filmed during 1971-74 at mainland and Santa Cruz Island study sites off Santa Barbara, southern California (Figure 1). Values are percent number of individuals.

| | Kelp canopy habitat | | | | | | | | | | Reef bottom habitat | | | | | | | | | |
| | Santa Barbara mainland | | | | | Santa Cruz Island | | | | | Santa Barbara mainland | | | | | Santa Cruz Island | | | | |
Family and species	1971	1972	1973	1974	1971-74	1971	1972	1973	1974	1971-74	1971	1972	1973	1974	1971-74	1971	1972	1973	1974	1971-74
Serranidae:																				
Paralabrax clathratus	9.96	2.87	6.85	2.51	4.56	1.39	3.12	5.47	4.70	3.34	20.78	12.48	6.30	7.01	10.86	9.92	13.39	21.20	10.88	13.82
P. nebulifer	—	—	—	—	—	—	—	—	—	—	0.17	0.05	—	—	0.04	—	—	—	—	—
Sciaenidae:																				
Cheilotrema saturnum	—	—	—	—	—	—	—	—	—	—	—	0.09	0.10	1.45	0.53	—	—	—	—	—
Kyphosidae:																				
Girella nigricans	12.45	—	—	1.11	1.12	1.19	4.21	0.59	3.43	2.72	2.04	10.79	5.92	3.50	7.00	18.39	8.24	10.95	8.46	11.27
Medialuna californiensis	6.51	3.27	1.86	5.09	3.42	0.08	0.26	0.46	0.46	0.28	0.17	0.70	0.67	7.01	2.12	1.13	0.59	0.70	1.40	0.94
Embiotocidae:																				
Brachyistius frenatus	—	—	7.30	0.22	2.28	52.99	37.07	24.70	11.79	34.60	—	—	0.29	0.08	0.08	1.05	1.58	0.16	0.37	0.81
Damalichthys vacca	0.19	0.03	—	0.15	0.06	0.16	0.08	0.13	0.06	0.10	9.03	4.77	6.69	4.70	5.66	2.58	4.22	4.12	2.87	3.48
Embiotoca jacksoni	—	0.07	—	0.44	0.11	—	—	0.13	0.58	0.13	23.34	22.62	43.55	25.90	27.91	8.63	7.92	7.22	6.84	7.64
E. lateralis	—	0.23	—	0.66	0.22	0.04	0.31	2.50	0.70	0.66	2.56	6.45	3.92	1.88	4.37	2.18	3.10	4.35	1.84	2.87
Hypsurus caryi	—	—	—	—	—	—	—	—	—	—	2.39	2.94	7.74	17.95	7.65	—	0.46	0.08	—	0.15
Phanerodon furcatus	2.68	—	2.81	0.44	1.15	—	—	0.33	0.58	0.16	0.17	0.75	2.20	0.51	0.93	0.32	0.59	0.31	0.81	0.52
Rhacochilus toxotes	0.19	—	0.04	—	0.03	0.04	—	—	—	0.01	5.96	1.92	1.62	0.77	2.04	0.16	1.91	1.24	1.18	1.17
Pomacentridae:																				
Chromis punctipinnis	51.92	29.00	37.48	42.03	35.79	39.72	35.46	11.13	39.95	33.49	9.03	7.71	2.20	10.68	7.44	16.69	7.26	0.54	25.88	12.51
Hypsypops rubicundus	—	—	—	—	—	—	—	—	—	—	—	1.26	0.76	1.45	1.05	13.14	17.08	10.87	12.35	13.51
Labridae:																				
Halichoeres semicinctus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.32	0.33	0.16	0.29	0.28
Oxyjulis californica	4.60	3.76	15.02	10.03	8.51	1.11	3.98	8.96	11.61	5.42	8.52	8.97	2.67	5.47	6.76	1.69	2.38	3.18	5.81	3.28
Pimelometopon pulchrum	—	0.03	0.04	—	0.03	—	0.05	—	0.06	0.03	2.22	4.16	2.10	1.11	2.77	13.39	11.68	9.86	8.31	10.79
Clinidae:																				
Heterostichus rostratus	0.19	0.07	0.27	0.30	0.18	0.08	0.03	0.07	—	0.04	—	0.09	0.76	0.94	0.42	—	0.13	—	0.15	0.07
Scorpaenidae:																				
Sebastes atrovirens	0.38	0.30	0.50	0.22	0.35	1.39	2.62	3.49	8.30	3.47	0.51	0.28	0.67	0.59	0.47	6.05	8.31	7.38	5.52	6.88
S. carnatus & S. chrysomelas	—	—	—	—	—	—	—	—	—	—	2.22	0.75	3.25	2.39	2.00	0.56	2.31	2.48	0.88	1.59
S. melanops	—	—	—	—	—	—	—	—	—	—	—	—	0.19	—	0.04	—	—	—	—	—
S. mystinus	10.92	59.81	27.49	35.18	41.26	0.04	10.63	3.82	9.76	6.67	7.16	11.03	4.20	2.74	7.12	0.56	5.08	11.57	3.68	5.24
S. rastrelliger	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.56	0.53	0.47	0.22	0.44
S. serranoides	—	0.56	0.36	1.62	1.67	1.72	2.18	38.21	8.01	8.85	1.02	0.28	0.10	0.68	0.42	1.05	1.38	1.94	1.47	1.46
S. serriceps	—	—	—	—	—	—	—	—	—	—	0.17	—	0.10	—	0.04	0.16	0.20	0.08	0.22	0.18
S. vexillaris	—	—	—	—	—	—	—	—	—	—	0.17	0.09	—	—	0.06	—	—	0.08	—	0.02
Hexagrammidae:																				
Ophiodon elongatus	—	—	—	—	—	—	—	—	—	—	—	0.05	0.38	—	0.10	—	—	—	—	—
Oxylebius pictus	—	—	—	—	—	—	—	—	—	—	2.39	1.68	3.25	2.91	2.39	1.45	1.12	0.85	0.59	1.00
Cottidae:																				
Leiocottus hirundo	—	—	—	—	—	—	—	—	—	—	—	—	0.10	—	0.02	—	—	0.08	—	0.02
Scorpaenichthys marmoratus	—	—	—	—	—	—	—	—	—	—	—	0.05	0.29	0.26	0.14	—	0.20	0.16	—	0.09
Number of individuals	522	3,031	2,204	1,356	7,113	2,442	3,847	1,518	1,722	9,529	587	2,140	1,047	1,170	4,944	1,240	1,516	1,288	1,360	5,404
Number of cinetransects	13	31	45	40	129	22	38	46	40	146	25	45	55	43	168	37	45	55	48	185

SIMILARITY (I)
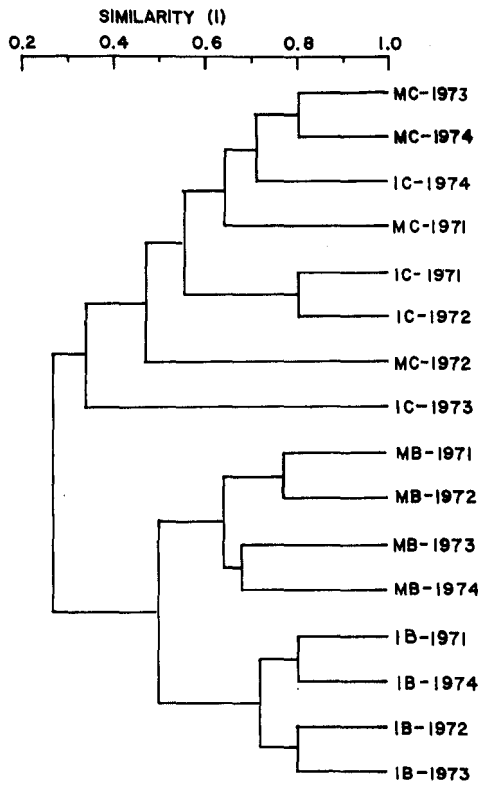
FIGURE 2.—Clustering, by year (right number), of canopy (C) and bottom (B) cinetransect samples of kelp-bed fishes filmed each September in 1971-74 at mainland (M) and Santa Cruz Island (I) study sites off Santa Barbara, southern California.

study sites. Samples from within mainland or island sites tended to be more alike than samples between these sites, particularly for bottom assemblages. Samples from within tended to form secondary subclusters nested in the principal ones distinguishing canopy and bottom assemblages (Figure 2), and within-site similarity values tended to be higher than between-site values (Table 2).

As indicated by clusters (Figure 2) and similarity values (Table 2), however, mainland and island canopy assemblages were more difficult to distinguish than bottom assemblages. The mean ratio of within- to between-site resemblance (I or tau) was comparatively large for arrays of canopy species (Table 2), indicating that canopy assemblages were only slightly more distinguishable between sites than among years. This, and the fact that variances of canopy similarities were relatively large (Table 2), explained why the clusters of canopy samples were poorly defined. What few between-site differences in canopy samples prevailed were due to greater numbers of kelp perch and juvenile olive rockfish observed in the canopy habitat of the island site, and of blue rockfish at the mainland (Table 1). Island canopy samples contained a few more species than mainland canopy samples (Table 3, S), and the average number of species per cinetransect (Table 3) was significantly greater (Table 4) at the island. (The significant year-site interaction as indicated in
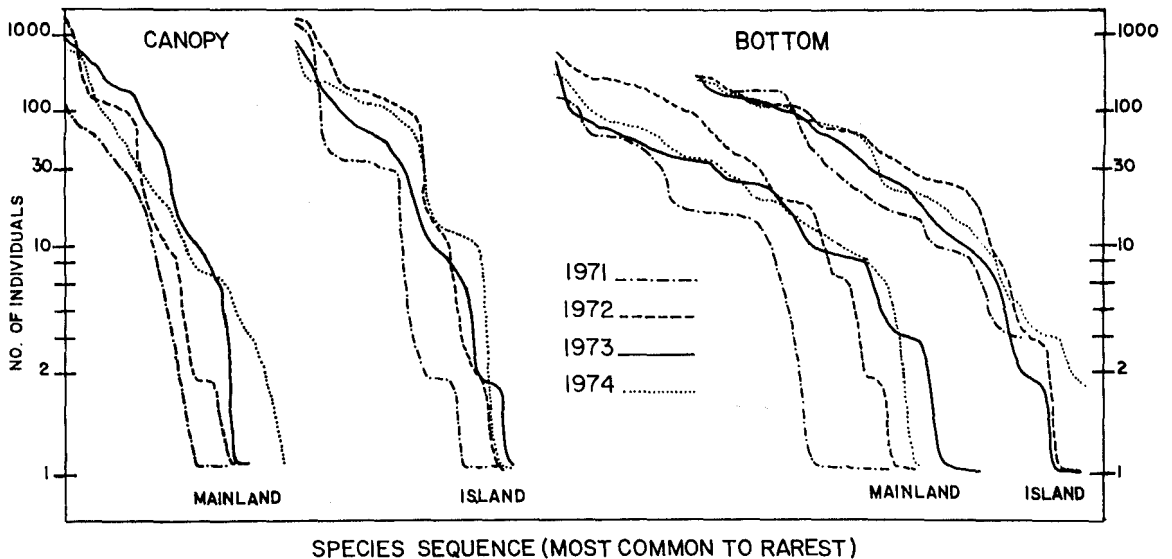

SPECIES SEQUENCE (MOST COMMON TO RAREST)

FIGURE 3.—Abundance-diversity curves for 31 species of kelp-bed fishes from canopy and bottom assemblages in yearly samples filmed during 1971-74 at mainland and Santa Cruz Island sites off Santa Barbara, southern California.

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TABLE 2.—Comparison of within-site and between-site means (±1 standard deviation) of similarity (I) and rank correlation (tau) between all pairs of species-abundance arrays from yearly cinetransect samples filmed during 1971-74 at mainland and Santa Cruz Island Study sites off Santa Barbara, southern California. Within-site means are of values for all pairs (1971 vs. 1972, 1971 vs. 1973, . . ., 1973 vs. 1974), both members of which were filmed in canopy or bottom habitats either at the mainland or island site; between-site means are of values for all such habitat-year pairs, one member of which was from an island sample, the other from a mainland sample; and mean ratio is the between-site value/mean within-site value (mainland and island). (Figure 2 is a cluster diagram of yearly samples, computed from all values of I.)

| Habitat | Within sites (n = 6)[1] | | | | Between sites (n = 10) | | Mean ratio between/within | |
| | Mainland | | Island | | | | | |
	I	Tau	I	Tau	I	Tau	I	Tau
Canopy	0.62±0.11	0.58±0.09*	0.61±0.13	0.59±0.09*	0.50±0.17	0.45±0.12	0.81	0.77
Bottom	0.68±0.05**	0.67±0.06***	0.75±0.06***	0.80±0.03***	0.53±0.09	0.49±0.06	0.74	0.67
Mean	0.65	0.625	0.68	0.695	0.515	0.495	0.775	0.72

[1]Difference of within- and between-site means significant at (t-test): *P · 0.05; **P · 0.01; ***P · 0.001.

Table 4 occurred because the relation was reversed in 1973 as indicated in Table 3.) Diversity and evenness (Table 3, $\bar{h}$ and J) of canopy assemblages, however, did not differ significantly between sites.

However, sporadically abundant endemic island seaperch were not included in these comparisons. Adding this species to 1974 counts of the island-canopy samples increased the fish total from 1,722 to 3,084 individuals, median fish counts per transect from 31 to 64 individuals, and median number of species per transect from 5.5 to 6.0. The slight increase in species diversity ($\bar{h}$) was

not significant (Table 3). Island seaperch were seldom observed in bottom transects.

In contrast to the canopy assemblages, mainland and island bottom assemblages were easily distinguishable. Because between-site resemblance was comparatively small for arrays of bottom species (Table 2), mainland and island clusters of samples were sharply defined (Figure 2). Island samples contained relatively more California sheephead, garibaldi, and opaleye, Girella nigricans, and included rock wrasse, Halichoeres semicinctus, which were not recorded from the mainland (Table 1). Mainland-site sam-

TABLE 3.— Yearly abundance and species diversity of canopy and bottom assemblages of kelp-bed fishes in cinetransect samples from mainland and Santa Cruz Island study sites off Santa Barbara, southern California. Columns include: n, no. of transects in sample; Geom. $\bar{x}$, the antilog of the mean transformed fish count with 95% confidence limits; S, total species in sample; n($\bar{h}$), sample size to compute $\bar{h}$; $\bar{h}$, the mean of successively pooled transect estimates of diversity per individual (see text); and J, evenness of distribution of individuals among species in the sample. Contrasts among means that were shown to differ significantly by analysis of variance (Table 4) were by the Student-Newman-Keuls procedure (Sokal and Rohlf 1969:239); means making up homogeneous subsets are indicated by X's in the same column.

| Habitat | Site | Year | n | Fish counts | | Species counts | | S | n($\bar{h}$) | $\bar{h}$±95% CI | J |
				Geom. $\bar{x}$, 95% CL	Contrasts	$\bar{x}$±95% CI	Contrasts				
Canopy	Mainland	1971	13	11.0<24.2<53.1	x x	2.7±0.63	x	11	7	1.33±0.555	0.54
		1972	31	47.4<70.6<105.0	x	4.7±0.57	x	12	19	1.32±0.297	0.39
		1973	45	32.2<39.9<49.3	x	5.0±0.42	x	12	27	1.80±0.161	0.64
		1974	40	16.2<22.5<31.2	x	4.3±0.57	x	14	29	1.82±0.216	0.52
		Unweighted $\bar{x}$		39.3		4.2		12.2		1.57	0.522
	Island	1971	22	30.6<58.8<112.5	x	4.6±0.69	x	13	16	1.17±0.187	0.40
		1972	38	51.0<70.6<97.9	x	6.2±0.67	x	13	29	1.63±0.137	0.61
		1973	46	19.6<25.4<32.6	x	3.5±0.45	x	14	32	1.70±0.301	0.58
		1974	40	21.5<29.0<39.3	x	5.7±0.63	x	14	27	2.18±0.199	0.71
		Unweighted $\bar{x}$		46.0		5.0		13.5		1.67	0.575
		1974[1]	40	30.3<43.9<63.7		6.3±0.71		15	29	2.32±0.272	0.64
Bottom	Mainland	1971	25	15.7<20.0<25.4	x x	7.3±0.82	x x	20	11	2.39±0.167	0.75
		1972	45	36.6<42.4<48.9	x	10.1±0.62	x	24	27	2.51±0.130	0.76
		1973	55	13.7<16.2<19.3	x	7.0±0.65	x	26	31	2.34±0.185	0.68
		1974	43	18.9<22.8<27.4	x	8.2±0.83	x	22	33	2.46±0.116	0.77
		Unweighted $\bar{x}$		25.4		8.2		23.0		[2]2.42	0.740
	Island	1971	37	23.6<28.6<34.6	x	8.7±0.65	x x	21	25	2.45±0.107	0.77
		1972	45	24.1<28.7<34.2	x	9.5±0.84	x	24	36	2.60±0.089	0.82
		1973	55	16.9<19.9<23.5	x	7.8±0.72	x	25	34	2.56±0.123	0.78
		1974	48	17.0<21.3<26.7	x x	7.6±0.66	x	22	28	2.69±0.169	0.77
		Unweighted $\bar{x}$		24.6		8.4		23.0		[2]2.58	0.785
		1974[1]	48	17.9<22.0<29.2		7.8±0.67		23	30	2.83±0.179	0.79

[1]Including counts of Cymatogaster gracilis.
[2]Difference between unweighted means of mainland and island values significant at P = 0.05.

TABLE 4.—Analysis of variance of kelp-bed fish counts ($\log_{10}$ transformed) and species counts from cinetransects composing yearly samples filmed during 1971-74 in canopy and bottom habitats. For the two-way ANOVA's, samples were classified by sites (Santa Barbara mainland and Santa Cruz Island, southern California) and years (four sequential Septembers). For the one-way ANOVA's, samples were classified by years for each site separately (Mainland and Island subheads).

Source	df	Fish counts MS	Fish counts F	Species counts MS	Species counts F
Canopy:					
Sites, S	1	0.062	<1	17.631	6.17**
Years, Y	3	2.802	16.78***	32.629	11.42***
SY	3	1.079	6.46***	46.414	16.24***
Error	267	0.167		2.858	
Mainland:					
Years	3	1.598	8.93***	19.744	8.37***
Error	125	0.179		2.360	
Island:					
Years	3	2.282	14.56***	59.298	17.99***
Error	142	0.157		3.296	
Bottom:					
Sites, S	1	0.001	<1	2.777	<1
Years, Y	3	1.408	19.51***	106.177	18.07***
SY	3	0.420	5.83***	19.187	3.26*
Error	345	0.072		5.877	
Mainland:					
Years	3	1.505	23.48***	88.720	15.99***
Error	164	0.064		5.547	
Island:					
Years	3	0.322	4.05**	36.639	5.93***
Error	181	0.080		6.176	

*$P \approx 0.02$; **$P \approx 0.01$; ***$P < 0.001$.

ples, on the other hand, included relatively more black perch, pile perch, and rainbow seaperch, *Hypsurus caryi*. Whereas one species—the black perch—usually dominated mainland samples, several species—the kelp bass; opaleye; blacksmith; garibaldi; and California sheephead—were often equally abundant in island samples. This more equitable spread of numbers over several common species resulted in significantly greater species diversity ($\bar{h}$) by increasing the evenness component (J) (Table 3), and is reflected in the flattened tops of dominance-diversity curves (Figure 3). Neither total species (Table 3, S) nor mean number of species per transect (Table 3, species counts) were significantly larger (Table 4) in island samples.

Mainland and island study sites differed significantly in certain characteristics of structural habitat (Table 5). Scored relief of reef bottom was significantly greater at the island site, although scored densities of giant kelp and bottom algae did not differ significantly between sites. Even though depth of reef over which bottom transects were filmed did not differ significantly between sites, it was more variable at the island site (Table 5) because the shore there sloped more steeply (Figure 4). Discounting 1973, when water at the island site was unusually turbid, underwater visibility was significantly greater by some 2.0 m at the island site (Table 6). Island water temperatures were significantly greater, though only slightly so, in all yearly sampling periods except 1973.

Yearly Differences

Species composition of bottom assemblages at mainland and island sites was more uniform (showed greater resemblance among years) than the corresponding canopy assemblages (Table 2), although significantly so only for the island site (*t*-tests, I between habitats, $P < 0.05$; tau, $P < 0.002$). Consequently, both measures of yearly resemblance (I, tau) of bottom-species arrays within sites were significantly greater than those between sites (Table 2). Furthermore, among-year variances of both resemblance measures for mainland- and island-bottom assemblages were less than those for both canopy assemblages, though significantly so only for island measure tau (*F*-test, $P \approx 0.05$). Comparing bottom assemblages only, the island assemblage was significantly more uniform (*t*-tests, I between sites, $P \approx 0.05$; tau, $P < 0.001$).

Fish and species counts also reflected the greater annual variability of canopy assemblages. We computed coefficients of variation (CV)—percentage ratios of standard deviation to

TABLE 5.—Means of habitat variables measured with each cinetransect for all bottom samples filmed during 1971-74 at mainland and Santa Cruz Island study sites off Santa Barbara, southern California. Scored from 1 (low) to 5 (high), plant density, other algae includes all understory forms. Time of day is the 4-yr range of median times at which transects making up yearly samples were filmed. CV is coefficient of variation and CI, confidence interval. Significance levels are from Mann-Whitney U-tests of rank differences between mainland and island values.

Site	No. of observations (n)	Time of day (h)	Mean bottom type score	Mean plant density score Giant kelp	Mean plant density score Other algae	Bottom depth (m) $\bar{x} \pm 95\%$ CI	Bottom depth (m) CV	Underwater visibility (m) $\bar{x} \pm 95\%$ CI	Underwater visibility (m) CV
Mainland	168	1205-1403	3.89	2.43	3.16	8.62±0.205	15.4%	6.11±0.157	17.4%
Island	185	1210-1400	4.43**	2.29	3.29	8.28±0.400	32.8%	[1]8.11±0.439	[1]34.8%

**$P < 0.01$.
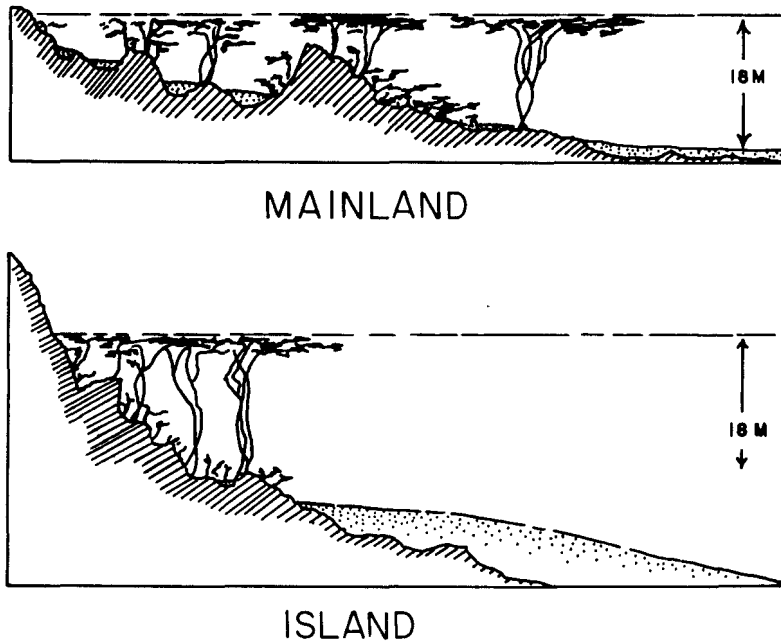[1]$n = 130$, excluding unusually low values for 1973 (see Table 6).

MAINLAND

ISLAND

FIGURE 4.—Offshore profiles (vertically exaggerated) at mainland (Naples Reef) and Santa Cruz Island (Fry's Harbor) study sites off Santa Barbara, southern California. Off the mainland, broad sand and cobble flats (stippled) separate rocky outcrops (hatched) between the shore and Naples Reef (highest outcrop), 1.6 km offshore. Off the island, the relatively steep rocky bottom meets sand within only about 50 m of shore.

TABLE 6.—Yearly means (±95% confidence interval) of diver estimated underwater visibility and temperature measured with each cinetransect in bottom-habitat samples filmed during 1971-74 at mainland and Santa Cruz Island study sites off Santa Barbara, southern California.

Site	Year	n	Underwater visibility (m)	Water temperature, surface (°C)	Thermocline depth (m)
Mainland	1971	25	5.61±0.436	16.51±0.309	8.90±0.704
	1972	45	7.07±0.222	18.00±0.081	8.72±0.219
	1973	55	6.43±0.317	17.31±0.060	8.72±0.326
	1974	43	4.97±0.347	19.16±0.076	8.78±1.036
Island	1971	37	7.96±0.363	19.42±0.063	10.00±0.329
	1972	45	8.84±0.991	18.56±0.335	10.45±0.951
	1973	55	2.97±0.082	16.63±0.250	Undetected
	1974	48	7.56±1.070	19.56±0.070	>10-11

mean—to compare variability of these different measures of different magnitudes (Sokal and Rohlf 1969:62). Averaged among eight yearly samples (four mainland + four island, summarized in Table 3), CV's for counts per transect of individuals and species in canopy samples ($\bar{x}$ = 75.5% and 36.9%) were significantly greater than corresponding values (61.1%, 29.0%) for bottom samples (t-tests, $P < 0.05$). Expectedly, therefore, the CV for species diversity (h) of canopy samples was also significantly greater ($\bar{x}$ = 33.8% vs. 13.6%, approximate t-test, unequal variances, $P < 0.05$).

Yearly differences in mean fish and species counts per transect (canopy and bottom) were highly significant (Table 4). All one-way ANOVA's revealed such differences (Table 4), and highs and lows generally coincided between mainland and island sites (Table 3). For example, counts were generally high in 1972, low in 1973, and intermediate in 1971 and 1974. Thus, most of the significant differences between means were due to a relatively abrupt decline from high counts in 1972 to low counts in 1973. The 1972 peak was most pronounced at the mainland site, when 10 of 16 species had greatest abundances, vs. 7 at the island (Table 7). Peaks of five species coincided: Paralabrax clathratus, D. vacca, E. lateralis, S. atrovirens, and S. mystinus. The only other coincident peak abundance was of S. serranoides in 1973. Despite the general correspondence between sites of overall changes in abundance and species number, however, significant year-site interactions (Table 4) indicated notable exceptions. For example, 1973 counts of individuals and species were relatively high in the mainland canopy, but low in the island canopy (Table 3).

Wolda's (1978) measures of annual variation revealed overall trends in species abundances

TABLE 7.—Annual variation of estimated density (individuals per hectare) of common kelp-bed fish species at mainland and Santa Cruz Island study sites off Santa Barbara, southern California. Variance $\sqrt{n}$, the variance of square roots of yearly densities, measures yearly variability discounting effects of means; $\bar{R}$ at bottom of table, the mean of log R's—the average difference in $\log_{10}$ density for the species array between two successive years, measures net change in the array; AV, the variance of log R's, measures the scope of change. Between-year totals yield these statistics for an array of all 32 log R's (See text and Wolda 1978). A dash (—) indicates that the number was too small for analysis.

Species	Mainland					Island				
	1971	1972	1973	1974	Variance $\sqrt{n}$	1971	1972	1973	1974	Variance $\sqrt{n}$
Paralabrax clathratus	377	384	171	121	19.3	214	329	301	220	3.1
Girella nigricans	204	246	53	59	19.2	340	272	128	167	10.6
Medialuna californiensis	97	132	· 39	153	8.1	21	19	13	26	0.4
Brachyistius frenatus	—	—	—	—	—	2,161	1,394	299	190	247.9
Damalichthys vacca	103	109	60	62	2.1	47	70	47	39	0.8
Embiotoca jacksoni	260	512	383	339	7.3	137	117	82	101	1.3
E. lateralis	28	154	35	32	11.6	37	61	48	36	0.7
Hypsurus caryi	27	66	70	231	18.0	—	—	—	—	—
Rhacochilus toxotes	67	43	15	10	5.5	5	30	14	16	1.8
Chromis punctipinnis	864	1,207	689	657	17.4	1,872	1,420	140	976	187.5
Hypsypops rubicundus	—	—	—	—	—	208	273	108	167	6.6
Oxyjulis californica	161	336	280	194	6.6	71	185	143	260	10.4
Pimelometopon pulchrum	25	95	20	14	7.4	213	189	109	113	4.5
Sebastes atrovirens	11	74	15	10	0.7	154	229	124	204	3.3
S. carnatus &										
S. chrysomelas	25	17	29	31	0.4	10	23	19	12	0.6
S. mystinus	238	2,379	531	470	217.3	11	472	175	203	57.2
S. serranoides	11	26	66	29	3.9	85	102	481	145	34.3
Oxylebius pictus	27	38	29	38	0.3	—	—	—	—	—
$\bar{R}$ Between years		0.29	−0.30	0.00			0.23	−0.24	0.06	
Between-year total		0.15					0.14			
AV Between years		0.12	0.12	0.06			0.20	0.12	0.09	
Between-year total		0.11					0.15			
Mean variance, midwater planktivores					117.3					164.2
Mean variance, all others					8.3					6.0

(Table 7). In general, mean log R's (Table 7, $\bar{R}$), which measure net annual change between species arrays, differed significantly within (t-tests, $P<0.01$), but not between ($P>0.05$) sites. This further indicated that species abundances varied concordantly on both sides of the Channel. For the mainland site, $\bar{R}$ for 1971-72 was positive, indicating net increases in most species between these years (Table 7) as total fish counts increased significantly both in canopy and bottom habitats (Table 3); was negative for 1972-73 as numbers decreased in both habitats; and was zero for 1973-74 as a decrease in total canopy numbers offset an increase in bottom numbers. Net annual changes at the island site were somewhat less marked (Table 7), and numbers of fish differed significantly between 1972 and 1973 only (Table 3). In general, variances of log R's (Table 7, AV), which measure the scope of annual differences between species arrays, did not differ significantly either within or between sites (F-tests, $P>0.1$). However, the within-site differences were more marked, which is consistent with the concordance of annual trends of the mainland and island sites.

Much of the yearly variation in fish abundance was due to fluctuations in species that aggregate in the kelp canopy, especially midwater plankti-vores (Table 7). The average among-year variance of transformed numbers of three abundant plank-tivores (B. frenatus, Chromis punctipinnis, and S. mystinus) was relatively large (145.4, $n = 5$); that for abundant species whose vertical distributions are somewhat broader (Paralabrax clathratus, G. nigricans, S. serranoides, and O. californica) was substantially less (13.4, $n = 8$); while that for abundant demersal species (E. jacksoni, Hypsypops rubicundus, and Pimelometopon pulchrum) was smaller still (5.4, $n = 5$).

Yearly differences were loosely related to underwater visibility, water temperature, and, perhaps, to kelp density in the canopy. Water was relatively clear and warm during September 1972 (Table 6) when counts of individuals and of species were high. Furthermore, water was turbid and cool at the island site during 1973 when counts were low. However, at the mainland site in 1973, where no such conditions prevailed (Table 6), bottom counts were also low (Table 3). Kelp density seemed to affect canopy counts at the mainland site, where lower scores for kelp density in 1974 (Table 5) coincided with lower counts of fish in the canopy (Table 3).

In sum, variation in composition (order of relative or ranked species abundances) was less

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between years than between habitats or sites, although canopy assemblages maintained less site-specific integrity than bottom assemblages. Coincident peak abundances of several species at both sites in 1972 contributed to significant yearly differences in fish counts, although significant year-site interactions revealed exceptions to the generally concordant annual trends. Fishes that aggregated in the canopy habitat, especially midwater planktivores, probably contributed most to annual variation measured by between-year log ratios of numbers per species. Yearly differences in fish abundances were loosely related to water clarity and temperature and kelp density, but correlations were not clear-cut.

DISCUSSION

Sampling

With limited time, personnel, and budget, visual transecting may be the most appropriate method for sampling fish populations in the complex reef environment, so long as it is understood that this method always underestimates densities of small, hidden, and/or cryptic species (Brock 1954; Jones and Chase 1975). Although some investigators aver that destructive methods (poisoning, dynamiting) provide broader sampling (Randall 1963; Goldman and Talbot 1976), others counter that visual methods are more representative because they record individuals of larger, stronger species that escape the slaughter (Smith and Tyler 1973). Hence, a thorough census of covert and overt species probably requires both methods (Quast 1968c).

Cinetransecting is analogous to visual transecting. Both methods may miss most covert fish (Alevizon and Brooks 1975), but record most overt individuals. For example, the rank order of species abundances from all mainland-bottom samples (Table 1) correlated significantly (tau = 0.66, $P<0.001$) with that of daytime visual transects made along a transect line about the reef crest at this site throughout the year (Ebeling and Bray 1976: table 3). Four of the five top-ranking species were the same in both studies, even though cinetransects covered a much broader area.

However, cinetransects have some advantages over visual transects. They can be made quickly, as many as 50/d in the present study. Cinetransects provide permanent records of the fish and their environment, not only for greater accuracy

in identifying and counting fish, but also for reuse in related studies (see Alevizon 1975; Bray and Ebeling 1975; Love and Ebeling 1978). Diver photographers can proceed slowly and steadily, not diverting their attention from sampling to record observations or follow a transect line. They do not need extensive training in quick recognition of fish species and numbers, so can be replaced by others if required; if cinetransect samples are sorted into subsets, each filmed by one or the other of two different divers, correlations between the corresponding diver-specific species arrays are very high. For example, the four habitat-site-specific samples filmed by two divers in 1973, when sorted to eight diver-specific subsets, gave tau rank correlations ranging from 0.71 to 0.89 ($P<0.001$).

Within broad limits, furthermore, water visibility and light levels probably do not appreciably affect the volume of water sampled by cinetransects filmed along the bottom. At a given focus distance, the camera lens' depth of field is inversely related to the diameter of its aperture. In bright light, the aperature is small, creating a greater zone in which objects are in focus. In the kelp forest, however, light was generally so dim, even on clear days, that the aperture was almost always fully open. Thus, shading probably creates a fairly constant depth of field. To check this, we estimated the distance at which objects were first identifiable on film. Two divers swam along a tape measure ending in a fishlike target, one filming the target and nearby fish, the other signaling distance from target. During the first trial when underwater visibility (distance at which target was discernible) was 15.2 m, fish were identifiable on film only when photographed within about 3.5 m of the camera. During the second when visibility was only about 4.0 m, fish were still identifiable when photographed within about 3 m. Hence, the fairly constant depth of focus of the camera's lens, which was always set at 2.0 m on the distance scale, standardized the maximum distance (about 3.5 m) at which a photographed fish was identifiable.

Linear regressions of $\log_{10}$-transformed fish counts on estimated underwater visibility provide further evidence that visibility had little effect on values. Mean fish and species counts for the 1973 and 1974 island-bottom samples were similar, so the two were combined as one large sample ($n = 103$) for regression analysis. Although visibility varied between 2.1 and 15.2 m, the regression was nonsignificant (ANOVA F-test, $P = 0.3$). Even in

the canopy habitat, the effect of more variable light levels is apparently not severe. A similar regression analysis of pooled 1971-72 island-canopy samples ($n = 60$) was nonsignificant ($P = 0.9$), though visibility ranged from 4.6 to 10.7 m.

But while such inferences from camera optics and counts-visibility relations indicate that estimates of relative abundance obtained from cine-transects are comparable over a wide range of sampling conditions, we feel that the calibration of absolute densities presents difficulties. The primary problem is that, particularly in the kelp canopy, our estimates of area or volume sampled are tenuous. For this reason, we used absolute densities only for computing Wolda's (1978) measure of annual variation, which required estimated abundances per species, standardized for differences in sampling effort among years and between canopy and bottom habitats. We feel that this is proper because a systematic error in estimating will have little effect on the measure's value, which is based on yearly ratios of population sizes, not on sizes per se.

Also, combining canopy and bottom transects may miss some fish at middepth. Canopy transects covered depths between 1 and 4 m, which included the greatest concentration of fish in the upper water column. Bottom transects covered depths between the reef and about 2 m upward, which included greatest concentrations in the lower column. Nonetheless, over bottoms averaging 8.5 m deep, cinetransects generally missed the top meter as well as midwater between 4 and 6.5 m. Hence, our fish counts, even of overt midwater species, probably underestimated true abundances.

Annual Variability

Species composition (order of relative or ranked species abundances), rather than richness (number of species), contributed most to differences between mainland and island fish assemblages, which were most marked for the bottom assemblages (see also Ebeling et al. in press). Yearly mainland and island samples had the same number of species, although island species diversity was slightly greater because individuals were more evenly distributed among species. At the island site, species in a "kelp-rock" habitat group (Ebeling et al. in press)—tropically derived species such as *Pimelometopon pulchrum* and *G. nigricans*—were relatively more abundant than at Naples Reef. We had no indication that fishing

intensity for such species (spear fishing, bottom angling) differed between the two sites. Nor was unnatural disturbance by kelp harvesting a factor. Furthermore, virtually unexploited kelp-rock species, such as *Hypsypops rubicundus*, were relatively more abundant at Santa Cruz Island. This indicates that much of the mainland-island difference in species composition probably reflected the observed differences in structure of natural habitat rather than differences in exploitation. Likewise, but on a broader scale, insular and continental shore-fish faunas are distinguished in the tropical western North Atlantic (Robins 1971; Gilbert 1972). Whereas turbid waters, muddy-silty bottoms, and few reefs characterize mainland habitats, clear water, coral reefs, and more stable conditions typify island habitats. Consequently, island fish assemblages contain relatively more specialized reef species, such as pomacentrids and labrids, that require the trappings and provisions of complex surfaces.

We felt that composition and abundance of the fish assemblages remained fairly constant among years, considering that they inhabit a presumed zone of faunal transition (Hubbs 1974; Horn and Allen 1978). Species composition varied more between sites and habitats than among years. This indicates that a particular assemblage persists, despite significant yearly variation in its fish and species counts. Yet we had few standards for comparison. Sale (1978:85) knew of no evidence that demonstrated "long-term local stability in reef fish communities," presumably because long-term monitoring studies were wanting. With a 7-yr study of fishes inhabiting a rocky tidal pool in the northern Gulf of California, however, Thomson and Lehner (1976) showed that fish abundance, diversity, and species order were seasonally predictable and varied little from year to year. In fact, the fish assemblage was remarkably resilient, recovering quickly from unpredictable and devastating disturbances, such as severe storms, winter kills, and rotenone poisoning. More generally, Wolda (1978) emphasized the need for actual measures of annual variability in tropical and other animal assemblages to test a plethora of theoretical speculation.

Our values of Wolda's (1978) measure of annual variation (AV) in arrays of species were in fact relatively low. AV's for fish assemblages at mainland and island sites (0.11, 0.15) did not differ significantly (F-tests of variance ratios) from most of those (0.06-0.33, averaging 0.15) for arthropods

living in humid, climatically stable and more pre-dictable areas, but were significantly less than most values (0.12-0.64, averaging 0.34) for ar-thropods living in dry, climatically unstable envi-ronments (Wolda 1978: table 2). Values of AV (0.17, 0.20) that we calculated from annual sight transects of reef fishes taken off central California by Miller and Geibel (1973) and Burge and Schultz (see footnote 6) exceeded our values, but not sig-nificantly so. But our AV's were significantly less than the value (0.55) that we calculated from Livingston's (1976) trawl samples of fish from a Florida estuary during two successive winters (F-tests of variance ratios, $P<0.01$). Thus, annual variation in species abundances of our fish as-semblages may be more typical of communities in relatively stable environments than of those from highly variable environments.

Climatic and other environmental anomalies may contribute to annual variation. Peak fish abundance in 1972 occurred in relatively clear and warm water, which may stimulate fish to be more active (Quast 1968a, b, c; Larson 1977), and perhaps more easily photographed. The summer and fall of 1972 followed a relatively calm winter of light rainfall (Harger 1979: append. B), and was a favorable period for growth of small benthic algae and associated animals, which are impor-tant forage for surfperches and other microcarni-vores. On the other hand, poor visibility may have caused abrupt decreases in counts of *Chromis punctipinnis* at the island site in 1973. An obliga-tory daytime planktivore (Bray 1978), this species may seek bottom shelter when water is turbid. Generally, midwater planktivores were more vari-able in numbers than other species. Decreased kelp cover at the mainland site in 1974 probably drove some fish bottomward, but not necessarily out of view; an aggregate decrease of eight indi-viduals per canopy transect of *C. punctipinnis*, *Paralabrax clathratus,* and *O. californica* accom-panied a corresponding increase of five per bottom transect.

However, less obvious factors may be more im-portant, because other periods of clear and warm water produced no such peak abundances. Time lags in responses of fish populations to environ-mental change preclude simple explanations of annual variation. Lags between bumper births and subsequent adult recruitment may cause populations to overshoot their environmental car-rying capacities (Hutchinson 1978). Alterna-tively, fixed spawning seasons coupled with an unpredictable cycle in food production may limit recruits independently of the carrying capacity of the environment for adults (Cushing 1969). From bottom-trawl catches, Mearns[12] concluded that re-cruitment of juvenile nearshore fishes occurs over relatively short periods off southern California and may vary markedly in success among species from one year to the next. Larson (1977) found that counts of *S. carnatus* and *S. chrysomelas* decreased significantly at several depths in an area near the island site during 1973-76. This decrease may have been the result of sparse juvenile settlement observed in 1974-75.

Migration and predation may play a role, espe-cially at the mainland site, a semi-isolated offshore reef; e.g., kelp perch, which are canopy specialists, occurred sporadically and sparsely there. Kelp cover has varied considerably over the years. But even though cover may vary at other places as well, the distance of this reef from exten-sive kelp beds inshore may have inhibited kelp-perch recolonization after periods of canopy loss. Several natural predators eat reef fishes, but we do not know if the rate varies from year to year. During the day, harbor seals and sea lions forage at both sites. Predatory fish such as kelp bass may eat relatively more young of species such as surfperches that do not hide in the reef itself, dur-ing periods when plant cover is sparse. At night, larger individuals of such prey fish may be par-ticularly vulnerable to large Pacific electric ray, *Torpedo californica*, which invade the reef then (Bray and Hixon 1978). Love (1978) concluded that olive rockfish, which grow slowly and seldom move between reefs, are decimated chronically by overfishing. Although kelp bass are equally exploited, adult replacements apparently move in to restore a portion of a contiguous population (Quast 1968d).

It is noteworthy that the constancy or "stability" in species composition of our fish assemblages was roughly correlated with species diversity. Canopy assemblages were relatively simple, with many individuals distributed unevenly among a few species. They were less constant in composition than the bottom assemblages, which were charac-terized by more species and more even distribution of individuals among species. Also, the island bot-tom assemblage, which was the more diverse

because of greater evenness, maintained a more constant species composition than the mainland-bottom assemblage. But there is no good basis, either theoretical (May 1973) or empirical, for assuming that this relation is a causal one. Some diverse communities of coral-reef fishes are reportedly not stable at all; in fact, fluctuations in their species composition may actually increase their diversity (Sale 1977, 1978; Talbot et al. 1978).

Rather, both constancy and diversity of the assemblages are probably determined by the type of habitat in which they live. Thus, the relatively low diversity and high temporal instability of the canopy assemblages probably reflect the simplicity and instability of the canopy habitat. Most fish meet in the canopy to eat plankton or planktivorous fishes. In this way, the canopy habitat is a concourse, where animals meet for one purpose (Elton 1927; Whittaker 1965). Here there are relatively few opportunities for diversifying form and function, and hence fewer species. Relatively few environmental factors strongly influence species distributions, as May (1975) suggested in general for simply structured communities. Ephemeral currents, turbidity, temperature, and kelp growth may influence the distribution of canopy dwellers. Bray (1978) has shown that the distribution of adult blacksmith is strongly affected by food-bearing currents. Adults have largely independent sources of food and shelter: the reef provides shelter but water currents carry in their planktonic food. Blacksmith feed in dense aggregations, and since local oceanographic conditions fluctuate rapidly (Quast 1968a) and plankton occurs in patches (Wiebe 1970), the location of their optimal area of foraging frequently shifts.

In contrast, our bottom assemblages depend on more stable commodities like rocks and infaunal prey, which are not so immediately affected by factors, like currents, that change rapidly. Many bottom species are solitary, parochial, or even territorial (Clarke 1970; DeMartini 1976; Larson 1977; Hixon 1979). Thus, their local density is not so likely to change from day to day.

The greater variability of the mainland-bottom assemblage than that of the island is curious. Perhaps the relative isolation of the mainland site may contribute to vagarious settlement of fish larvae and other recruitment (Larson 1977). Also, the mainland site has relatively large areas of reef flat and a surrounding plain of sand and cobble, creating more of a "transitional" type of habitat.

Periodic occurrences of such species as the black croaker, *Cheilotrema saturnum*, and rainbow surfperch, which are atypical of continuous high-relief rocky habitats, lend discontinuity to the Naples fish assemblage.

ACKNOWLEDGMENTS

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