FISH ASSEMBLAGES IN *MACROCYSTIS* AND *NEREOCYSTIS* KELP FORESTS OFF CENTRAL CALIFORNIA

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ABSTRACT

The abundance and species composition of conspicuous fishes were compared within two canopy forming kelp forests (giant kelp, *Macrocystis pyrifera*, and bull kelp, *Nereocystis luetkeana*) in Central California. The primary investigative method was a subtidal belt transect, in which visual observation was used. The species composition of fish assemblages in the two canopy types was similar. Densities of fish were generally greater in *Macrocystis* than in *Nereocystis* forests. The major difference was the density of midwater species of the genus *Sebastes*. The blue rockfish, *Sebastes mystinus*, was the numerically dominant species in both canopy types. Estimates of the biomass of fish were about 2.4 times greater in *Macrocystis* beds than in *Nereocystis* beds.

Many species of fish exhibit an affinity for substrate and cover within their habitat, such as rock or coral reefs or kelp beds, as well as man-made objects such as piers, jetties, and offshore oil platforms. This structure may provide shelter, a base for foraging activity, or nursery habitat for young fish. Within the temperate nearshore marine environment, macroalgae may provide a large portion of this substrate and cover. Kelp forests are one of the major features of the nearshore environment along the west coast of North America. The two most conspicuous canopy-forming kelps are the giant kelp, *Macrocystis pyrifera*, a perennial, and the bull kelp, *Nereocystis luetkeana*, an annual (Abbott and Hollenberg 1976). Besides the difference in perennial versus annual growth pattern, *Macrocystis* and *Nereocystis* differ markedly in physical structure (Fig. 1) and seasonal patterns of abundance. *Macrocystis* plants typically have many stipes originating from a single large holdfast, and large fronds attached to each stipe throughout its length. *Nereocystis* plants consist of a single stipe, with large fronds only at the distal end. During periods of full development (typically late summer), *Macrocystis* can develop a completely closed canopy, whereas *Nereocystis* typically has a broken canopy. Winter storms usually remove large portions of the *Macrocystis* canopy, but many plants remain secured to the substrate and provide structure within the water column to varying depths throughout the year. *Nereocystis* canopies are also typically removed during these storms, and, because *Nereocystis* is an annual, it provides little or no structure from midwinter through late spring.

Nereocystis may be more abundant than *Macrocystis* in the presence of severe and persistent disturbances such as continued exposure to large swells or heavy grazing pressure (Dayton et al. 1980). In the absence of this pressure, *Macrocystis* may be competitively dominant, in that it forms a dense and often complete surface canopy earlier in the year, and thus may exclude or limit *Nereocystis* which has light-sensitive germination requirements (Dayton et al. 1980, 1984).

This study was designed to test the hypothesis that the fish component of the *Macrocystis pyrifera* community differs from that of the *Nereocystis luetkeana* community in Central California.

METHODS

Studies were conducted from 6 km south to 15 km north of Point Piedras Blancas, San Luis Obispo County, CA (lat. 35°40′N, long. 121°17′W) (Fig. 2). Additional studies were also done near Big Creek, Monterey County, CA (lat. 36°04′N, long. 121°36′W). The surface canopies of kelp beds consist almost exclusively of *Nereocystis* from Point Piedras Blancas north to Ragged Point, an area about 13 km long, but are dominated by *Macrocystis* south of Piedras Blancas. I searched 74 transects in the Piedras Blancas study area and 4 in the Big Creek area: 26 transects in *Macrocystis* forests and 14 in *Nereocystis* in 1982 and 17 in *Macrocystis* and 21 in *Nereocystis* in 1983. Field studies extended from June

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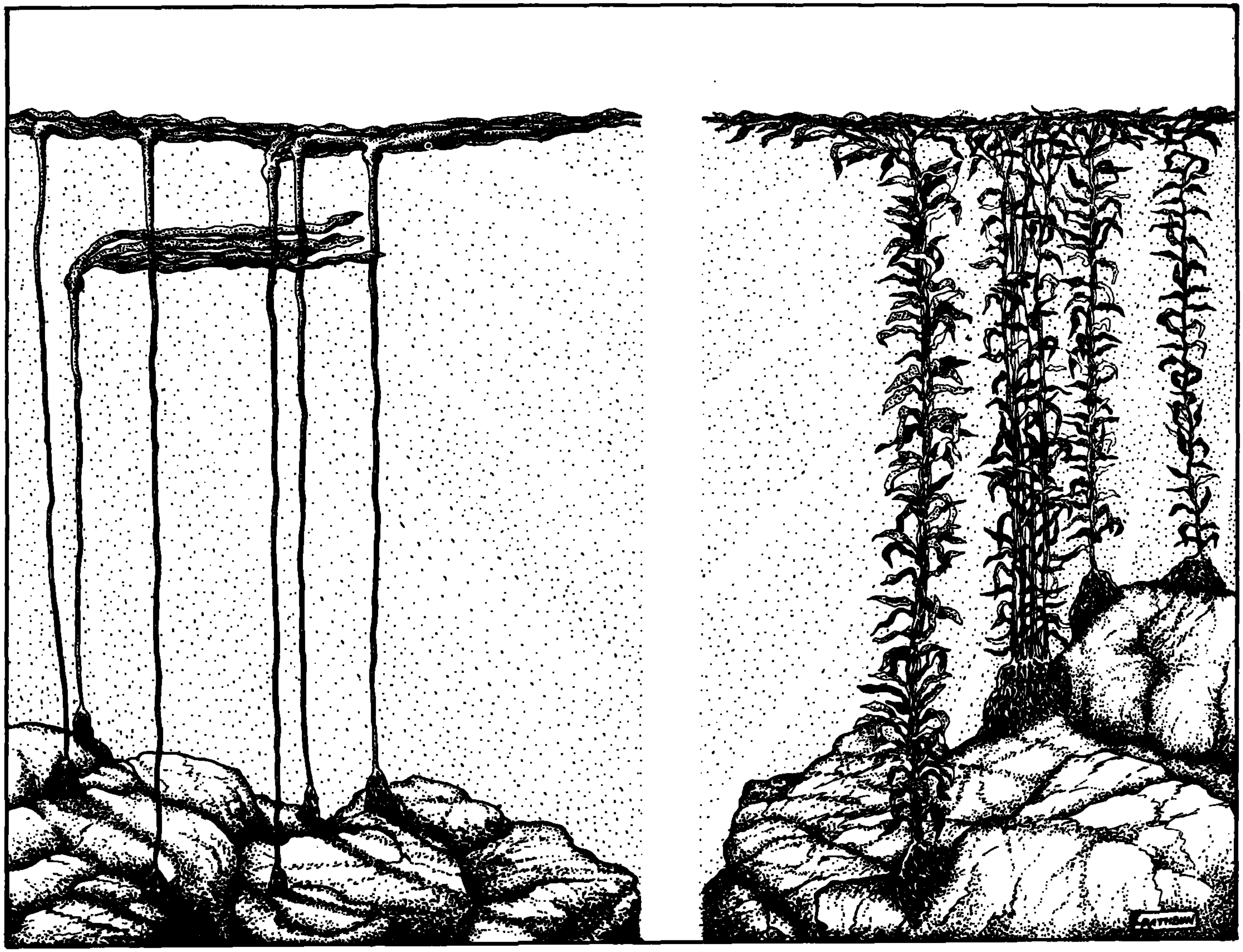

FIGURE 1.—A comparison of the physical structure of *Nereocystis luetkeana* (left) and *Macrocystis pyrifera* (right) kelp forests.

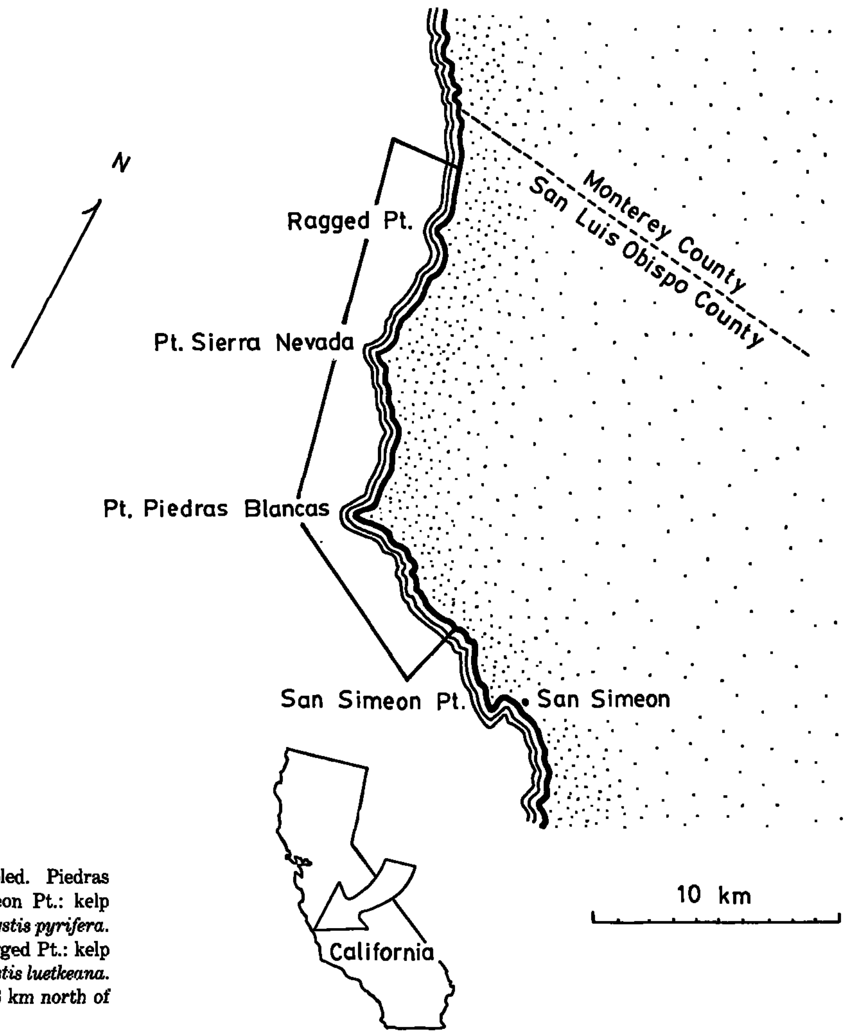

FIGURE 2.—Location of areas sampled. Piedras Blancas Pt., south, to San Simeon Pt.: kelp canopies are dominated by *Macrocystis pyrifera*. Piedras Blancas Pt. north, to Ragged Pt.: kelp canopies are dominated by *Nereocystis luetkeana*. Big Creek (not shown) is about 38 km north of Ragged Pt.

1982 to October 1983. Transects were apportioned evenly throughout early summer to late fall in each of the forest types.

A belt transect, as described by Brock (1954) and modified by Quast (1968), was used with the aid of scuba to conduct subtidal fish surveys. Each survey consisted of two components, benthic and midwater. A 50 m fiberglass tape was extended across the ocean floor in differing compass courses, extending from eye bolts permanently embedded in the substrate, or from the anchor of a dive boat on haphazardly located transect sites. The width of the midwater transect was determined by measuring the horizontal water visibility 2 m above the substrate. This was done by sighting down the transect line (fiberglass tape) toward the zero end, where a small bicolored float (13.5 × 5.5 cm) was suspended 2 m off the bottom. The observer moved away from the float along the line. When the float could not be readily discerned, the position on the tape was recorded. This value was doubled (to include observations on either side of the transect line) to obtain the width of the midwater transect. This survey technique may lead to a slight underestimation of fish densities due to decreasing searching efficiency with increasing distances from observer to observed (Caughley 1977). Surveys were conducted only when visibility exceeded 4.4 m. Horizontal water visibility ranged from 4.4 to 12.1 m (*Macrocystis* $\bar{x}$ = 6.6 m, SE = 2.6; *Nereocystis* $\bar{x}$ = 7.4 m, SE = 0.49). The width of the benthic survey was 4 m (2 m on each side of the transect tape). All sampling was conducted beneath and within either of the two forest types, in water 6 to 22 m deep. Underwater observations were recorded on formated data sheets using plastic paper.

In conducting the benthic survey, I slowly swam from one end of the transect to the other and identified and enumerated the fish that were observed. A fish was included in the benthic survey if it was observed within 0.5 m of the bottom and was not a member of a school of typically midwater fish located momentarily near the bottom. A fish observed swimming through the transect in front of the diver was included. An effort was made to inspect all crevices, caves, and ledges, and to move aside algae to locate fish. A description of unfamiliar fish was made in the field and its identity later determined in field guides if possible. Small, relatively cryptic species were probably underestimated in the process of these visual surveys (Brock 1982).

The midwater transect was searched about 3 m above the tape. Repetitive ascents and descents were made at 5 m intervals to detect fish occurring throughout the water column. The sizes of very large schools were estimated. All fish observed within the length of the 50 m tape were recorded. Unidentified species were treated as they were during the benthic survey.

After the survey was completed, an index of the bottom profile was recorded by measuring the water depth at each meter mark along the tape. Two methods of determining bottom profile were used: first, an objective, and later, a subjective measure. The objective relief index was the sum of the differences between each of the 50 consecutive depth measurements along the 50 m transect. During the second half of this study (1983) a subjective relief index was assigned to the general vicinity of each transect; this was determined by the greatest vertical relief observed along the transect line: 0 = flat, no relief; 1 = low relief <1 m); 2 = moderate relief (1 to 2 m); 3 = high relief (2 to 4 m); and 4 = extreme relief (more than 4 m).

Two measures of species diversity were used to compare the fish assemblages in *Macrocystis* and *Nereocystis* forests: 1) total number of species found on all transects within one canopy type and 2) the Shannon-Weaver index of diversity, H′ (Pielou 1966).

Because of heterogeneity between sample variances, fish density distributions were compared with the nonparametric Mann-Whitney test. A minimum acceptable level of significance of 0.05 was assigned.

RESULTS

Twenty-seven species of fish were identified within the spatial limits of the transects (Tables 1, 2, 3). An additional 8 species were identified within the kelp forest, but outside the transect limits. Juvenile rockfish were considered a single group, and occasionally an unidentified fish was observed.

In *Macrocystis* forests, 26 species were identified within the transects and 10 species outside the transects; in *Nereocystis* forests, the respective totals were 23 and 4 species. Three additional types of fish were observed that could be identified only to the family level (Table 3). Four species observed only in *Macrocystis* forests were white seaperch, *Phanerodon furcatus*; rainbow seaperch, *Hypsurus caryi*; China rockfish, *Sebastes nebulosus*; and black-eye goby, *Coryphopterus nicholsi*. One species was observed only in *Nereocystis* beds, the jacksmelt, *Atherinopsis californiensis*. Species not observed within both transect types were relatively uncommon, but were observed in and around both forest types during this study.

Fishes that could not be identified to species or family level were rare, occurring on only 6 (8%) of the transects (Table 3).

TABLE 1.—Summary of presence/absence of fish species encountered [midwater (M) and benthic (B), years pooled] throughout study.

Species	*Macro-cystis*	*Nereo-cystis*	Principal habitat
Sebastes mystinus	X	X	M
Sebastes serranoides	X	X	M
Sebastes atrovirens	X	X	M
Sebastes melanops	X	X	M
Sebastes chrysomelas	X	X	B
Sebastes carnatus	X	X	B
Sebastes miniatus	X	X	B
Sebastes rastrelliger	X	X	B
Sebastes caurinus	X	X	B
Sebastes nebulosus	X		B
Sebastes sp. (juveniles)	X	X	M/B
Oxyjulis californica	X	X	M
Aulorhynchus flavidus	X	X	M
Atherinopsis californiensis		X	M
Phanerodon furcatus	X		M
Oxylebius pictus	X	X	B
Hexagrammos decagrammus	X	X	B
Embiotoca lateralis	X	X	B
Embiotoca jacksoni	X	X	B
Orthonopias triacis	X	X	B
Scorpaenichthys marmoratus	X	X	B
Ophiodon elongatus	X	X	B
Rhachochilus vacca	X	X	B
Coryphopterus nicholsi	X		B
Anarrhichthys ocellatus	X	X	B
Jordania zonope	X	X	B
Hypsurus caryi	X		B

Midwater Transects

Differences in abundance of fish in the *Macrocystis* and *Nereocystis* forests were most apparent among the midwater species, primarily within the genus *Sebastes*. Of the nine species of midwater fish (juvenile *Sebastes* treated as a single "species"), three were significantly more abundant in *Macrocystis* than in *Nereocystis* forests: blue rockfish, *S. mystinus*; kelp rockfish, *S. atrovirens*; and olive rockfish, *S. serranoides* (Tables 1, 2). A fourth species, the black rockfish, *S. melanops*, was not observed on *Nereocystis* transects, though it was only occasionally seen in *Macrocystis*.

Although there were no general changes in fish abundance between 1982 and 1983 among the midwater species, some individual species differences were noted. Densities of blue rockfish were significantly lower in 1983 than in 1982 (Table 2). During this same period there was an insignificant increase in the density of juvenile rockfish. Densities of the señorita, *Oxyjulis californica*, appeared to increase within both forest types in 1983, but the increase was significant only when canopy types were combined for each year. This annual variation should be considered in light of the extremely anomolous El Niño event which occurred during this period (Cane 1983), and may be atypical.

Benthic Transects

Among the 19 principally benthic species found in both the *Macrocystis* and *Nereocystis* benthic transects, three (16%) were significantly more abundant in *Macrocystis* forests: Striped seaperch, *Embiotoca lateralis*, painted greenling, *Oxylebius pictus*, and the gopher rockfish, *Sebastes carnatus* (Tables 1, 3). One other species, the kelp rockfish, which occurred on benthic transects, was considered as primarily a midwater species. Gopher rockfish are bathymetrically segregated from the sibling species, *S. chrysomelas* (black-and-yellow rockfish). Gopher rockfish are relatively more abundant at depths >12 to 14 m (Larson 1980). In my study, the densities of black-and-yellow rockfish increased significantly in the second year while during the same period, densities of gopher rockfish decreased.

Due to sampling methodology and the occurrence

TABLE 2.—Mean densities (no. fish/100 m^2) and frequency of occurrence of fishes on midwater transects through kelp (standard error of mean in parenthesis).

	Mean densities (fish/100 m^2)						Frequency of occurrence	
	Macrocystis			*Nereocystis*				
Species	1982	1983	1982-83	1982	1983	1982-83	*Macrocystis*	*Nereocystis*
Sebastes mystinus[1,2] Blue rockfish	19.4	8.25	15.0 (1.8)	6.68	2.09	3.9 (1.0)	1.00	0.82
Sebastes serranoides[1] Olive rockfish	0.51	0.36	0.45 (0.09)	0.17	0.07	0.11 (0.03)	0.74	0.34
Sebastes atrovirens[1] Kelp rockfish	0.19	0.16	0.18 (0.05)	0.007	0.005	0.006 (0.004)	0.44	0.06
Sebastes melanops[1] Black rockfish	0.03	0.01	0.02 (0.009)	0	0	0	0.16	0
Sebastes sp. Juvenile rockfish	3.4	7.7	5.1 (3.1)	0.06	0.95	0.59 (0.5)	0.19	0.11
Oxyjulis californica[2] Señorita	3.1	26.6	12.4 (6.6)	1.6	18.7	11.9 (6.2)	0.40	0.40
Aulorhynchus flavidus Tube-snout			0.43 (0.4)			0.014 (0.01)	0.07	0.06
Atherinopsis californiensis Jacksmelt			0			6.0 (6.5)	0	0.20
Phanerodon furcatus White seaperch			1.37 (1.4)			0	0.05	0
Species observed incidental to transects								
Scomber japonicus Chub mackerel							0	0.09
Myliobatis californica Bat ray							0	0.03
Sphyraena argentea Pacific barracuda							0.02	0
Torpedo californica Pacific electric ray							0.02	0

[1] Difference significant between *Macrocystis* and *Nereocystis*, years combined.
[2] Difference significant between years, kelp canopies combined.

TABLE 3.—Mean densities (no. fish/100 m²) and frequency of occurrence of fishes on benthic transects through kelp forests (standard error of mean in parenthesis).

Species	Mean densities (fish/100 m²)						Frequency of occurrence	
	Macrocystis			*Nereocystis*				
	1982	1983	1982-83	1982	1983	1982-83	*Macrocystis*	*Nereocystis*
Sebastes chrysomelas[1] Black-and-yellow rockfish	1.52	1.91	1.67 (0.25)	1.11	2.21	1.77 (0.26)	0.74	0.91
Oxylebius pictus[2,3] Painted greenling	1.13	1.35	1.2 (0.1)	0.21	0.79	0.56 (0.1)	0.86	0.51
Hexagrammos decagrammus Kelp greenling	0.33	0.35	0.34 (0.07)	0.36	0.43	0.40 (0.07)	0.44	0.57
Sebastes carnatus[1,2] Gopher rockfish	1.29	0.76	1.04 (0.2)	0.75	0.22	0.43 (0.15)	0.61	0.31
Embiotoca lateralis[2] Striped seaperch	0.63	1.1	0.84 (0.2)	0.25	0.12	0.17 (0.08)	0.58	0.20
Sebastes atrovirens[2] Kelp rockfish	0.52	0.97	0.70 (0.1)	0.04	0.15	0.11 (0.05)	0.58	0.14
Sebastes sp. Juvenile rockfish	0.87	0.21	0.62 (0.2)	0.23	0.14	0.17 (0.07)	0.42	0.26
Embiotoca jacksoni Black perch	0.39	0.44	0.41 (0.1)	0	0.27	0.16 (0.06)	0.42	0.17
Orthonoplas triacis Snubnose sculpin	0.20	0.23	0.21 (0.06)	0.04	0.13	0.09 (0.04)	0.33	0.14
Sebastes mystinus Blue rockfish	0.08	0.26	0.15 (0.05)	0.04	0.17	0.15 (0.05)	0.23	0.17
Scorpaenichthys marmoratus Cabezon			0.107 (0.04)			0.11 (0.04)	0.16	0.20
Ophiodon elongatus Ling cod			0.13 (0.04)			0.09 (0.04)	0.21	0.09
Sebastes melanops[2] Black rockfish			0.209 (0.06)			0.029 (0.02)	0.23	0.06
Rhachochilus vacca Pile perch			0.135 (0.04)			0.0149 (0.01)	0.21	0.06
Sebastes miniatus Vermilion rockfish			0.042 (0.03)			0.094 (0.04)	0.07	0.14
Coryphopterus nicholsi Blackeye goby			0.198 (0.09)			0	0.21	0
Sebastes rastrelliger Grass rockfish			0.0116 (0.01)			0.0143 (0.01)	0.05	0.11
Sebastes caurinus Copper rockfish			0.035 (0.02)			0.0143 (0.01)	0.07	0.03
Anarrhichthys ocellatus Wolf-eel			0.023 (0.02)			0.0143 (0.01)	0.05	0.03
Jordania zonope Longfin sculpin			0.014 (0.01)			0.0143 (0.01)	0.02	0.03
Hypsurus caryi Rainbow seaperch			0.034 (0.01)			0	0.05	0
Sebastes nebulosus China rockfish			0.019 (0.02)			0	0.02	0
Unidentified fish			0.128 (0.09)			0.29 (0.3)	0.05	0.11
Species observed incidental to transects								
Sebastes serriceps Treefish							0.02	0.03
Cephaloscyllium ventriosum Swellshark							0.05	0
Sebastes auriculatus Brown rockfish							0.02	0
Sebastes pinniger Canary rockfish							0.02	0
Clinidae Clinids							0.12	0
Cottidae Sculpins							0.07	0
Gobiesocidae Cling fishes							0.02	0
Unidentified fish							0.12	0.06

[1]Difference significant between years, kelp canopies combined.
[2]Difference significant between *Macrocystis* and *Nereocystis* years combined.
[3]Difference significant between years, *Nereocystis*.

of *Macrocystis* in water up to 4 m deeper than that occupied by *Nereocystis* within the study area, the mean water depth at which surveys were made differed between sites (*Macrocystis* mean depth = 12.2 m; *Nereocystis* mean depth = 10.5 m, t = 2.73, P = 0.008 (two sample t-test)). When the five transects in *Macrocystis* which occurred at depths beyond the maximum depth of *Nereocystis* transects (16 m) were excluded from analysis, the difference in water depths between sites became insignificant. Following the removal of these deep transects, all species of fish, both midwater and benthic, were reevaluated. There were no changes in the results presented above following this treatment.

There was little correlation between densities of fish and either of the bottom relief indices (r values, 0.025 to 0.482). Throughout the study, bottom relief typically ranged from 1 to 4 m and relief <1 m was not encountered. Mean values of the objective relief index were 44.1 (SE = 2.8) for *Macrocystis* transects and 37.2 (SE = 2.2) for *Nereocystis* transects. This difference resulted in a P value of 0.061 (two sample t-test), which I considered significant. However, when all species of fish which demonstrated significantly different densities between canopy types were reevaluated, after excluding the six *Macrocystis* transects with relief values more than one standard deviation above the mean, no change in results was observed for any species tested.

The total number of species encountered on the transects was 26 in *Macrocystis* and 23 in *Nereocystis*. The two kelp forests had 22 species in common. Five species were found in only one of the two canopy types, although none of these were present in more than 21% of the transects within the canopy in which it was found. The H′ values calculated were 1.76 for *Macrocystis* transects and 1.58 for the *Nereocystis* transects. Although the value of diversity indices has been questioned (Goodman 1975), such indices are widely used in ecological literature. Neither measure of diversity used in the present study indicated differences in the diversity of fish assemblages between the two kelp forest types investigated.

DISCUSSION

Several measures of comparison were considered in the analysis of these two kelp communities: species composition, species diversity, and abundance of fishes. The data presented here demonstrate very little difference in either composition or diversity of fish assemblages (Table 1), while estimates of biomass were markedly higher in giant kelp compared with bull kelp (Table 4).

The single most obvious difference between the two kelp communities was in the abundance of the blue rockfish: mean density of fish (no./100 m^2) was

TABLE 4.—Estimates of biomass of fish of *Macrocystis* and *Nereocystis* kelp forests. Species that were uncommon, (<20% of transects), or small are not included.

	Macrocystis			*Nereocystis*		
Species	Density (#/100 m^2)	Mean weight[1] (kg)	Biomass (kg/100 m^2)	Density (#/100 m^2)	Mean weight[1] (kg)	Biomass (kg/100 m^2)
Midwater transects						
Sebastes mystinus	15.0	0.44	6.6	3.92	0.50	1.96
Sebastes serranoides	0.45	0.63	0.28	0.11	0.72	0.08
Sebastes atrovirens	0.18	0.54	0.09	0.006	0.57	0.003
Sebastes melanops	0.02	0.44	0.009	0	0	0
Oxyjulis californica	12.4	0.024	0.30	11.9	0.024	0.29
Benthic transects						
Sebastes chrysomelas	1.7	0.36	0.61	1.8	0.36	0.65
Sebastes carnatus	1.0	0.36	0.36	0.43	0.36	0.15
Sebastes atrovirens	0.70	0.38	0.27	0.11	0.38	0.04
Sebastes mystinus	0.15	0.44	0.07	0.15	0.50	0.07
Sebastes melanops	0.21	0.44	0.09	0.03	0.44	0.01
Sebastes miniatus	0.04	2.0	0.08	0.09	2.0	0.18
Hexagrammos decagrammus	0.34	0.5	0.17	0.40	0.5	0.2
Embiotoca lateralis	0.84	0.47	0.39	0.17	0.47	0.08
Embiotoca jacksoni	0.41	0.47	0.19	0.16	0.47	0.08
Scorpaenichthys marmoratus	0.11	0.7	0.08	0.11	0.7	0.08
Ophiodon elongatus	0.13	2.6	0.34	0.09	2.6	0.23
Rhachochilus vacca	0.13	0.47	0.06	0.01	0.47	0.005
Total			9.99 kg/100 m^2 = 0.0999 kg/m^2			4.11 kg/100 m^2 = 0.0411 kg/m^2

[1]Mean weights from collections at Piedras Blancas Field Station, U.S. Fish and Wildlife Service, or estimated from mean total lengths.

15.0 in *Macrocystis* and 3.9 in *Nereocystis*. Blue rockfish probably are the largest contributor to the total biomass of kelp forest fish communities in Central California. Miller and Geibel (1973) estimated blue rockfish densities at 6.66 fish/100 m^2 in 1969 and 8.35 in 1970 in *Macrocystis* beds at Hopkins Marine Life Refuge, Monterey County, CA. They suggested that this represents about 50% of the actual biomass because their survey method underrepresented midwater species. Considering this adjustment, my data for blue rockfish in *Macrocystis* forests agree well with theirs. Near Pt. Piedras Blancas, blue rockfish made up 33% and 18% of the mean number of fish within the *Macrocystis* and *Nereocystis* forests, respectively. Assuming an average weight of 440 g (Table 4), blue rockfish contributed about 70% of the total biomass of the *Macrocystis* fish assemblage and about 50% of *Nereocystis* (species weighing a few ounces or less were not included in this analysis). The importance of juvenile blue rockfish as forage for large carnivorous kelp forest fishes (primarily *Sebastes* sp.) has been well documented (Miller and Geibel 1973; Burge and Schultz 1973; Hallacher and Roberts 1985). Tagging studies have suggested that the home range of blue rockfish is relatively small (Miller and Geibel 1973). The evidence given here illustrates the important role that blue rockfish play in the kelp forest communities of central California.

My estimate of the biomass of fish within each of the two canopy types (Table 4) included only species that were relatively common and of sufficient size to contribute significantly to the total. For example, although the estimated mean weight of *Oxyjulis californica* was only 24 g, its abundance made its total contribution rather large.

My data showed that in this study area off Central California *Macrocystis* supported a larger standing crop of fish, primarily midwater species of the genus *Sebastes*, than did forests of *Nereocystis* (Table 4). The following explanations are offered for the observed differences. These explanations are not mutually exclusive; several or all of the proposed explanations may have contributed to the observed patterns.

1) The amount of algae consumed by blue rockfish fluctuates seasonally. Hallacher and Roberts (1985) showed that blue rockfish may use algae as a major source of energy during the non-upwelling period (September through March), which partly coincides with the period of minimum development in *Nereocystis* forests. During this period blue rockfish may rely on *Macrocystis* directly as a food source, or indirectly as a substrate from which invertebrates are taken. The resulting increased biomass of blue rockfish in *Macrocystis* may help support larger numbers of other carnivorous fish. Four of the seven species that were densest in *Macrocystis* (Table 5) forests are known to rely heavily on juvenile rockfish for food (Hallacher and Roberts 1985). Although juvenile rockfish densities were not statistically greater in the *Macrocystis* forest (Table 2) because of large variations in densities (occurring on transects in either very large or very small schools), they were generally more available in *Macrocystis* forests. Subsequent field observations of juvenile rockfish in central California kelp forests have indicated that kelp forest rockfish recruitment may have been poor during the course of this study.

TABLE 5.—Summary of species for which densities in the two kelp types differed significantly.

Species	Canopy type which presented significantly higher density
Midwater	
Sebastes mystinus Blue rockfish	*Macrocystis*
Sebastes serranoides Olive rockfish	*Macrocystis*
Sebastes atrovirens Kelp rockfish	*Macrocystis*
Sebastes melanops Black rockfish	Observed on *Macrocystis* midwater transects only
Benthic	
Sebastes carnatus Gopher rockfish	*Macrocystis*
Embiotoca lateralis Striped seaperch	*Macrocystis*
Oxylebius pictus Painted greenling	*Macrocystis*
Sebastes atrovirens Kelp rockfish	*Macrocystis* (considered primarily as a midwater species)

2) The perennial nature of *Macrocystis* forests compared with the annual nature of *Nereocystis* forests may contribute to increased fish densities in *Macrocystis* forests. *Macrocystis* forests provide some structure throughout the year with new growth providing both vertical and canopy structure 1 to 3 mo earlier than *Nereocystis*. This temporal stability may afford necessary habitat structure within the water column permiting relatively higher densities of fish.

3) Differences in abiotic factors such as the physical orientation of the reef systems to oceanic swells and the resultant surge and scour effects may play a role in determining habitat suitability for some species of fish. The effects of sediment transport and scouring, caused by water movement,

would be most evident at the sea floor and may in fact have contributed to the observed differences in densities in the bottom dwelling surf perch (Table 5). My data indicated that the major differences in densities of fish were in midwater species, suggesting that exposure to bottom disturbance per se was not a primary influence on observed patterns.

4) The differing physical characteristics of the *Macrocystis* and *Nereocystis* plants themselves may play a role in determining their suitability as habitat for kelp bed fishes. During periods of full development, within this study area, *Macrocystis* typically has widely spaced, thick bundles of stipes with large fronds throughout the water column, leading to a canopy that is frequently closed. *Nereocystis*, in contrast, has single, frondless stipes with large terminal fronds that generally form a broken surface canopy (Fig. 1). Due to the distinct physical structure of these two plants, both within the water column and at the canopy, the foliage biomass is usually considerably greater within the *Macrocystis* forest. This abundance of structure, combined with its persistance over time, may enhance the carrying capacity of giant kelp forests compared with those of bull kelp (Leaman 1980).

A comparison of the standing crop estimates presented in this study is made with those from other marine reef systems in Table 6. While values for both *Macrocystis* and *Nereocystis* forests are below those representing fringing coral reefs (Brock 1954; Randall 1963), my estimates for *Macrocystis* forests compare favorably with the upper values obtained in Monterey, CA (Miller and Geibel 1973) and northeast New Zealand (Russell 1977), while the *Nereocystis* estimate corresponds to the estimates from Southern California *Macrocystis* forests (Quast 1968; Larson and DeMartini 1984).

In conclusion, *Macrocystis* forests supported a biomass of fish about 2.4 times greater than that supported by *Nereocystis* forests (Table 4) where perennial, water column foliage provided a more persistant, structurally diverse habitat. Larger numbers of midwater fish, primarily *S. mystinus*, found in the *Macrocystis* forest can account for this difference.

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TABLE 6.—Comparison of biomass estimates of fish from marine communities (after Russell 1977).

Location and reference	Bottom type	Standing crop ($kg.m^2$)
Hawaii (Brock 1954)	Fringing coral reef: open sand, broken rock, coral reef, reef flat	0.001-0.0184
Virgin Islands (Randall 1963)	Fringing coral reef: boulders, coral	0.160
Southern California (Quast 1968)	Kelp bed: broken rocky bottom, dense algal cover	0.035[1]
Southern California (Larson and DeMartini 1984)	Cobble, low relief *Macrocystis* forest	0.039-0.065
	Cobble, low relief kelp-depauperate	0.024
Monterey Bay, CA (Miller and Geibel (1973)	Kelp bed: broken rocky bottom dense algal cover, rocky reef	0.001->0.112
N.E. New Zealand (Russell 1977)	Rocky reef: open low relief, sparse algal cover.	<0.001
	Rocky reef: high bottom relief, extensive algal cover	0.103
Central California (Present study)	Rocky reef: high bottom relief;	
	Macrocystis canopy	0.0999
	Nereocystis canopy	0.0411

[1]Average estimate.

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