Habitat Groups and Island-Mainland Distribution of Kelp-bed Fishes off Santa Barbara, California

Alfred W. Ebeling, Ralph J. Larson,[1] and William S. Alevizon[2]

Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara, California 93106.

INTRODUCTION

The islands off southern California diversify the coastal environment by doubling the length of shoreline and extending coastal habitats (Horn 1974). Geologically, and perhaps biologically, these islands may be classified into northern (bordering the Santa Barbara Channel) and southern groups (Hewatt 1946, Valentine and Lipps 1967, Weaver and Doerner 1967). Yet classification of the insular shore fish fauna is more complex. On a broad scale, distributions of shore fishes are influenced by water temperature and associated currents: the cool, southerly-flowing California Current offshore, and the warmer, inshore countercurrent and eddy (Hubbs 1967, 1974, Neushul *et al.* 1967). Also, the specific assemblage of fishes in a given area will depend very strongly on the habitat structure there. And finally, isolation at islands may be brought about either by differential transport of species having planktonic larvae (Kanter 1980, Seapy and Littler 1980) or by chance transport of species that have no planktonic dispersal stage (*cf.* Haldorson 1980). Our study analyzes the effects of habitat on the composition of one element of the inshore fish fauna, the kelp-bed fishes, and applies this analysis to compare the kelp-bed fish assemblages at Santa Cruz Island with those from the adjacent Santa Barbara mainland.

Some papers in this symposium dealt with large-scale biogeography of inshore organisms on the California Islands (Seapy and Littler 1980, Silva 1978). Even though we do not address this problem directly, we realize that interpretations of habitat effects must consider geographic affinities of the fauna. On the other hand, habitat effects may confound broad-scale geographic effects (*cf.* Kanter 1980, Littler 1980). Our objective, therefore, is to show how assemblages of kelp-bed fishes may be classified into particular habitat groups, and how differences in structural habitat affect the composition of fish assemblages making up such groups.

We did our study off Santa Barbara, at the southern end of a transitional zone between a warm-temperate biota to the southeast and a cool-temperate biota at San Miguel Island and north of Point Conception (*cf.* Hewatt 1946, Hubbs 1948, 1960, 1974, Neushul *et al.* 1967, Quast 1968b, Ebeling *et al.* 1971). The mixed composition of the fauna reflects water temperature and exposure to currents. The California Current carries cool water seaward past Point Conception, although a small branch of this current feeds a counterclockwise eddy in the western part of the Santa Barbara Channel (Reid 1965, Kolpack 1971). This eddy meets warmer currents from the southeast at the eastern end of the Channel, near Santa Barbara and Santa Cruz Island (Kolpack 1971). Therefore, even though oceanographically complex, our study areas are warmer and more exposed to southern currents than is San Miguel Island at the western end of the channel.

Given the geographic affinities of the fish fauna in our study areas, we investigated the influence of structural habitat on the composition of fish assemblages in and about beds of giant

[1] Present address: MRC Research Center, 533 Stevens Ave., Solana Beach, California 92075.

[2] Present address: Department of Biological Sciences, Florida Institute of Technology, Melbourne, Florida 32901.

kelp (*Macrocystis*). In this way, we hoped to explain any "island effect" on these assemblages, as expressed by differences in species abundance and composition between Santa Cruz Island and the Santa Barbara mainland. Inshore habitats vary along several environmental gradients (Limbaugh 1955, North 1963, Quast 1968a, Frey 1971). For example, density of giant kelp varies with depth and several other factors (Neushul *et al.* 1967, North 1963, 1971, Quast 1968a, Pearse and Lowry 1974). A depth-related gradient in dominant plants extends from surfgrass, boa kelp, or *Pterygophora-Eisenia* communities inshore, through giant kelp and red algae at intermediate depths, to depauperate plant communities in deeper water (Clarke and Neushul 1967, Neushul *et al.* 1967). Such biotic gradients follow abiotic gradients in temperature, light, wave surge, and productivity (Quast 1968a, Pequegnat 1964). A gradient in substrate type extends from flat and soft bottoms of sand and/or mud, through flat and hard bottoms, to high-relief rocky reefs; the "turf" of sessile animals and plants that covers these reefs varies with degree of water movement, silting, scouring, light penetration, and grazing (McLean 1962, Pequegnat 1964, Turner *et al.* 1965, 1968, Clarke and Neushul 1967, North 1971, Pearse and Lowry 1974, Neushul *et al.* 1976). Much like a forest, giant kelp provides a vertical gradient along which animals tend to stratify in the water column. Kelp stipes in midwater and the dense canopy near the surface provide shelter, food, and landmarks for a variety of fishes (Hobson 1965, Quast 1968b, Feder *et al.* 1974, Alevizon 1976).

Limbaugh (1955) and Quast (1968b, 1968c) analyzed kelp-bed fish assemblages mainly in the San Diego area of southern California. Miller and Geibel (1973) and Burge and Schultz (1973) analyzed such assemblages off central California, north of Point Conception. These investigators evaluated specific responses of individual species to their natural environment and were concerned with how assemblages may respond to changes in structural habitat. Excepting a few fragmentary observations and species lists (Hewatt 1946, Clarke and Neushul 1967, Neushul *et al.* 1967, Quast 1968c), however, there was almost no published information from the Santa Barbara area.

We supplement these seminal studies of southern and northern regions by taking a more synthetic approach to analyzing species assemblages in the less well-known transitional region off Santa Barbara. Thus, although we must interpret our results in terms of behavior of particular species, our results provide an overall view of changing fish assemblages. Hopefully, our synecological approach reveals general trends not immediately obvious from autecological studies.

We compared kelp-bed fish assemblages sampled at different localities along Santa Cruz Island with assemblages sampled at different localities along the Santa Barbara mainland. We first determined the structure of assemblages by identifying subgroups of species ("habitat groups") that tend to associate with different positions on environmental gradients in and about areas of reef and kelp. We then compared the density, diversity, and composition of assemblages among localities, between mainland and island, and between seasons. With this information, we were better able to distinguish and explain any island effect on the assemblages, in light of the faunal complexity of the region.

METHODS

Cinetransect Samples

We sampled fish populations and associated habitat variables by means of cinetransects. Cinetransects are 2.5-min, Super-8 mm, high-speed color movie films from 15.24-m film cartridges, taken by scuba divers starting out in a randomly chosen direction (Alevizon 1975a, Alevizon and Brooks 1975, Bray and Ebeling 1975, Love and Ebeling 1978, Ebeling *et al.* in press). To take cinetransect samples, we drove our skiff to any open area in the kelp where we could conveniently anchor. Diver photographers then swam with underwater cameras at about

3 m depth below the kelp canopy (canopy transects), or just above the bottom (bottom transects). We sampled in as many different habitats as we could find, but in each transect the photographer tried to stay within the same general depth, terrain, and microhabitat type (*e.g.*, sandy bottom, reef crest, surfgrass beds), so that each cinetransect could be classified by discrete habitat characteristics. For some of our analyses, we divided bottom transects into those made over rocky reefs and those made in inshore or sandy areas at or beyond the reef or kelp-bed margins (sandy-marginal transects). Bottom transects (in kelp beds over rocky reefs) outnumbered canopy and sandy-marginal transects (Table 1). The photographers swam at a fairly constant rate and never doubled back, so as not to photograph fish that tend to follow. The camera was pointed ahead (or slightly downward for bottom transects) and panned in a 10-degree arc as steadily as possible. Occasionally, the camera was pointed to include all fish sighted in a particular school or cluster. Measurement of variables was made *in situ* (*e.g.*, temperature, overcast, surge) or from the movies (*e.g.*, species counts, scored bottom relief, kelp density). Ebeling *et al.* (in press) concluded that cinetransecting is effective for rapidly sampling large, mobile fishes in complex environments where water is reasonably clear. Cinetransects provided permanent records of fish densities and general habitat structure. Compared with destructive sampling such as poisoning, cinetransects provided more realistic counts of larger and stronger fishes, but tended to underestimate densities of small and cryptic species.

During 1970, 175 cinetransects were filmed in reef and sandy-marginal habitats at four localities along the Santa Barbara mainland and five localities along Santa Cruz Island (Fig. 1 and Table 1). Cinetransects served three purposes: first, we used them as a large, heterogeneous sample to identify habitat groups (species with intercorrelated densities, along with associated environmental features). Second, we used them as smaller, homogeneous samples to compare fish assemblages among nearby localities that differed slightly in habitat characteristics, and to compare island and mainland assemblages. We divided the cinetransects into 20 samples, one each for canopy and bottom at each of nine localities, and one each for island and mainland sandy-marginal habitats. Third, we used mainland canopy and bottom cinetransects to see if fish assemblages varied seasonally by comparing samples taken during winter and spring with others taken in summer and fall. Off Santa Barbara, winter-spring (December through May) is an oceanographic period of cooler water, maximum vertical mixing, upwelling, storms, and fish spawning. Summer-fall is a period of warmer and generally clearer water, thermal stratification, calm weather, and rapid fish growth (Brown 1974, Love and Ebeling 1978).

Habitat Group Identification

To identify habitat groups (*i.e.*, to recognize environmentally induced patterns in the co-occurrence of kelp-bed fishes), we carried out a factor analysis of species densities and environmental variables (*cf.* Smith *et al.* 1973). In factor analysis, a large part of the covariation of observed variables is attributed to only a few, presumably causative, factors (Harman 1967). Thus, our factors can be thought of as a smaller number of hypothetical variables (habitat groups) that summarize the relations among a larger number of real variables (fish counts, habitat measures).

After selecting (as described below) 10 environmental variables (*e.g.*, measures of habitat, fish abundance and diversity) and 24 species variables (fish counts), we computed a factor analysis from a correlation matrix of all 34 variables. The analysis was such that factors were not necessarily orthogonal and could be correlated (Program BMDX72, with oblique rotation for simple loadings, from Dixon 1967). Appropriate criteria (Harman 1967, Fisher 1968, Thomas 1968) suggested that five factors were sufficient to describe the major relationships in the system. The degree of relationship between a variable and a factor is expressed by its

TABLE 1. Physical characteristics of 175 cinetransects filmed in kelp-canopy, bottom, and sandy-marginal habitats and grouped by localities along the mainland and Santa Cruz Island off Santa Barbara, California (Fig. 1). *Season* reflects periods of different hydrography: WS (December-May) and SF (June-November). *Bottom depth* is scored: 1 (1.5-4.6 m), 2 (4.8-7.6 m), 3 (7.9-10.7 m), 4 (11.0-13.7 m), and 5 (14.0-17.0 m). *Bottom relief* is scored subjectively from 1 (almost flat) to 5 (high ridges, large boulders, etc.). Each entry represents the number of cinetransects.

			Season		Bottom depth (score)					Bottom relief (score)				
Habitat	Area	Locality	WS	SF	1	2	3	4	5	1	2	3	4	5
Canopy	Mainland	HE	3	3		4	2			4	2			
		IV	6	4	1	3	6			7	3			
		CO	2	5			5	2		7				
		NA	4	3			2	4	1		1	3	2	1
	Island	SC		7		6	1				3	2	1	1
		PE		5			4	1			1			4
		FR		4	1	1		1	1			1	1	2
		VA		5		2	3					2	2	1
		WI		6		3	3					4	1	1
Bottom	Mainland	HE	5	7		9	3			2	2	5	2	1
		IV	6	5		3	8			1	4	6		
		CO	6	10	5	4	5	1	1	6	8	1	1	
		NA	5	6		1	6	3	1			3	4	4
	Island	SC		11	5	4	1	1				4	2	5
		PE		7	3	4							2	5
		FR		7	1		3		3			2	1	4
		VA		7		2	2	3					4	3
		WI		14	5	6	3				1		6	7
Sandy margin	Mainland*		6	6	9	3				8	4			
	Island*			10	2	2	6			6	2	2		

* Sandy-marginal cinetransects taken at a variety of mainland and island locations.

FIGURE 1. *Localities (circled) for cinetransect sampling of fish assemblages in areas of reef and kelp off Santa Barbara, California. Mainland: CO, Coal Oil Point; HE, Hendry's (Arroyo Burro) Beach; IV, Isla Vista; NA, Naples Reef. Santa Cruz Island: FR, Frys Harbor and vicinity; PE, Pelican Bay and vicinity; SC, Scorpion Anchorage; VA, Cueva Valdaze; WI, Willows Anchorage.*

"loading" on the factor. Loadings vary from −1.0 to +1.0 and are analogous to partial regression coefficients (Harman 1967). Because there is no significance test for loadings, we followed Sokal and Daly (1961) and arbitrarily took the absolute value 0.40 as about the lower limit of important loadings. Each of our five habitat groups was defined by the variables loading at least this high on a particular factor. Thus, most species could be unequivocally assigned to the habitat group represented by the factor on which they had the highest loading, although some species were difficult to place because they had intermediate loadings on two or more factors. The latter species may be interpreted as transgressing habitat groups more than is characteristic of the other species (*cf.* Angel and Fasham 1973).

The 24 fish species analyzed were those that occurred at a frequency of about 5 per cent (8 of 175 cinetransects) or more (Table 2). Fish counts per species often included many zeros, so the species' frequency distributions among cinetransects were strongly skewed. Since log-transformations of counts did not normalize most distributions, we used Kendall's rank correlations (instead of the usual parametric product-moment correlations) as the basis for our factor analysis.

Selecting the "best" environmental variables from the huge number observable was more difficult. We began with the largest number we could measure practicably and then, using several criteria, eliminated those considered less important. This large initial set included variables that measured (1) fish abundance and diversity, (2) habitat structure, (3) seasonal progression, and (4) changes in the weather. We subsequently eliminated seasonal and weather variables because their correlations with species densities were relatively small (Table 3).

TABLE 2. Fish species recorded by 175 cinetransects filmed in areas of reef and kelp off Santa Barbara, California (Fig. 1). *Common names* are arranged alphabetically as in an index (names and classification follow Miller and Lea 1972). *Occurrence* is: *c*, common; *m*, moderately common; *r*, rare but characteristic of such areas; and *u*, rare and uncharacteristic. An *X* marks the species' *inclusion* in the numerical analyses.

Common name	Scientific name	Family	Occurrence	Inclusion
Elasmobranchs				
Guitarfish, shovelnose	*Rhinobatos productus*	Rhinobatidae	u	
Ray				
bat	*Myliobatis californica*	Myliobatididae	u	
Pacific electric	*Torpedo californica*	Torpedinidae	u	
Shark				
horn	*Heterodontus francisci*	Heterodontidae	u[6]	
leopard	*Triakis semifasciata*	Carcharhinidae	u	
swell	*Cephaloscyllium ventriosum*	Scyliorhinidae	u[6]	
Teleosts				
Bass				
barred sand	*Paralabrax nebulifer*	Serranidae	m	X
kelp	*P. clathratus*	Serranidae	c	X
Blacksmith	*Chromis punctipinnis*	Pomacentridae	c	X
Cabezon	*Scorpaenichthys marmoratus*	Cottidae	r[1]	
Croaker, black	*Cheilotrema saturnum*	Sciaenidae	r	
Garibaldi	*Hypsypops rubicundus*	Pomacentridae	c	X
Goby, blackeye	*Coryphopterus nicholsii*	Gobiidae	r[1]	
Greenling				
painted	*Oxylebius pictus*	Hexagrammidae	m	X
kelp	*Hexagrammos decagrammus*	Hexagrammidae	r	
Halfmoon	*Medialuna californiensis*	Scorpididae	m	X
Kelpfish				
giant	*Heterostichus rostratus*	Clinidae	m	X
sp.	*Gibbonsia* sp.	Clinidae	r[1]	
Lingcod	*Ophiodon elongatus*	Hexagrammidae	r	X
Mola	*Mola mola*	Molidae	u	
Opaleye	*Girella nigricans*	Girellidae	c	X
Pipefish	*Syngnathus* sp.	Syngnathidae	r[1]	
Rockfish				
black	*Sebastes melanops*	Scorpaenidae	r	
black-and-yellow	*S. chrysomelas*	Scorpaenidae	m	X[2]
gopher	*S. carnatus*	Scorpaenidae	m	X[2]
blue	*S. mystinus*	Scorpaenidae	c	X
grass	*S. rastrelliger*	Scorpaenidae	r	X[2]
kelp	*S. atrovirens*	Scorpaenidae	c	X
olive	*S. serranoides*	Scorpaenidae	c	X
whitebelly	*S. vexillaris*	Scorpaenidae	r[3]	X[2]
Sculpin, lavender	*Leiocottus hirundo*	Cottidae	r	
Señorita	*Oxyjulis californica*	Labridae	c	X
Sheephead, California	*Pimelometopon pulchrum*	Labridae	c	X

TABLE 2. (Cont.)

Surfperch				
barred	*Amphistichus argenteus*	Embiotocidae	u	
black	*Embiotoca jacksoni*	Embiotocidae	c	X
dwarf	*Micrometrus minimus*	Embiotocidae	r[3]	X
island	*Cymatogaster gracilis*	Embiotocidae	c[4]	
kelp	*Brachyistius frenatus*	Embiotocidae	c	X
pile	*Damalichthys vacca*	Embiotocidae	c	X
rainbow	*Hypsurus caryi*	Embiotocidae	m[5]	X
rubberlip	*Rhacochilus toxotes*	Embiotocidae	m	X
sharpnose	*Phanerodon atripes*	Embiotocidae	r	
shiner	*Cymatogaster aggregata*	Embiotocidae	u	
striped	*Embiotoca lateralis*	Embiotocidae	c	X
walleye	*Hyperprosopon argenteum*	Embiotocidae	u[6]	X
white	*Phanerodon furcatus*	Embiotocidae	m	X
Topsmelt	*Atherinops affinis*	Atherinidae	u	
Treefish	*Sebastes serriceps*	Scorpaenidae	r[2]	
Turbot, C-O	*Pleuronichthys coenosus*	Pleuronectidae	u	
Whitefish, ocean	*Caulolatilus princeps*	Branchiostegidae	r[3]	
Wrasse, rock	*Halichoeres semicinctus*	Labridae	r	

[1] Apparently rare only because small and/or well camouflaged.
[2] All counted in one category of "bottom rockfish."
[3] Apparently rare because its distribution centers on deeper (whitebelly rockfish, ocean whitefish) or shallower (dwarf surfperch) reefs.
[4] Island endemic.
[5] Seasonally (spring, summer) common at Naples Reef.
[6] Active on reef only at night.

We then reduced the set of 20 habitat variables to minimize redundancy. Using the results of a separate, preliminary factor analysis of correlations among the habitat variables, we selected the most representative by the following criteria (Table 3): (1) every habitat factor resolved should be represented by at least one variable, (2) the variable should have a relatively large mean correlation with species densities (*i.e.*, be a likely causative agent), and (3) the variables should have a relatively large "communality" (Table 3) with the other environmental variables (*i.e.*, be most predictive of variation of the factor group as a whole). Hence, most were chosen by weighting the mean correlation (to bring it within the same magnitude as communalities), and adding the communality. For example, all variables loading on habitat factor 1 (Table 3) were highly intercorrelated, but the rocky, high-relief bottom type had the highest mean correlation-communality. Thus, this variable was chosen to represent the factor (and it is likely that variation in bottom relief induces variation in other correlates such as invertebrate and bottom-algal densities). Hence, bottom relief was selected as the best single variable to measure the whole substrate aspect of habitat structure. We made some exceptions: for habitat factor 3, bottom depth and plant density-surfgrass equally met the criteria, so both were included; for habitat factor 2, positional variables were selected, along with plant density-giant kelp (which met the criteria) for better spatial resolution of the groups; and for habitat factor 4, "area" (scored mainland or Santa Cruz Island localities) was omitted because mainland-island faunal and habitat differences were analyzed later.

TABLE 3. Correlative properties of environmental variables measured with each of 175 cinetransects filmed in areas of reef and kelp off Santa Barbara (Table 1). *Mean correlation* is the average of absolute values of correlations of the variable with densities of 24 fish species (Table 2). *Communality*, scaled from 0.0-1.0, measures covariation with others in a subgroup of 20 habitat variables subjected to a preliminary factor analysis. Variables with low communalities do not correlate strongly with others as factors; variables with high communalities and the same *factor number* are intercorrelated relatively strongly. The symbol "(−)" after factor number means that the variable is negatively correlated with others with the same factor number (see text).

Variable	Mean correlation with species variables	Usual sign of correlation	Communality with other habitat variables in factor analysis	Factor number
Abundance-diversity variables				
Number of fish per transect*	0.199	+		
Number of species per transect*	0.270	+		
Mean	0.234			
Habitat variables				
Area (scored localities)	0.205	+	0.80	4
Bottom depth (m)*	0.166	+	0.57	3(−)
Bottom type (score)				
boulders	0.185	+	0.75	1
rocky high relief*	0.185	+	0.84	1
rocky low relief	0.131	−	0.62	4(−)
sand	0.166	−	0.81	1(−)
Invertebrate density (score)				
crabs, etc.	0.175	+	0.81	1
urchins	0.111	+,−	0.67	1
Plant density (score)				
surfgrass*	0.173	+,−	0.54	3
giant kelp*	0.197	+	0.77	2
other brown algae, short	0.135	+		
other brown algae, tall	0.122	+,−	0.49	1
red algae	0.144	+	0.54	3
Position of transect relative to kelp bed (score)			0.72	1
outside of, but near*	0.145	−		
outside of, but not near	0.123	−	0.80	2(−)
toward shoreward margin*	0.126	+	0.42	3
toward middle	0.156	+	0.64	5(−)
toward seaward margin	0.114	−	0.82	2
Position of transect in water column (score)*	0.203	+,−	0.67	5
Underwater visibility (m)*	0.129	+	0.37	2
Mean	0.155		0.42	4
Seasonal variables				
Month (winter-summer)	0.107	+	0.76	
Thermocline depth (m)	0.076	+		
Water temperature (°C)				
bottom	0.095	+		
surface	0.078	+		
Mean	0.089		0.78	
Weather variables				
Overcast (score)	0.116	+		
Surge strength (score)	0.085	−		
Swell height (m)	0.112	−		
Wind				
direction to NW (score)	0.097	−		
speed (mph)	0.113	−		
Mean	0.105			

* Included in final factor analysis based on 10 environmental variables and 24 species.

TABLE 4. Habitat groups of kelp-bed fishes identified by factors relating 34 habitat and species variables from 175 cinetransects filmed off Santa Barbara (Table 1). *Factor loading* measures the contribution of the variable to the factor, and is scaled from −1.0 (correlates negatively with other variables in group) to +1.0 (correlates positively) (see text). *Communality* is explained in Table 3.

Factor number/Habitat group/Variable	Factor loading	Communality
1. Kelp-rock group		
Bottom type: rocky high relief	0.75	0.57
Plant density: giant kelp*	0.51	0.67
Underwater visibility	0.42	0.24
Number of species per transect	0.51	0.72
Number of fish per transect*	0.40	0.57
Blacksmith	0.65	0.52
Opaleye	0.62	0.50
Striped surfperch	0.60	0.45
Halfmoon	0.49	0.29
California sheephead	0.49	0.53
Garibaldi	0.45	0.32
Blue rockfish*	0.40	0.44
2. Canopy group		
Position of transect in water column*	−0.61	0.78
Number of fish per transect*	0.59	0.57
Kelp surfperch	0.56	0.56
Giant kelpfish	0.55	0.39
Señorita	0.41	0.24
Olive rockfish	0.41	0.31
Kelp rockfish*	0.36	0.42
3. Inner-marginal group		
Plant density: surfgrass	0.78	0.60
Bottom depth	−0.67	0.49
Position re. kelp bed: toward shoreward margin	0.56	0.39
Dwarf surfperch	0.64	0.41
Walleye surfperch	0.63	0.54
Rainbow surfperch	0.50	0.32
Black surfperch*	0.39	0.52
4. Commuter group		
Number of fish per transect*	0.51	0.57
Pile surfperch	0.71	0.50
Rubberlip surfperch	0.65	0.44
Kelp bass	0.42	0.37
White surfperch	0.40	0.39
Kelp rockfish*	0.39	0.42
5. Bottom group		
Position re. kelp bed: outside of, but near	0.64	0.63
Plant density: giant kelp*	−0.55	0.67
Position of transect in water column*	0.52	0.78
Lingcod	0.58	0.34
Painted greenling	0.50	0.28
"Bottom rockfish"†	0.48	0.31
Sand bass	0.47	0.28
Blue rockfish*	0.40	0.44
Black surfperch*	0.36	0.52

TABLE 4. (Cont.)

* Variables loading on more than one factor.

† Includes mostly black-and-yellow and gopher rockfishes; more rarely, grass and whitebelly rockfishes and treefish.

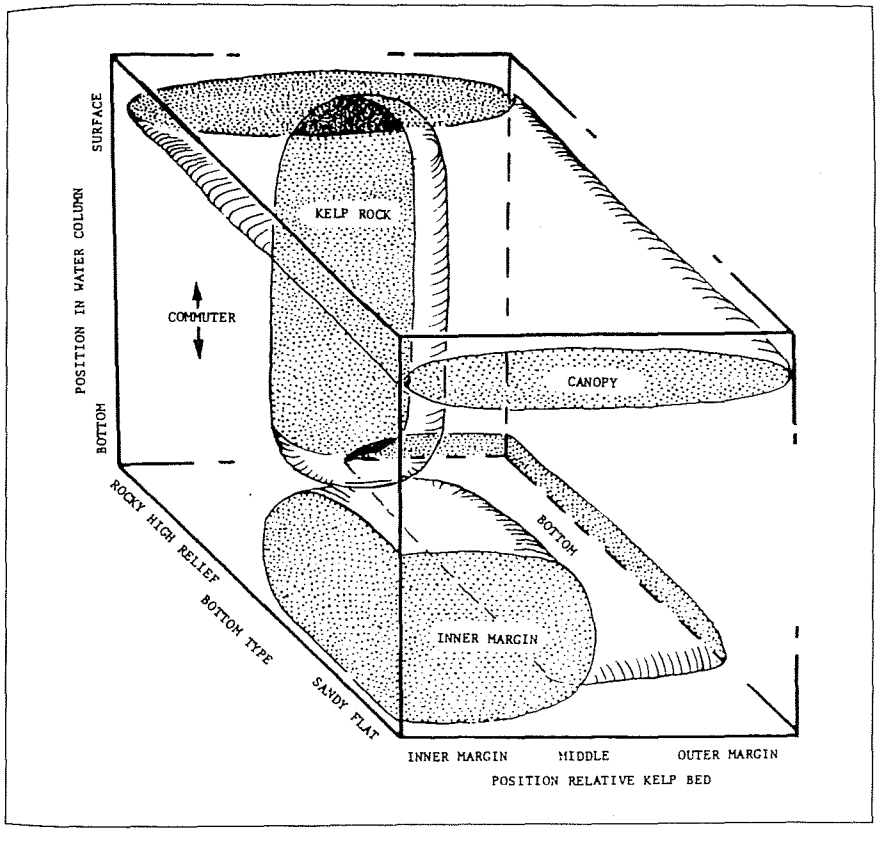

FIGURE 2. *Principal daytime space occupied by habitat groups (Table 4) of kelp-bed fishes identified by factors relating habitat and species variables from 175 cinetransects filmed off Santa Barbara (Fig. 1 and Table 1). Stippling is intersection of a group's principal space with a plane defined by axes of any two habitat variables. For example, species in the inner-marginal group transgress the sandy flat (lower values along transverse axis) beyond the edge of the kelp bed (lower values along horizontal axis) toward shore, so are not necessarily most abundant over well-developed offshore reefs. Species in the commuter group may occur commonly from bottom to canopy throughout the kelp bed.*

In summary, we computed a final factor analysis of rank correlations among 34 variables: density of each of 24 species, total fish and species per transect, and eight measures of habitat structure (Table 4).

Interlocality Comparisons

For canopy and bottom zones, mean fish density (number of individuals/cinetransect), biomass (wet weight estimated from length-weight regressions), and diversity (number of species) were compared among localities by one-way analyses of variance (anovas) for unequal sample sizes, and were compared for localities *vs.* seasons or areas (mainland, island) by two-way anovas for disproportionate, as well as unequal, subclass sizes (Nie *et al.* 1975). For two-way analyses of locality and area main effects, each of four "localities" was made up of a mainland-island pair in the Santa Barbara Channel (see Table 7). Since sample distributions of density and biomass were skewed to the right (relatively few large values), we $\log_{10}$-transformed variates to minimize extremes (Sokal and Rohlf 1969). This corrected for skewness and equalized variances (*cf.* Quast 1969c). Sample distributions of diversity were not significantly different from normal and had equal variances, and were therefore left untransformed. *A posteriori* contrasts between means were made (Table 8) by finding the smallest subgroups of means whose largest and smallest values were not significantly different (Sokal and Rohlf 1969, Dunnett 1970).

Differences in species composition among localities were measured by a similarity index (Whittaker 1960), based on proportionate differences in numbers of individuals: $I = 1.0 - (0.5 \sum_{i=1} |p_{ij} - p_{ik}|)$, or $\min(p_{ij}, p_{ik})$, where p_{ij} is the proportionate abundance of species i in cinetransect j. Outcomes were similar whether proportionate differences between samples were based on density, biomass, or frequency of occurrence of the included species because the three kinds of arrays were highly intercorrelated. Rank correlations between species arrays based on pooled mainland bottom samples were large and highly significant ($P<0.001$): 0.60 between biomass and density, 0.64 between biomass and frequency, and 0.78 between frequency and density.

RESULTS

The 175 cinetransects recorded 51 fish species in 23 families, although only about half were common enough to be analyzed (Table 2). This large heterogeneous sample was the basis for identifying habitat groups of species. Showing little or no seasonal variation, subsamples revealed significant differences in kelp-bed fish assemblages among localities, which varied considerably in structural habitat along the mainland. Overall, however, mainland-island differences overshadowed interlocality differences.

Habitat Groups

Factor analysis resolved five factors of intercorrelated species and habitat variables. We interpreted the factors as identifying loose spatial associations or habitat groups of common kelp-bed fishes (Table 4 and Fig. 2): a kelp-rock group (factor 1) of species that co-occurred most abundantly in clear-water areas of high bottom relief and kelp density, where species diversity was greatest; a group (2) of species that co-occurred high in the water column, beneath the kelp canopy; an inner-marginal group (3) of surfperches that co-occurred shoreward at shallower depths, where surfgrass was plentiful; a commuter group (4) of species that co-occurred throughout the water column in areas of high species diversity; and a bottom group (5) of sedentary species that co-occurred most abundantly on the reef bottom, where kelp was less dense.

Correlations between the factors themselves indicated interrelationships among the habitat groups (Table 5). The kelp-rock (factor 1), bottom (5), and commuter (4) groups were positively correlated, while canopy (2) and inner-marginal (3) groups were uncorrelated or negatively correlated with this triad.

TABLE 5. Correlations among five factors relating 34 habitat and species variables from 175 cinetransects filmed off Santa Barbara (see Table 4).

Factor	1. Kelp rock	4. Commuter	5. Bottom	2. Canopy
4. Commuter	0.13			
5. Bottom	0.05	0.12		
2. Canopy	−0.01	0.02	−0.11	
3. Inner margin	−0.13	0.06	0.02	−0.10

TABLE 6. Locality-*vs.*-season analysis of variance of kelp-bed fish density, biomass, and diversity from cinetransects filmed along Santa Barbara mainland and classified by four localities and two semiannual periods, December-May and June-November (Fig. 1 and Table 1).

	Degrees of	Density ($\log_{10}$ nos. of individuals)		Biomass ($\log_{10}$ kg)		Diversity (nos. of species)	
Source	freedom	Mean square	F	Mean square	F	Mean square	F
Canopy							
Localities, L	3	0.263	1.73	0.235	1.77	10.279	3.48*
Seasons, S	1	0.037	<1	0.002	<1	1.884	<1
L × S	3	0.387	2.54	0.397	2.99	12.316	4.18**
Error	22	0.152		0.133		2.949	
Bottom							
Localities, L	3	0.677	6.94***	0.784	6.50***	33.476	8.14***
Seasons, S	1	0.090	<1	0.015	<1	0.328	<1
L × S	3	0.037	<1	0.013	<1	7.366	1.69
Error	42	0.097		0.121		4.359	

Significant at: $*0.05<P<0.02$. $**P=0.02$. $***P<0.001$.

Interlocality Differences

Habitat structure varied more among mainland than among island localities, and mainland-type habitats as a whole were different from island-type habitats (Table 1). Along the mainland, locality NA (Fig. 1) had a better-developed and deeper reef than the other three localities. All four localities, however, had relatively large expanses of sand and flat rock separating relatively small areas of well-developed reef. In contrast, most of the island localities were segments of a continuous, well-developed reef system.

Within sampling limits, seasonal variation in fish density, biomass, and diversity was nil. Fish densities were but weakly correlated with seasonal variables (Table 3), and no significant differences distinguished semiannual periods (Table 6).

Interlocality variation in density, biomass, and diversity was also nil in the canopy zone. We detected little or no significant differences among canopy means, either within areas or between the mainland and Santa Cruz Island (Table 7). Of all contrasts, in fact, only one mean of one variable was indicated as different from others (Table 8).

In the bottom zone, however, significant differences in these variables, both within areas and between mainland and island (Table 7), reflected differences in habitat type. In general, means from deeper localities with higher bottom relief were significantly greater than the others (Table 8; see NA and HE of mainland, and most island localities, all of which had moderate to high

TABLE 7. Locality-*vs.*-area (mainland, island) and among-locality analyses of variance of kelp-bed fish density, biomass, and diversity from cinetransects filmed along Santa Barbara mainland and Santa Cruz Island (Fig. 1 and Table 1). For the two-way analyses, localities are four mainland-island pairs in the Santa Barbara Channel: CO-PE, IV-SC, HE-FR, and NA-VA (WI, on the island's seaward side, is excluded). The one-way analyses include all nine localities.

Source	Degrees of freedom	Density (log_{10} nos. of individuals) Mean square	F	Biomass (log_{10} kg) Mean square	F	Diversity (nos. of species) Mean square	F
Canopy							
Localities, L	3	0.101	<1	0.230	1.29	8.737	1.76
Areas, A	1	0.036	<1	0.288	1.62	9.890	1.99
L x A	3	0.262	1.20	0.097	<1	7.752	1.56
Error	43	0.219		0.178		4.957	
Localities	8	0.141	<1	0.163	<1	8.740	1.87*
Error	48	0.232		0.178		4.666	
Bottom							
Localities, L	3	1.200	15.14***	1.164	13.93***	77.56	17.01***
Areas, A	1	1.716	21.64***	2.275	27.24***	101.58	22.28***
L x A	3	0.170	2.14	0.369	4.42**	7.09	1.55
Error	74	0.079		0.084		4.56	
Localities	8	0.863	11.77***	1.067	13.87***	50.70	12.38***
Error	87	0.073		0.077		4.10	

Significant at: *$P=0.09$. **$P=0.006$. ***$P<0.001$.

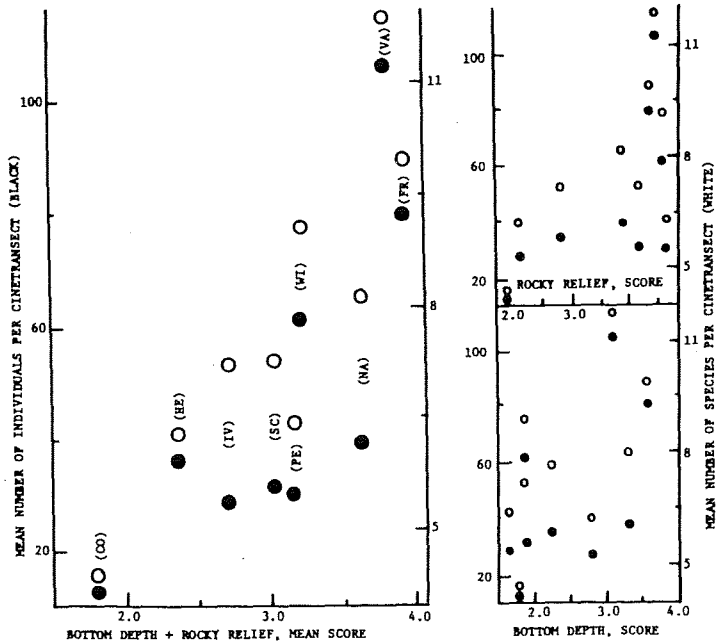

TABLE 8. Among-locality contrasts between means of kelp-bed fish density, biomass, and diversity from (*n*) cinetransects filmed at nine localities (*Loc.*) along Santa Barbara *mainland* and Santa Cruz *Island* (Fig. 1 and Table 1). Mainland observations are pooled between semiannual periods (Table 6). Using the Student-Newman-Keuls procedure, means are ordered by size into subsets (marked by columns of *X*s under *SNK*) judged homogenous by the least significant range (LSR) criterion ($P=0.05$ level); no subset contains means that differ more than the LSR determined for a subset of that size, so means that differ significantly are in different subsets (Nie *et al.* 1975; see Table 6 and text).

Habitat/ Area	Density (antilog nos. of individuals) Loc.	*n*	Mean	SNK	Biomass (antilog kg.) Loc.	Mean	SNK	Diversity (nos. of species) Loc.	Mean	SNK
Canopy										
Mainland	NA	7	43.7	X	IV	7.63	X	NA	4.14	X
	IV	10	46.6	X	NA	8.02	X	IV	4.50	X
	HE	6	54.5	X	HE	8.39	X	CO	6.14	X
	CO	7	95.8	X	CO	15.5	X	HE	6.50	X
Island	FR	4	41.4	X	FR	8.72	X	WI	4.17	X
	PE	5	54.1	X	WI	9.62	X	FR	5.00	X
	WI	6	60.6	X	SC	13.2	X	SC	5.29	X
	SC	7	78.3	X	PE	16.7	X	VA	6.80	X
Bottom										
Mainland	CO	16	12.7	X	CO	4.56	X	CO	4.37	X
	IV	11	28.4	X	HE	11.35	X	IV	6.27	X X
	HE	12	36.6	X X	IV	11.45	X	HE	7.33	X X
	NA	11	38.0	X X	NA	16.6	X X	NA	8.09	X X X
Island	PE	7	29.8	X X	SC	10.8	X	PE	6.43	X X
	SC	11	31.7	X X	PE	15.5	X X	SC	7.27	X X
	WI	14	61.5	X X	WI	28.5	X X	WI	9.07	X X
	FR	7	79.8	X	FR	35.7	X	FR	10.0	X X
	VA	7	107.1	X	VA	41.9	X	VA	12.0	X

FIGURE 3. *Variation of kelp-bed fish density and diversity with bottom depth and degree of rocky relief among bottom assemblages at four mainland and five Santa Cruz Island localities sampled from 175 cinetransects filmed off Santa Barbara (Fig. 1 and Table 1). Vertical axes: left, density (black circles); right, diversity (white circles). Horizontal axes: large graph on left, combined bottom depth and rocky relief; small graphs on right, bottom depth or rocky relief plotted separately. Localities are identified parenthetically between vertical black-white pairs of points on left graph.*

TABLE 9. Relative abundance and frequency of occurrence of 24 species in mainland *(Main.)* and Santa Cruz Island *(Is.)* samples of canopy, bottom, and sandy-marginal assemblages of kelp-bed fishes, as represented in 175 cinetransects filmed off Santa Barbara. Samples are pooled among localities (Fig. 1 and Table 1).

	Per cent numbers of individuals						Per cent frequencies of occurrence					
	Canopy		Bottom		Sandy margin		Canopy		Bottom		Sandy margin	
Species	Main.	Is.	Main.	Is.	Main.	Is.	Main.	Is.	Main.	Is.	Main.	Is.
Bass												
barred sand	-	-	0.83	-	-	-	-	-	12.0	-	-	-
kelp	9.39	3.26	16.00	9.09	4.62	17.28	86.7	66.7	80.0	87.0	33.3	80.0
Blacksmith	8.92	50.44	6.93	23.27	-	3.40	30.0	77.8	26.0	58.7	-	20.0
Garibaldi	-	-	0.36	9.43	-	-	-	-	12.0	67.4	-	-
Greenling, painted	-	-	0.89	0.88	-	-	-	-	16.0	21.7	-	-
Halfmoon	2.02	1.74	0.24	2.42	-	3.40	13.3	29.6	6.0	41.3	-	20.0
Kelpfish, giant	0.65	0.12	0.18	-	0.66	-	33.3	14.8	6.0	-	16.7	-
Lingcod	-	-	0.53	-	-	-	-	-	12.0	-	-	-
Opaleye	0.22	1.34	2.31	15.25	-	0.93	6.7	40.7	24.0	69.6	-	20.0
Rockfish												
blue	5.76	6.25	6.58	7.39	-	1.54	33.3	29.6	38.0	43.5	-	20.0
"bottom"*	-	-	1.01	0.66	-	0.62	-	-	30.0	28.3	-	10.0
kelp	2.20	4.12	1.42	4.21	-	0.62	50.0	66.7	22.0	87.0	-	20.0
olive	0.86	1.19	0.30	1.16	-	-	36.7	51.8	10.0	26.1	-	-
Señorita	6.08	4.30	6.52	3.40	2.64	22.2	63.3	51.8	44.0	43.5	25.0	70.0
Sheephead, California	-	0.24	3.02	10.03	-	11.73	-	11.1	32.0	84.8	-	70.0
Surfperch												
black	1.66	0.12	30.33	5.63	35.97	8.95	16.7	7.4	92.0	84.8	91.7	80.0
dwarf	-	-	-	0.13	3.96	0.93	-	-	-	6.5	25.0	10.0
kelp	35.16	25.74	0.36	0.13	-	0.31	76.7	74.1	6.0	6.5	8.3	10.0
pile	1.44	0.37	7.76	1.95	1.98	1.24	26.7	14.8	66.0	52.2	33.3	30.0
rainbow	-	-	1.30	0.13	7.59	0.31	-	-	22.0	4.35	25.0	10.0
rubberlip	1.04	0.34	5.15	1.95	0.34	1.85	23.3	11.1	46.0	45.6	8.3	30.0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
walleye	23.46	-	2.19	-	34.00	4.32	10.0	-	6.0	-	33.3	20.0
white	1.15	0.21	5.09	0.25	8.25	19.44	23.3	11.1	30.0	6.5	41.7	20.0
Total number of individuals	2779	3279	1688	3180	296	324						
Total number of transects							30	27	50	46	12	10

* Includes mostly black-and-yellow and gopher rockfishes; more rarely, grass and whitebelly rockfishes and treefish.

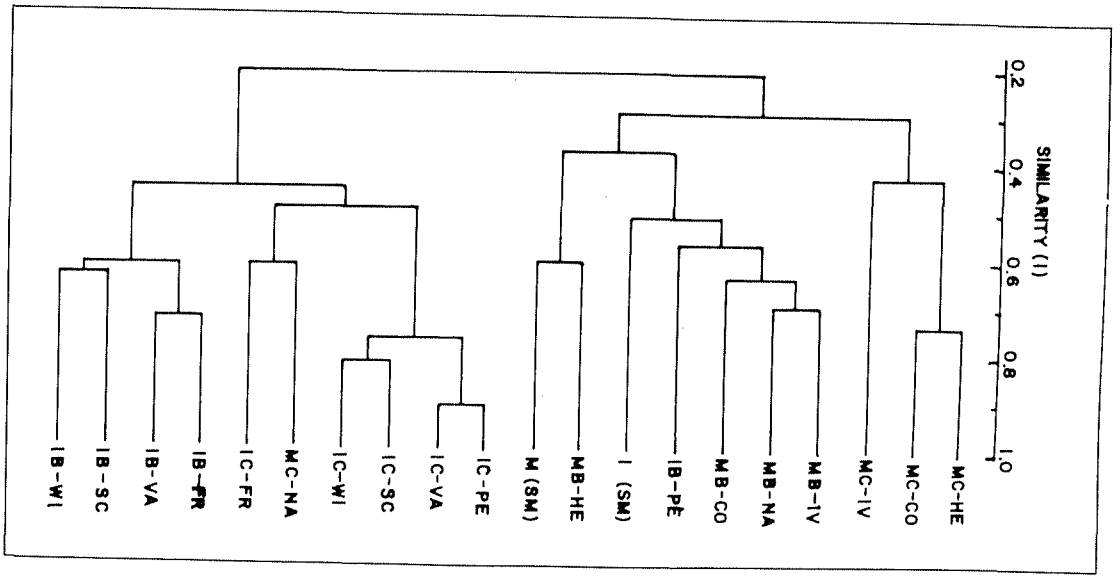

FIGURE 4. *Interlocality cluster analysis of kelp-bed fish assemblages sampled from 175 cinetransects filmed off Santa Barbara. Units are mainland (M) or Santa Cruz Island (I) canopy (C) or bottom (B) samples from the localities (right-hand letter pairs) in Figure 1 and Table 1. The dendrogram was derived from a similarity matrix based on relative species abundances (see text) by means of the unweighted pair-group clustering method using arithmetic averages (Sneath and Sokal 1973).*

bottom relief). Hence, island localities with lowest means (PE, SC) were about as abundant and diverse as mainland localities with highest means (NA, HE). A plot using mean score of depth and bottom relief (from Table 1) revealed the synergistic effect of these two abiotic variables on fish density and diversity, in that plotting either depth or relief separately showed less correlation (Fig. 3). Poorest island localities (PE, SC) were probably the most heavily used and disturbed anchorages. Also, locality SC, like mainland locality CO, had patches of relatively flat, barren rock where turf was sparse.

Species composition differed predictably among localities of different habitat type (Table 9 and Fig. 4). Along the mainland shore, localities HE, CO, and IV (Fig. 1) typically had pockets of sandy, flat bottom interspersed among high-relief reefs or flat pavement rock (Table 1). Many transects were taken near shore, where walleye surfperch schooled during the day. The canopy zone at these near-shore localities also harbored large numbers of such commuter species as kelp bass and pile and rubberlip surfperches. These habitat generalists, including more benthically-oriented, inner-marginal and commuter species (black, rainbow, white, and dwarf surfperches), also frequented sandy-marginal habitats (Table 9 and Fig. 4 [SM]). On the other hand, locality NA was a relatively well-developed reef located farther offshore in clearer water. Its canopy harbored large numbers of kelp-rock species (blacksmith and blue rockfish). Thus, the NA canopy sample clustered with the island samples. Differences between locality NA and the other mainland localities in relative numbers of habitat generalists *vs.* reef specialists were less clear for bottom samples. Only locality HE contained comparatively large numbers of inner-marginal and commuter species. All island localities were clear-water areas over continuous, high-relief rocky bottom. This was reflected in greater rank concordance in species arrays among island samples (Table 10). Island samples generally contained relatively more individuals of kelp-rock species, although the bottom sample from disturbed locality PE contained more commuter and inner-marginal individuals (kelp bass, pile perch, black surfperch).

The island assemblages differed from those of the mainland not so much in presence or absence of species as in the relative abundance or frequency of occurrence of species. Only two species (rock wrasse and endemic island surfperch) were recorded from Santa Cruz Island but not from mainland localities. Two others occasionally encountered along the mainland (black croaker and lingcod) were not recorded from island localities. Yet we have since seen lingcod during winter-spring, the period unrepresented in island transects.

In the canopy zone, the most obvious island-mainland differences were the absence of island surfperch from the mainland assemblage (Table 2), and the presence of higher densities of tropically-derived kelp-rock species, especially blacksmith, in the island assemblage (Table 9). Also, mainland locality NA had a relative dearth of kelp surfperch, but this dearth was a local phenomenon peculiar to such semi-isolated reefs. Kelp-surfperch populations may be decimated during sporadic decreases in kelp density on such reefs. Also, locality NA, in particular, was swept by relatively strong currents, which often pulled the kelp stipes beneath the surface and may have made it difficult for the small fish to maintain station. Elsewhere along the mainland, kelp surfperch were common in the thicker canopies of inshore kelp beds, where currents were weaker.

Likewise, the island-bottom assemblage had higher densities of tropical derivatives in the kelp-rock habitat group (Table 9). Besides having abundances of California sheephead, opaleye, halfmoon, and garibaldi, it contained rock wrasse (Table 2), which were not recorded from the Santa Barbara mainland. On the other hand, the mainland-bottom assemblage contained higher densities of commuter and inner-marginal species, especially black, pile, white, and rainbow surfperches. The sandy-marginal assemblages also reflected such island-mainland differences. At Santa Cruz Island, kelp-rock species were photographed together

TABLE 10. Among-locality concordance of rank-ordered abundances of 24 species in mainland and Santa Cruz Island samples of canopy and bottom assemblages of kelp-bed fishes, as represented in cinetransects filmed off Santa Barbara (Fig. 1 and Table 1). *n* represents number of localities; *N*, range in number of cinetransects at localities (Table 8); *W*, Kendall's coefficient of rank concordance (Tate and Clelland 1957).

	Island			Mainland		
Habitat	*n*	*N*	*W*	*n*	*N*	*W*
Canopy	5	4-7	0.60**	4	6-10	0.41*
Bottom	5	7-14	0.63**	4	11-16	0.49**

*Significantly different from zero at $0.025>P>0.01$.
**Significantly different at $P<0.005$.

with habitat generalists of the inner-marginal and commuter groups. Such intermingling of specialists and generalists accounted for higher diversity of the island assemblage (Table 9).

DISCUSSION

Southern California kelp beds harbor some 125 fish species, although no more than 20 to 30 are common enough to occur with a frequency of more than 5 to 10 per cent (*cf.* Quast 1968b, Feder *et al.* 1974). Hence, the number of species recorded by cinetransect and analyzed in the present study composes a representative array. In the following discussion, we first show how habitat groups merge to form the main fish assemblages of canopy and bottom zones in areas of reef and giant kelp. We suggest that a group composed mostly of reef specialists, many of which retain the more stereotyped behaviors of their close tropical relatives, will be more strongly or weakly represented in the assemblages, depending on habitat structure. We then discount seasonal effects to show that areal differences in assemblages, both among longshore localities and between mainland and island, reflect differences in structural habitat. Therefore, we argue that extensive areas of well-developed reef and clear water, which characterize the island habitats, have an "island effect" on assemblages favoring "tropical derivatives" contributing to higher fish density and diversity, and that this effect is manifest in such habitats whether of the island or mainland shores.

Habitat Groups

In some ways, our habitat groups resemble species associations differentiated subjectively by other authors (*cf.* Limbaugh 1955, Hobson 1965, Quast 1968b, Feder *et al.* 1974). Yet our habitat-group classification based strictly on correlations of species abundances does not always coincide with that of Quast (1968b) based on the fishes' behavior and use of different forms of substrate. He distinguished (1) bottom, (2) kelp-holdfast, (3) kelp-column, and (4) canopy habitats, and, within each habitat, species that (a) sit in interstices or on surfaces, (b) continuously roam about surfaces, or (c) use the open-water spaces. Fish behavior contributes indirectly to the formation of our habitat groups, but the prime requisite is that member species coincidentally occupy the same space or volume of water whether they act the same way or not. So, for example, our kelp-rock habitat group contains species of Quast's surface-roaming (b) and open-water (c) categories. However, our bottom habitat group resembles Quast's bottom-surface-sitting category (1, a) because all members are sedentary and limited to one surface in one space, *i.e.*, the reef bottom.

We emphasize that the habitat groups resolved by factor analysis are not the smallest that

may occur over the reef. Members of the same group may actually prefer different microhabitats. For example, gopher and black-and-yellow rockfishes of the bottom group tend to segregate by bottom depth along Santa Cruz Island (Larson 1977). Off Los Angeles, black and rainbow surfperches of the inner-marginal group select different temperature regimes (Terry and Stephens 1976). Whenever the two co-occur abundantly at Naples Reef, rainbow surfperch typically concentrate in depressions, while black surfperch prefer the reef flat (D. Laur, pers. comm.). As in tropical coral reefs, certain species may be mostly restricted to microhabitats distinguishable by their depth and position in the water column, overgrowth and cover structure, height on the reef, consolidation and texture of substrate, currents and surge, and exposure to the open sea (Hiatt and Strasburg 1960, Gosline 1965, Jones 1968, Sale 1968, Talbot and Goldman 1972, Smith *et al.* 1973, Goldman and Talbot 1976). Yet space may be occupied in ways apparently unrelated to observable microhabitat differences, perhaps by chance (Sale 1974, 1977, Sale and Dybdahl 1975, Bradbury and Goeden 1974).

Most fish bypass the mid-kelp region and occupy the bottom or canopy zones. The kelp canopy and its supports provide a vertical extension of the substrate, allowing fuller use of the entire water column (Quast 1968b, Feder *et al.* 1974). Many juveniles, like those of olive rockfish, concentrate in the canopy (Quast 1968c, Miller and Geibel 1973, Hobson and Chess 1976), although others, like small juvenile blacksmith, remain close to shelter near the bottom. Bottom and canopy assemblages merge wherever the two habitats meet along the steep, rocky, island shore, and whenever surface disturbance and poor visibility drive the canopy fishes bottomward (*cf.* Quast 1968a, 1968b, 1968c; pers. obs.). Many canopy and commuter species intermingle, especially over high, rocky areas where kelp bass, opaleye, various surfperches, and blacksmith swim through the water column and extend their zone of activity along the kelp stipes (Limbaugh 1955, Hobson 1965, Alevizon 1975a, 1975b, 1976). Nonetheless, some habitat group members must stay in particular zones; for example, demersal rockfish seldom leave the bottom, and kelp surfperch seldom leave the canopy. In general, therefore, the kelp-bed habitat has an added structural dimension over that of the tropical reef, which supports no canopy of giant algae. But Quast (1968b) observed that even though fish species diversity increases with bottom habitat diversity, it does not increase noticeably with foliage height diversity. He suggested that the kelp forest merely extends the bottom algal zone and does not really provide an entirely new habitat for species diversification. However, our results indicate that a few species, such as the kelp surfperch, occur only when a kelp canopy is present.

Species contributing to more than one factor may be either habitat generalists or species that for some reason congregate near the top and bottom of the water column. An inner-marginal species, the black surfperch, also contributed to the bottom group factor; in fact, it occurs almost everywhere inside and outside the reef. The contribution of blue rockfish to both kelp-rock and bottom group factors supports field observations that their behavior changes markedly with age. Juveniles and subadults usually pick plankton in midwater with aggregations of blacksmith (Love and Ebeling 1978), while larger individuals often approach or rest on the bottom like bottom group species. Yet large blue rockfish may also leave kelp beds to school in midwater over deep reefs (Miller and Geibel 1973). Kelp rockfish contributed almost equally to canopy and commuter group factors. Adults hang motionlessly on or among kelp blades in the canopy or midwater (Alevizon 1976) and occasionally rest on rocks on the bottom. Hobson and Chess (1976) observed that, at Santa Catalina Island, kelp rockfish usually rest on the bottom during the day and rise at night to eat plankton.

Correlations among the factors indicate interrelationships among the habitat groups. The intercorrelated kelp-rock, bottom, and commuter groups compose much of the fish fauna in rocky-bottom kelp beds. Members of kelp-rock and bottom groups differ in their vertical mobility, but are more or less restricted to rocky reefs. Like some kelp-rock species, members

of the commuter group occur throughout the water column, but unlike kelp-rock species, they do not depend on the rocky bottom for shelter. Among the commuter species, kelp bass occupy the whole kelp forest from bottom to canopy, where they eat a variety of prey from plankton and small epiphytic animals to small fish and other nekton (Quast 1968d, Love and Ebeling 1978). Pile and rubberlip surfperches, though often foraging over turf-covered bottom (Laur and Ebeling in prep.), also aggregate well up in the water column (Alevizon 1975a). On the other hand, bottom group members usually sit motionlessly, either in the open and camouflaged, ready to ambush relatively large benthic prey (Larson 1972), or hidden in shelters, often to escape heavy surge (Larson 1977). Though confined to rocky reefs, they are not necessarily limited to kelp beds and also occur in deeper water. Canopy group members complete the array of species more or less restricted to areas of reef and kelp. Unlike canopy-dwelling kelp-rock species (blacksmith, halfmoon, blue rockfish), however, canopy species may occupy the kelp-canopy zone whether near rocky reef or not. Kelp surfperch and giant kelpfish are well camouflaged and act to blend in with the moving kelp blades. Señoritas, which are strictly diurnal, actually bury themselves in areas of sand and gravel at night (Ebeling and Bray 1976). Negatively correlated with the other groups, the inner-marginal group contains species of dark or silvery surfperches that are equally at home on the reef, in areas of sand and cobble outside the reef, and in shallow beds of boa kelp and surfgrass farther inshore. These species frequent jetties and piers, where they are caught readily by hook and line (DeMartini 1969, Pinkas *et al.* 1967, Frey 1971).

Most kelp-rock species (Table 4) are members of, or closely allied with, the primarily tropical families of wrasses (Labridae), damselfishes (Pomacentridae), and rudderfishes (Kyphosidae). Like their counterparts on coral reefs, these tropical derivatives actively seek shelter at night, and some (California sheephead and garibaldi) are brightly colored. Their feeding habits also resemble those of their tropical relatives. For example, adult blacksmith congregate upcurrent to eat incoming plankton (Bray in prep.), just like individuals of a tropical congener (Russell 1971). Kyphosid-like opaleye and halfmoon ingest plants, as do tropical rudderfishes, although these temperate species are not strictly herbivorous (Quast 1968c), as are their tropical counterparts (Randall 1967). Tropical derivatives are reluctant to stray far from shelter. Fager (1971) observed that garibaldi and opaleye were among the few kelp-bed fishes that did not colonize experimental reefs made of simple 1-m cubes set out on a sandy bottom some distance from natural reefs off San Diego.

In contrast, the other habitat groups contain, for the most part, members of primarily temperate families or genera such as surfperches (Embiotocidae), rockfishes (*Sebastes*), and greenlings (Hexagrammidae). In general, these temperate derivatives do not actively seek shelter at night (Ebeling and Bray 1976). Most are generalized carnivores, broad-based microcarnivores, and/or facultative planktivores (Limbaugh 1955, Quast 1968d, 1968e, Bray and Ebeling 1975, Love and Ebeling 1978).

Interlocality Differences

In comparing fish assemblages among localities, we discounted seasonal variation because previous studies support our observations that such variation is relatively small. Miller and Geibel (1973) concluded that most species remain in kelp-bed habitats the year around off Monterey, central California. Fager (1971) observed "surprisingly little" seasonal change in fish abundance and diversity about small experimental reefs, although he noted some changes in species composition of the assemblages. Alevizon (1975a) concluded that four surfperch species (black, striped, pile, and rubberlip) showed no significant seasonal variation in habitat distribution off Santa Barbara. Ebeling and Bray (1976) observed very high seasonal concordance of rank-ordered species abundances in sight-transect samples at Naples Reef.

Kelp-bed fishes, in fact, show little seasonal movement as compared with, for example, bottom fishes in the temperate North Atlantic (*cf.* Tyler 1971, 1972). Adults of many kelp-bed species may spend most of their lives within an area of but a few hundred square meters (Limbaugh 1955, Clarke 1970, Frey 1971, Quast 1968c, Miller and Geibel 1973, Larson 1977, M. Hixon, pers. comm.). In this they resemble herbivores, omnivores, and smaller carnivores of tropical coral reefs (Talbot and Goldman 1972, Goldman and Talbot 1976, review by Ehrlich 1975) and other parochial fish populations (Gerking 1959).

Nonetheless, recent observations show that certain species occur seasonally at Naples Reef (Fig. 1), which is semi-isolated and located 1.6 km offshore (Ebeling and Bray in prep.). Rainbow surfperch and señoritas may disappear during the winter and reappear in the spring. Also, long-term temperature changes may alter the fish assemblages (Carlisle 1969, Mearns and Smith 1976), especially in a transitional zone like the Santa Barbara Channel (Hewatt 1946, Hubbs 1948, 1960, Radovich 1961, Neushul *et al.* 1967, Ebeling *et al.* 1971). Quast (1968d) noted that kelp bass fished out of a particular area of reef and kelp seem to be replaced quickly by immigrants. During our study, however, sportfishing was relatively light in most localities sampled (*cf.* Love and Ebeling 1978).

Interlocality differences in kelp-bed fish density, diversity, and composition reflect differences in habitat structure. Depth and bottom relief may have a synergistic effect on the fish assemblages in that higher densities of more species tend to inhabit deeper parts of rocky, high-relief reef, where water is often relatively clear and calm. More specifically, rocky reefs of greater bottom relief, kelp density, and water clarity harbor habitat specialists in the kelp-rock group, as well as habitat generalists and canopy species in other habitat groups, and the whole heterogeneous assemblage is best represented over deeper, less turbulent areas. Shallow waters show considerable wave action, surge, and increasing turbidity. Thus, especially when surge is strong, fish remaining in water shallower than about 5 m depth may have trouble maintaining station and viewing their immediate environment. Larson (1977) showed that two bottom species, the gopher and black-and-yellow rockfishes, hide in holes and are inactive during periods of heavy surge. Other investigators also observed increases in fish species diversity with greater bottom relief (Limbaugh 1955, Quast 1968a, 1968b, Feder *et al.* 1974). Quast (1968b) showed that diversity increased with depth only over bottoms of moderate to high relief. In a factor analysis of variables affecting the spatial distribution and density of Hawaiian reef organisms in Kaneohe Bay, Smith *et al.* (1973) concluded that the most important determinants of fish distribution are, first, bottom relief, and, second, water circulation and surge.

Island Effect

The island effect we observed is not primarily caused by the varied oceanographic regime of the Northern Channel Islands (*cf.* Hubbs 1967, 1974). Unlike San Miguel Island and the western half of Santa Rosa Island, the north side of Santa Cruz Island, where we did most of our sampling, is not strongly influenced by the cool California Current. Like the mainland, it receives warmer water from the southeast (Hubbs 1967, Neushul *et al.* 1967) and is influenced by local gyres characterizing the surface waters of the Santa Barbara Channel (Kolpack 1971). Therefore, the fish fauna on both sides of the Santa Barbara Channel is mostly southern Californian, with intrusions of central Californian species (Hubbs 1974, Ebeling *et al.* 1971). Tropical derivatives are typical southern, not central, Californian species.

Nor is the island effect primarily caused by isolation. Only one species, the island surfperch, is an island endemic. Furthermore, Ebeling (in prep.) showed that an array of Santa Cruz Island species more closely resembles an array of species from off San Diego, some 340 km to the southeast (*cf.* Quast 1968c), than an array of mainland species from Naples Reef directly across the channel.

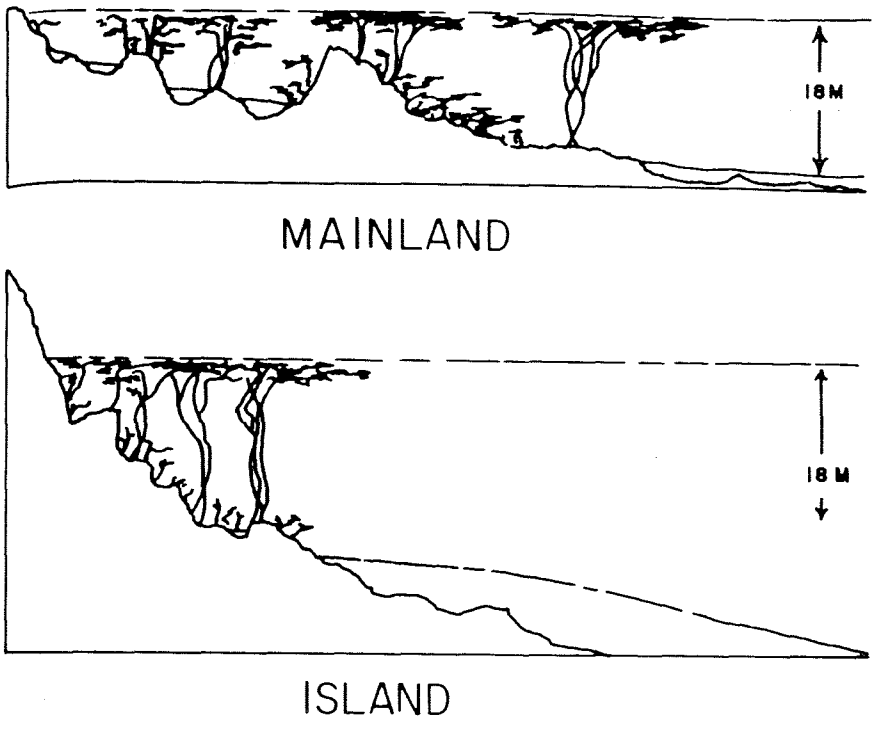

FIGURE 5. *Vertically exaggerated offshore profiles at the mainland and Santa Cruz Island near Santa Barbara. Off the mainland, broad sand flats (upper bottom lines) separate rocky outcrops (upward extensions of lower bottom lines) between the shore and Naples Reef (highest outcrop) 1.6 km offshore. Off the island, the relatively steep rocky bottom meets sand within only 50 m of shore.*

Hence, the differences in composition between island and mainland species assemblages seem to reflect structural-habitat differences rather than oceanographic or areal differences. The mainland bottom consists of broad sand and pebbly flats between scattered reefs (Fig. 5). Even Naples Reef, the best-developed reef system among the mainland localities, is structurally less complex than the steep, rocky, island bottom, which is strewn with boulders and deeply sculptured with holes and caves. The greater continuity of well-developed reef along the island shore probably accounts for the greater concordance of species abundance among island localities. Underwater visibility averages 1 to 2 m more at Santa Cruz Island than at Naples Reef (Ebeling *et al.* in press). Density of turf, an important source of fish food, is significantly greater at Santa Cruz Island than at Naples Reef (D. Laur, pers. comm.), which may account for island-mainland differences in foraging behavior of striped surfperch (Alevizon 1975b). Clarke and Neushul (1967) emphasized these environmental differences between Anacapa Island, which typifies such areas, and the adjacent mainland. Yet extensive, high-relief, rocky bottoms and clear water also characterize areas of reef and kelp at headlands off La Jolla near San Diego, and these areas also support an island-like biota (Limbaugh 1955, Clarke and Neushul 1967). It

seems, therefore, that off southern California it is the island-like habitats, rather than islands *per se*, that attract "island-like" fish assemblages.

The composition of sandy-marginal fish assemblages reflects the mainland-island difference in structural habitat. Typical kelp-rock species commonly venture over the relatively small sandy stretches between extensive rocky reefs. Thus, the precipitous island shore (Fig. 5) leaves little room for a typical shallow, sandy-bottom fauna, and many kelp-rock species were photographed in the sandy-marginal habitat while skirting their favored reefs. Also, we observed some kelp-rock species (*e.g.*, California sheephead) foraging over sandy areas at the bases of reefs.

Perhaps the complex substrate, clear water, and greater food supply of "island-like" environments offer more opportunities for the tropical derivatives to find shelter at night and partition space and food during the day. Several authors have pointed out that the coexistence of tropical-reef fishes depends on the availability of defensible holes and other shelter sites (Randall 1963, Collette and Talbot 1972, Smith and Tyler 1973, 1975, Sale 1974, 1975). Russell *et al.* (1974) showed that experimental reefs made of concrete blocks with holes are more heavily colonized by coral-reef fishes than are reefs made of plain blocks. Smith and Tyler (1975) concluded that a greater variety of hole sizes should provide shelter for a greater variety of sizes of fish. On the other hand, primarily temperate species like surfperches remain mostly exposed at night (Ebeling and Bray 1976). Miller and Geibel (1973) noted that surfperches are usually among the most abundant species on reefs where water is turbid.

In summary, the composition of kelp-bed fish assemblages along Santa Cruz Island reflects the high bottom-relief and clear-water character of island-like habitats. Such habitats support higher densities of kelp-rock species than do simpler and more turbid mainland habitats, and "superimposing" the extra numbers of tropically-derived reef specialists on the usual reef contingent also increases total fish diversity per unit area. This island effect was so profound that fish species sampled from various localities tended to group by area (mainland *vs.* island) rather than by habitat (canopy *vs.* bottom), as they did when sampled only from deeper, well-developed mainland (Naples Reef) and island reefs (Ebeling *et al.* in press).

SUMMARY

The kelp-bed fish fauna off Santa Barbara is mainly warm-temperate, but includes abundances of some primarily cool-temperate species from the north. Using underwater movie strips (cinetransects), we sampled assemblages of this fauna, near the kelp canopy and just over the reef bottom, in nine localities along Santa Cruz Island and the adjacent mainland coast. Factor analysis of these samples indicated that the species are loosely organized into five "habitat groups," which are characteristic of (1) areas of high-relief rock and dense kelp, (2) the kelp canopy, (3) shallow areas at or beyond the margins of reefs and kelp beds, (4) the midwaters, from kelp canopy to bottom, and (5) areas of reef bottom and sparse kelp. Mean fish density, biomass, and diversity varied significantly among localities and between mainland and island, but not between winter-spring and summer-fall. Means increased with rocky relief and bottom depth, and were generally greatest for island localities. Relatively more habitat generalists from the marginal and midwater groups (*e.g.*, surfperches) occurred in areas of mixed bottom types and turbid water. More reef specialists from the kelp-rock group, many of which require shelter holes at night, occurred in areas of extensive rocky bottom and clear water. Phylogenetically, these sheltering species have comparatively close tropical relatives (*i.e.*, are "tropical derivatives"). The island assemblages contained greater abundances of tropical derivatives, which contributed to the higher fish density and diversity. This "island effect" on species composition is probably caused by habitat differences rather than oceanographic differences or isolation between mainland and island. Island habitats, as well as island-like habitats along the mainland, have clearer water, more continuous high-relief rocky bottom, and perhaps more fish food. Thus, they may offer more opportunities for tropical derivatives to shelter at night and to partition the available space and food during the day.

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