ABUNDANCE AND VERTICAL DISTRIBUTION OF FISHES IN A COBBLE-BOTTOM KELP FOREST OFF SAN ONOFRE, CALIFORNIA

RALPH J. LARSON[1] AND EDWARD E. DEMARTINI[2]

ABSTRACT

Using visual belt transects on the bottom and vertically stratified belt transects taken with movie cameras in the water column, we assessed the species composition, vertical distribution, and standing stock of fishes in a forest of giant kelp and a nearby kelp-depauperate area off San Onofre, California. The volume of water-column "cinetransects" was calibrated for water clarity. Species such as garibaldi, blacksmith, and various rockfishes, which depend on high-relief rocky substrates, were rare or absent in these low-relief, cobble-bottom habitats. The species present in the kelp forest apparently did not depend on high-relief rock, at least in the presence of kelp. These species fell into three groups, based upon their vertical distributions: "canopy" species (kelp perch, giant kelpfish, and halfmoon), which occurred mainly in the upper water column; "cosmopolites" (kelp bass, white seaperch, and señorita), which occurred throughout the water column; and "bottom" species (California sheephead and various seaperches), which occurred mainly near the bottom. Despite the absence of reef-dependent species, estimated standing stocks of 388-653 kg/ha in the San Onofre kelp forest were as large or larger than estimates made by others in kelp forests located on higher relief bottoms. The kelp-forest areas at San Onofre also supported a larger standing stock of fishes (other than barred sand bass) than the adjacent area with little kelp. The relatively large standing stock of fishes in the kelp forest can be attributed to the presence of kelp and to the depth of the kelp forest. Located in relatively deep water (15 m), this kelp forest possessed an extensive midwater zone. The attraction of fish in moderate densities to the midwater zone of this kelp forest contributed substantially to overall biomass. We conclude that kelp per se can enhance the standing stock of fishes on a temperate reef, at least in areas of low bottom relief.

Rocky reef and giant kelp, *Macrocystis pyrifera*, habitats off the coast of southern California support a diverse and abundant assemblage of fishes (Limbaugh 1955; Quast 1968 a, b; Feder et al. 1974; Ebeling et al. 1980 a, b). Much of the richness of this ichthyofauna has been attributed to the rocky substrate; areas with a rugose, rocky bottom and little kelp seem to support more fish than areas with a flat bottom and dense kelp (Quast 1968 a, b; Ebeling et al. 1980a). However, kelp itself also provides a unique habitat for some fishes (Coyer 1979; Ebeling et al. 1980a) and a point of orientation in the water column for others (Quast 1968 a, b; Bray 1981). The kelp canopy may also serve as a nursery area for some species of fish (Miller and Geibel 1973; Feder et al. 1974; M. Carr[3] Unpubl. data).

Several approaches have been used to assess the influence of habitat on the abundance and composition of fish assemblages in nearshore kelp and rock habitats off California. Perhaps the best analytical approach is experimental, as employed by Miller and Geibel (1973), Bray (1981), and Carr (footnote 3) ; however, the comparative approach of Limbaugh (1955; also reported in Feder et al. 1974), Quast (1968 a, b), and Ebeling et al. (1980a) is also of value. Based on observations in a variety of areas, Limbaugh described the habits and habitats of many nearshore fishes. Quast and Ebeling et al. employed broad-scale quantitative sampling of fish assemblages in different areas. Quast's interpretation of data extended Limbaugh's natural history approach, and added to it the actual comparison of abundances in different habitats. Ebeling et al. (1980a) employed a multivariate analysis of habitat characteristics and relative abundances of species to define subassemblages of fishes, and also compared abundances in areas of different habitat characteristics.

In this paper we examine the abundance, vertical distribution, and species composition of noncryptic fishes in a forest of giant kelp near San Onofre, Calif. We also report the abundance and species composition of fishes in a nearby area with little kelp. This study, undertaken initially to predict the effects of a

[1]Marine Science Institute, University of California, Santa Barbara. Calif.; present address: Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132.
[2]Marine Science Institute, University of California, Santa Barbara, Calif.; present address: Marine Review Committee Research Center, 531 Encinitas Boulevard, Encinitas, CA 92024.
[3]M. Carr, Moss Landing Marine Laboratories, Moss Landing, CA 95039.

possible loss of kelp (Dean[4]) on the indigenous fish fauna, also allowed us to extend the comparative approach of Quast and Ebeling to assess two features of kelp-forest fish faunas and to further evaluate a sampling technique.

The portion of the kelp forest we examined was located in relatively deep water (15 m) and was anchored on a low-relief cobble bottom. Since it lacked a highly heterogeneous substrate, we were able, by comparison, to further evaluate the effects of kelp per se on nearshore fishes. Because the kelp forest was in deep water, we also had the opportunity to examine the vertical distribution of fishes in greater detail than other workers, by sampling four vertical strata, rather than the two strata (canopy and bottom) sampled by Quast (1968b) and Ebeling et al. (1980a, b).

Besides visual transects to sample fish on or near the bottom, we used underwater movies ("cinetransects") to estimate the abundance of fishes in the water column above the bottom. Alevizon and Brooks (1975) and Ebeling et al. (1980b) discussed the advantages and disadvantages of cinetransects, but provided only rough estimates of the area sampled in a cinetransect. In this paper we more carefully evaluate cinetransect volume, emphasizing the effect of underwater visibility on cinetransect width.

Our objectives in this paper are 1) to estimate cinetransect volume as a function of underwater visibility; 2) to examine the vertical distribution of fishes in a deep-water kelp forest; 3) to estimate the overall abundance and biomass of fishes, integrated over depth, in this kelp forest; and 4) to evaluate the importance of kelp to nearshore fishes, by comparing our data from the San Onofre kelp forest with that from an adjacent kelp-depauperate area and with other published data from kelp forests located on more rugose substrates.

MATERIALS AND METHODS

Study Areas

This study was conducted in and near the offshore portion of a giant kelp, *Macrocystis pyrifera*, forest near the San Onofre Nuclear Generating Station, between San Clemente and Oceanside, Calif. (Fig. 1).

San Onofre kelp (SOK) varied in areal extent from <5 to 95 ha during the mid- to late 1970's, and covered about 75 ha during the fall of 1979 (Dean footnote 4). SOK occupied a shallowly sloping, low-relief (<1 m) cobble and sand substrate between the depths of about 10 and 15 m. Two relatively permanent, offshore portions of SOK, and an area with little kelp located ≤100 m upcoast from SOK, served as our study areas. The upcoast (SOK-U) and downcoast (SOK-D) areas within SOK, and the kelp-depauperate area ("kelpless" cobble), were all about 15 m deep and 2-3 km from shore. Because of its depth, low relief, and periodic inundation by sand, the cobble substrate in all areas was relatively bare of understory algae and sessile invertebrates. However, some stands of the 1 m tall laminarian kelp *Pterygophora californica* were present, especially along the fringes of the *Macrocystis* forest and throughout the kelpless cobble area.

Sampling Methods

Our general sampling plan was to stratify fish censuses by depth and to replicate these samples over several dates. In the two kelp-forest areas, we censused each of three, equally spaced strata in the water column, plus a bottom stratum. Only the bottom stratum was censused at the kelp-depauperate area, since few kelp-associated fishes were observed above the bottom in this area. Sampling at each stratum was replicated hierarchically: A number of replicate transects were made within an area on a given sampling day, and counts from these transects were averaged. This was repeated on 4 or 5 d at each site. The daily averages at each stratum and area were themselves used as replicates that provided reasonably precise estimates of means per stratum and that allowed estimates of variability due to sampling error. Because of time and manpower constraints, the various study areas were usually sampled on different dates. All three water-column strata in a given area were sampled on the same day; the bottom stratum, however, was usually sampled on a different day.

All sampling took place from October through December 1979. This time of year offers the most consistently clear and calm water conditions. Since most migratory and transient species were excluded from analysis (see below), our fall study should reasonably characterize the general distribution and abundance of "resident", kelp-associated fishes at SOK. Within this period, sampling was generally limited to dates when horizontal visibility exceeded 3 m.
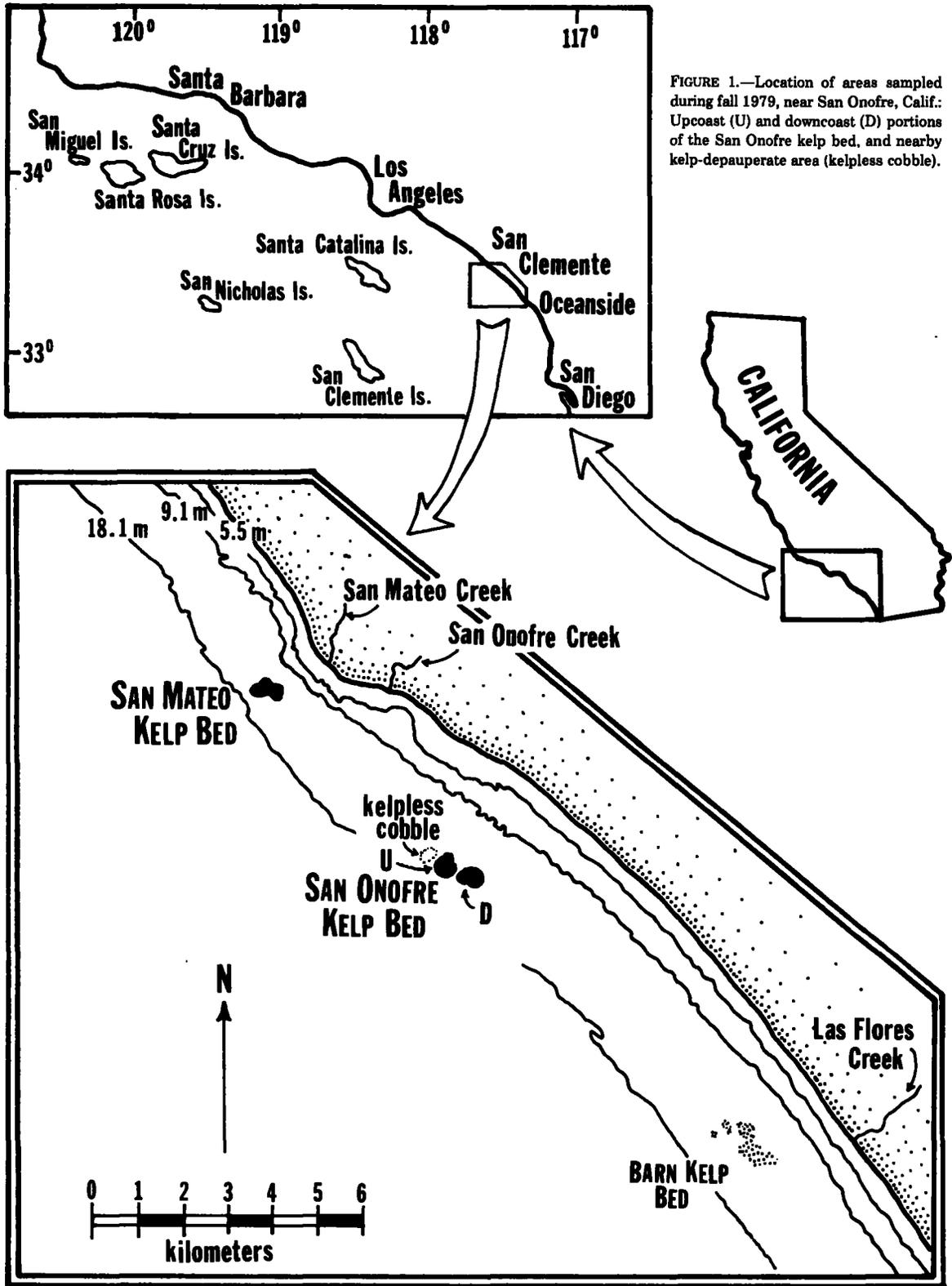
FIGURE 1.—Location of areas sampled during fall 1979, near San Onofre, Calif.: Upcoast (U) and downcoast (D) portions of the San Onofre kelp bed, and nearby kelp-depauperate area (kelpless cobble).

In each area, two permanently buoyed stations served as foci for sampling. At each station, we determined a range of suitable compass headings for transects. To assure complete coverage of the area, we divided each range of suitable headings into five equal subarcs and randomly chose transect headings from each subarc. Headings were selected separately for each sampling stratum. One transect per subarc was made on each sampling day for bottom sampling. In the water-column strata, where fish patchiness necessitated more samples, we made one transect in each subarc and added another transect from one of the subarcs (randomly chosen). Thus, five transects were usually made from each station per date on the bottom, and six at each station and depth stratum in the water column. Regardless of sampling method, transects began 7-10 m from the station hub. Transects were taken from both sampling stations on a sampling day. Data from the two stations at an area were pooled, since the abundances of major species were generally indistinguishable between stations in an area on a given date.

On the bottom, fish sampling was conducted visually in 75 m long strip transects. Divers (one per station) counted fish in bands estimated to be 3 m wide and 1.5 m high, while reeling out 75 m long lines along the predetermined compass headings. All non-

cryptic fishes within this band were identified and counted, with separate tallies kept for juvenile, subadult, and adult members of each species (Table 1). All subadult and adult *Macrocystis* plants >1 m tall (Dean footnote 4) were counted in the same 3 m wide band while reeling in the transect line on the return trip.

Transects in the water column at the two kelp-forest areas were made with underwater movie strips, using Elmo Super 311 Low Light[5] movie cameras (F/1.1), Giddings Cine-Mar housings, and Kodak Ektachrome 164 super-8 film cartridges. At 18 frames/s, the transects lasted about 3 min. Divers swam predetermined compass headings and photographed fish occurring in a 120° horizontal arc about the transect axis and 1.5 m above and below the diver's depth. The transect ended when the film cartridge was exhausted. Water-column transects were made in three depth strata: 3 m, 7.6 m, and 12 m (Table 2). Horizontal visibility was measured with each set of transects (at a depth on a sampling date), as the distance at which an olive-tan colored, 10 cm long float ("fish mimic") became indistinct. Films were later viewed in slow motion by at least two observers, at

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

TABLE 1.—Common and scientific names of fishes observed at the San Onofre kelp bed and adjacent kelpless cobble area during fall 1979 with the estimated weight of juveniles, subadults, and adults. Body weights for teleosts were estimated from average observed lengths, converted to weights using the length-weight regressions of Quast (1968a: Appendix B), after adjusting for the bias (underestimate) from the use of average body length to predict average body weight (see Pienaar and Ricker 1968). Weights of elasmobranchs were estimated from fishes trapped in the intakes of the San Onofre Nuclear Generating Station, Unit 1, during 1976-79.[1] Asterisks indicate species not included among kelp-bed "residents." Common names after Robins et al. (1980).

Family and species	Weight (g) Juvenile	Weight (g) Subadult	Weight (g) Adult	Family and Species	Weight (g) Juvenile	Weight (g) Subadult	Weight (g) Adult
Serranidae				Scorpaenidae			
Paralabrax clathratus, kelp bass	7	200	1,050	*Scorpaena guttata*, California scorpionfish	—	—	550
Paralabrax nebulifer, barred sand bass	20	300	1,500	*Sebastes rastrelliger*, grass rockfish[2]	—	—	400
Embiotocidae				*Sebastes serranoides*, olive rockfish[2]	4	175	—
Brachyistius frenatus, kelp perch	—	—	25	*Sebastes* spp., juvenile rockfish[2]	1	—	—
Embiotoca jacksoni, black perch	10	75	350	Sciaenidae			
Phanerodon furcatus, white seaperch	10	50	175	*Cheilotrema saturnum*, black croaker	—	—	225
Damalichthys vacca, pile perch	15	175	500	Pristopomatidae			
Rhacochilus toxotes, rubberlip seaperch	15	150	700	*Xenistius californiensis*, salema	—	—	75
Hypsurus caryi, rainbow seaperch	10	60	150	Atherinidae			
Labridae				*silversides spp.	—	—	20
Oxyjulis californica, señorita	0.5	5	55	Carangidae			
Semicossyphus pulcher, California sheephead	50	250	875	*Trachurus symmetricus*, jack mackerel	—	115	—
Halichoeres semicinctus, rock wrasse	25	100	250	Sphyraenidae			
Girellidae				*Sphyraena argentea*, Pacific barracuda	—	150	—
Girella nigricans, opaleye	—	—	950	Carcharhinidae			
Scorpididae				*Triakis semifasciata*, leopard shark	—	—	2,000
Medialuna californiensis, halfmoon	—	—	250	Rhinobatidae			
Pomacentridae				*Platyrhinoides triseriata*, thornback	—	—	240
Chromis punctipinnis, blacksmith	2	—	—	Myliobatidae			
Hypsypops rubicundus, garibaldi	25	120	500	*Myliobatis californica*, bat ray	—	—	6,700
Clinidae				Torpedinidae			
Heterostichus rostratus, giant kelpfish	3	30	175	*Torpedo californica*, Pacific electric ray	—	—	9,450
Cottidae							
Scorpaenichthys marmoratus, cabezon	—	—	1,500				

[1]E. DeMartini and R. Larson. 1980. Predicted effects of the operations of San Onofre Nucler Generating Station Units 1, 2, and 3 on the fish fauna of the San Onofre region. Report submitted to the Marine Review Committee of the California Coastal Commission. Unpubl. rep., 27 p. Marine Science Institute, University of California, Santa Barbara, CA 93106.
[2]Members of the genus *Sebastes* will be grouped under "rockfish spp." in subsequent tables.

TABLE 2.—Bathymetric sampling strata at the San Onofre kelp bed. Weighting factors (W_h) are shown for the above-bottom strata and for the above-bottom versus bottom strata.

Sampling depth (m)	Depth Range represented (m)	Extent of range (m)	W_h (above-bottom only)	W_h (all strata)
3	0-5.3	5.3	0.3926	
7.6	5.3-9.8	4.5	0.3333	[1]0.9
12	9.8-13.5	3.7	0.2741	
15 (bottom)	13.5-15.0	1.5	—	0.1
	0-15		1.0	1.0

[1]Weighting factor for above-bottom strata combined.

which time fish that were distinguishable on film were identified, counted, and assigned to maturity classes as above.

Transect Volume

The volume of visual bottom transects was considered to be fixed, and the volume of water-column cinetransects to be dependent on underwater visibility. The volume of bottom transects was fixed at $75\text{ m} \times 3\text{ m} \times 1.5\text{ m} = 337.5\text{ m}^3$, since the length of transects was measured, and the height and width of transects were fixed at values less than horizontal visibility. Cinetransect length was taken as the average distance covered in simulated, 3-min cinetransects swum by three divers over a metered line. Each diver swam two simulations against the current, and two with the current. The cross-sectional area of a cinetransect was treated as an ellipse with a minor (vertical) axis of 1.5 m, the distance above and below the diver that fish were photographed. The major axis of the ellipse was a function of camera range, the distance at which fish could be distinguished on film. The particular function was cos 30° × camera range,

since divers photographed fish within a 120° arc (60° on each side of the transect axis) (Fig. 2). Thus, the volume of cinetransects at a given depth on a given day was calculated as

$$V = 1.5\ \pi L\ (\cos 30° \times CR),$$

where V was cinetransect volume in cubic meters; 1.5, the minor axis of the ellipse; L, the cinetransect length as determined above; and CR, the camera range at that depth on that day. Camera range itself was estimated as a function of the horizontal visibility at a depth on a sampling date.

The relationship between camera range and horizontal visibility was estimated empirically under different conditions. The main "other condition" that we evaluated was the orientation of the camera to the sun. In trials run at different visibilities, two fish of similar appearance (usually a kelp perch, *Brachyistius frenatus*, and a white seaperch, *Phanerodon furcatus*) were held on a spear by one diver and photographed with our usual equipment by another diver at distances decremented from the limits of horizontal visibility (measured as described above). At each visibility, trials were run with the camera facing into the sun and with the camera facing away from the sun. Two observers viewed the film from each trial and determined camera range as the greatest distance at which the two fish could be distinguished on film. The criteria for distinguishability were the same as those used in evaluating whether or not to count a fish when we viewed regular cinetransects.

Data for camera range versus horizontal visibility were fit to several asymptotic functions. The fitting

CINETRANSECT VOLUME

A. CINETRANSECT SHAPE

B. CINETRANSECT CROSS SECTION
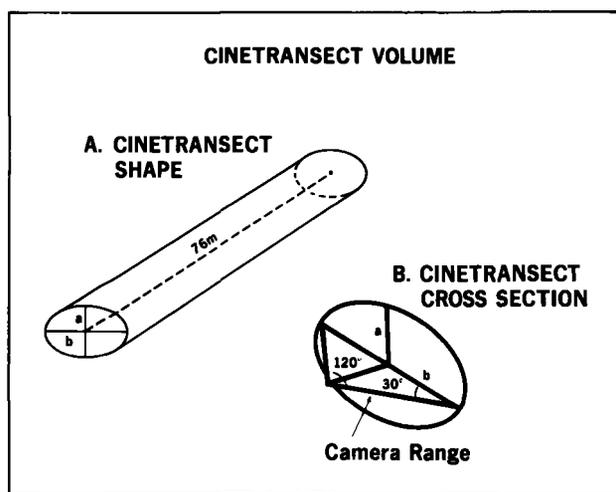
Camera Range

FIGURE 2.—A. Estimated shape of area sampled in underwater transects taken with motion pictures (cinetransects). The length of 76 m was estimated from simulated transects. B. Elliptical cross section of a cinetransect, with minor axis (a) of 1.5 m and major axis (b) calculated from camera range when divers surveyed a 120° horizontal arc about the central axis of the transect.

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routine was BMDP program P3R, nonlinear regression (Dixon and Brown 1979). The function with the smallest residual mean square was selected to represent the relation between camera range and horizontal visibility, and was employed in estimating camera range at a depth on a sampling date.

Data Analysis

We reduced data into two general forms: densities (number or biomass per unit volume) in different strata, and abundances integrated throughout the entire water column. The first was used to examine the vertical distribution of individual species or of the entire assemblage and to compare the relative abundances of species in a stratum. The second was used to estimate the overall abundance of the assemblage and to compare the overall abundances of different species. In both cases, the final point and interval estimates were based on the means and variances, over dates, of daily means.

The daily estimate of density (per 1,000 m³) for each species in a depth stratum was estimated as the mean number or biomass per transect on that day, times the ratio (1,000/transect volume), where transect volume was estimated as above. Biomass of a species on a given transect was estimated by counts of individuals in different maturity classes, converted to wet weights by the key in Table 1.

Our estimate of a species' density in a depth stratum was calculated as the mean of the daily density estimates in that stratum. Similar estimates were made for the sum of all "resident" teleosts. Excluded from the analysis of total fish density and abundance were elasmobranchs and certain teleosts (silversides, jack mackerel, Pacific barracuda, black croaker, and salema) that were rare at SOK, are seasonal visitors to kelp beds, or are not primarily associated with rock reefs and kelp forests (Feder et al. 1974). Species such as white seaperch and barred sand bass often occur in other habitats, but were included in our analysis because they may have at least a marginal association with kelp-rock habitats and were frequently encountered and abundant in our samples.

By weighting the average density of a species (or the assemblage) in a stratum by the volume of water represented by samples in that stratum, we were able to obtain estimates of abundance integrated from surface to bottom (Snedecor and Cochran 1980:444). The sampling day was an integral component of our analysis, but only the above-bottom strata were sampled on the same day at a given site. To obtain accurate estimates of variance for integrated abundances, then, we assembled our integrated estimates in two stages. We first estimated stratified mean density for the above-bottom strata on each day and averaged these values over days. We also computed mean density (over days) in the bottom stratum. Secondly, we computed stratified mean density (and its standard error) for the above-bottom and bottom strata, using the means and variances calculated above. The stratified mean density estimates for the entire water column were then scaled to represent abundances over 100 m² of bottom.

Samples in each stratum were assumed to represent a range of depths extending to the midpoints between strata, with the 3 m stratum also extending to the surface (Table 2). Weighting factors for the strata were determined from the relative extents of the depth ranges represented. Among the above-bottom strata, relative weighting factors were the vertical ranges of these strata divided by 13.5 m. For the bottom versus above-bottom strata the depth ranges were divided by 15 m.

Daily estimates of stratified mean density in the above-bottom strata were calculated as

$$D_{wc} = \sum_h W_h D_h,$$

where D_{wc} was the estimate of stratified mean density in the 3 m, 7.6 m, and 12 m strata; W_h, the weighting factor; and D_h, the mean density on that day in stratum h (Snedecor and Cochran 1980). The mean ($\bar{D}_{wc}$) and variance (S^2_{wc}) of these daily estimates were then computed. The mean ($\bar{D}_b$) and variance (S^2_b) of estimated daily densities on the bottom were also calculated.

Stratified mean abundance throughout the entire water column was estimated as

$$\bar{A}_{st} = \left(\frac{1,500}{1,000} \right) \sum_h W_h D_h,$$

where $\bar{A}_{st}$ was the stratified mean estimate of integrated abundance over 100 m² of bottom, W_h was the weighting factor, and $\bar{D}_h$ was the mean density in either the above-bottom strata ($\bar{D}_{wc}$) or in the bottom stratum ($\bar{D}_b$). The term in the summation is the estimate of stratified mean density (per 1,000 m³) over all strata, and the ratio (1,500/1,000) converts this value to abundance over 100 m² of bottom.

The standard error of $\bar{A}_{st}$ was calculated as

$$S_{\bar{A}_{st}} = \sqrt{\left(\frac{1,500}{1,000} \right)^2 \sum_h W^2_h S^2_h / n_h},$$

where S^2_h was the variance of daily density estimates in either the above-bottom (S^2_{wc}) or bottom (S^2_b)

strata; W_h, the weighting factor; and n_h, the number of days sampled in stratum h. The portion of the formula included in the summation is the usual estimate of variance for stratified means (Snedecor and Cochran 1980), and the root of this sum is the standard error of mean density (per 1,000 m³) throughout the water column. Multiplying by $(1,500/1,000)^2$ adjusts the standard error for the larger volume of water in the column over 100 m².

Estimates of integrated abundance at the kelp-depauperate site were obtained by converting mean density on the bottom to mean density over 100 m².

Arithmetic means (of untransformed data) were used for all estimates of density and abundance. Geometric means (obtained by back-transforming the means of log-transformed data) underestimate absolute densities in a manner proportional to their variances. Adjustments for this underestimation (Elliott 1971) are usually based on the assumption of log-normal distributions, and we could not make such an assumption. However, some statistical comparisons were made with log-transformed data to avoid the problem of heterogeneous variances. These were comparisons of mean numbers and biomass on the bottom, where varying transect volume did not confound the calculation of variance. Other comparisons, however, were made with untransformed data. These included tests for dif-

ferences in numbers or biomass in the above-bottom strata arid in the entire water column. When all three areas were compared, a one-way ANOVA was used if variances were not heterogeneous. T-tests for unequal variances (Bailey 1959) were used for pairwise comparisons of areas when variances were unequal.

RESULTS

Cinetransect Calibration

We estimated cinetransect length to be about 76 m. Six down-current trials averaged 78.3 m in length (standard error (SE) = 1.5 m, range = 74-82 m), 6 upcurrent trials averaged 72.8 m in length (SE = 2.3 m, range = 67-82 m), and the overall average was 75.6 m (SE = 1.5 m).

Camera range was an asymptotic function of horizontal visibility, with little increase in camera range at visibilities beyond 7-9 m (Fig. 3). Camera range was appreciably lower when the camera was facing the sun than vice versa, particularly at greater visibilities. This was reflected in each of the curves fit (Table 3). Since divers did not record whether actual transects faced into or away from the sun, we used the curve fit to all camera range-horizontal visibility values to calibrate cinetransect volume. The logistic equation provided, by slight margin, the best fit to
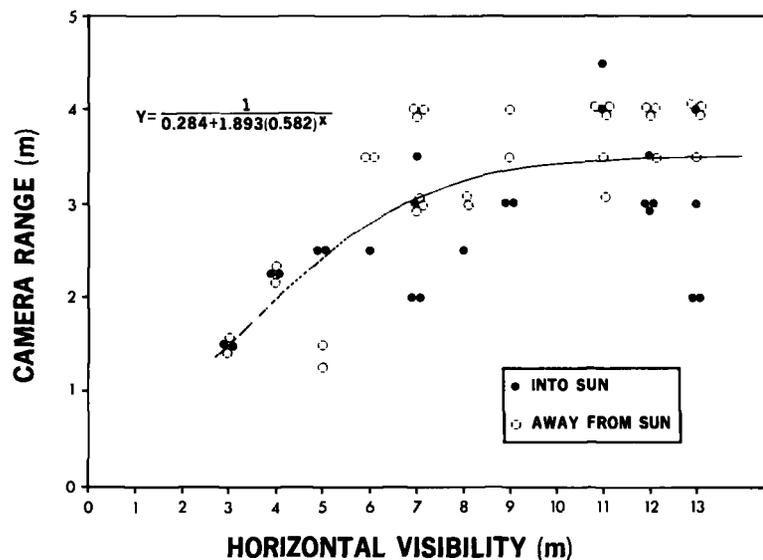

FIGURE 3.—Relation of camera range (the distance at which fish could be distinguished on film) and horizontal visibility. Points are observations of maximum camera range at different visibilities with the camera facing into and away from the sun. The equation and line show the logistic function fit to these points.

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these data (Table 3) and was the one employed in calculating cinetransect volume.

Distribution and Abundance of Fishes

Five sets of bottom transects were made in each study area. Water-column samples were taken on five dates at SOK-U and on four at SOK-D. Transect number and visibility at depth on each date are shown in Table 4.

Of the 28 species recorded in this study, 19 were "resident" teleosts. Of these, 13 species were recorded on more than two transects in the two kelp-forest areas (Table 5). These 13 common species could be assigned to bathymetric categories, based on their vertical patterns of frequency of occurrence (Table 5) and density (Tables 6, 7) within SOK.

Kelp perch, halfmoon, and giant kelpfish were most common in the upper strata and are designated "canopy" species. While halfmoon and giant kelpfish were observed in all strata, all three species were most abundant in the 3 m stratum. Only halfmoon reached moderate abundances at 7.6 m in the SOK-D area (Tables 5, 6, 7).

Señorita, white seaperch, and kelp bass were common throughout the water column (Tables 5, 6, 7) and are designated "cosmopolites". These three species were among the most common and abundant fishes in all strata. The white seaperch was the most cosmopolitan of the three in 1979, its density and frequency of occurrence on transects varying little with depth. The señorita was the most abundant species in nearly all strata. The kelp bass was also abundant at all depths. Its numerical density varied little among the water-column strata, but was generally greater on the bottom. Its biomass was greater in the lower strata (Tables 6, 7). Young kelp bass concentrated in the upper water column (Table 8), contributing to the relatively low biomass per fish for kelp bass in the 3 and 7.6 m strata. Our data indicate

TABLE 3.—Functions fit to camera range (Y) versus horizontal visibility (X) relationship, and the best fit parameters as determined by BMDP program P3R (Dixon and Brown 1979). Also noted are the asymptotes calculated for each equation and data set, and the residual mean squares. Into= trials made with the camera facing into the sun; Away = trials made with the camera facing away from the sun; All = curves fit to all data. P_1, P_2, and P_3 are arbitrary symbols for the parameters of each function; there is no implied correspondence between the numbered parameters of different functions.

Function name and formula	Set of trials	P_1	P_2^2	P_3	Asymptote (m)	Residual mean square
Logistic $Y = 1/(P_1 + P_3)$	All	0.284	1.89	0.582	3.52	0.369
	Away	0.259	2.63	0.560	3.86	0.250
	Into	0.317	1.20	0.618	3.15	0.355
Gompertz $Y = e^{(P_1 + P_2 P_3^X)}$	All	1.27	−3.19	0.647	3.56	0.370
	Away	1.37	−3.88	0.648	3.94	0.255
	Into	1.15	−2.35	0.656	3.16	0.354
Von Bertalanffy $Y = P_1 (1 - e^{P_2(X - P_3)})$	All	3.60	0.334	1.43	3.60	0.372
	Away	4.03	0.301	1.62	4.03	0.261
	Into	3.17	0.361	1.07	3.17	0.353
Michaelis-Menton $Y = \dfrac{P_1 (X - P_2)}{P_3 + X - P_2}$	All	4.21	1.92	2.03	4.21	0.377
	Away	4.94	1.91	2.79	4.94	0.269
	Into	3.51	2.01	1.28	3.51	0.354
Beverton-Holt $Y = 1/(P_1 + P_2/X)$	All	0.194	1.06	—	5.15	0.388
	Away	0.158	1.17	—	6.33	0.284
	Into	0.241	0.92	—	4.15	0.352

TABLE 4.—Sampling dates, number of transects, and visibilities measured during fall 1979 sampling in two areas within the kelp bed at San Onofre (SOK-U and SOK-D) and in a nearby cobble-bottom area with little kelp (Cobble). Horizontal visibility (vis.) measured in meters

	SOK-U								SOK-D								Cobble	
	3 m		7.6 m		12 m		Bottom		3 m		7.6 m		12 m		Bottom		Bottom	
Date	ν	vis.	ν	vis.	ν	vis.	ν	vis.	ν	vis.	ν	vis.	ν	vis.	ν	vis.	ν	vis.
10 Oct.							10	2.95										
15 Oct.															9	2.14		
17 Oct.							9	2.89									7	3.00
22 Oct.							10	2.75							9	3.42		
24 Oct.																	10	2.60
26 Oct.									11	14.00	12	8.50	11	3.50				
31 Oct.							10	3.85									10	5.00
7 Nov.															10	3.90		
12 Nov.	12	7.30	12	5.10	12	4.75												
14 Nov.																	10	5.50
16 Nov.															10	4.50	10	4.85
21 Nov.							10	8.75										
26 Nov.									12	10.25	12	7.00	12	4.00				
28 Nov.															10	4.00		
30 Nov.	12	12.55	12	7.05	12	3.15												
5 Dec.									12	16.00	12	13.75	12	7.25				
7 Dec.	12	10.50	12	5.85	12	5.10												
10 Dec.									12	8.25	12	7.80	12	6.90				
12 Dec.	12	9.45	12	6.95	12	8.50												
19 Dec.	13	10.50	12	8.50	12	5.25												
Total	61		60		60		49		47		48		47		48		47	
Mean		10.06		6.69		5.35		4.24		12.13		9.26		5.41		3.59		4.19

that the upper kelp canopy serves as a nursery for young-of-the-year kelp bass, and these cryptic fish were probably much more abundant there than shown by our counts. We examined vertical segrega- tion of size classes only for kelp bass. This is because our 1979 data were too few to evaluate vertical segregation by size that has since been noted for two other species (señorita and blacksmith) in several

TABLE 5.—Percent of transects on which species were observed during fall 1979, in two portions of a kelp forest near San Onofre, Calif. (SOK-U and SOK-D) and in a nearby kelpless cobble area (Cobble). Species' ranks are shown in parentheses. Number of transects is noted in the column heading.

Species	SOK-U 3 m n=61	SOK-U 7.6 m n=60	SOK-U 12 m n=60	SOK-U Bottom n=49	SOK-D 3 m n=47	SOK-D 7.6 m n=48	SOK-D 12 m n=47	SOK-D Bottom n=48	Cobble Bottom n=47
kelp bass	52(3)	50(3)	60(1.5)	61(2.5)	74(2)	77(2)	81(1)	81(2)	26(4.5)
barred sand bass		2(10)	8(4.5)	59(4)		9(8)		58(5)	53(1)
kelp perch	59(2)	13(4)	2(13)		49(3)	10(6.5)	9(8)		
black perch			8(4.5)	41(5)		9(8)		65(3)	26(4.5)
white seaperch	41(4)	58(2)	60(1.5)	39(6.5)	40(4)	56(3)	62(3)	44(7.5)	15(8)
pile perch		2(10)	3(10)	20(9)	4(9)		17(5)	42(9)	11(9)
rubberlip seaperch			3(10)	18(10)				19(10)	4(12.5)
rainbow seaperch				39(6.5)				44(7.5)	19(6.5)
señorita	93(1)	87(1)	58(3)	61(2.5)	96(1)	94(1)	66(2)	63(4)	43(2)
California sheephead			5(7.5)	58(1)	2(10.5)	19(5)	36(4)	90(1)	36(3)
rock wrasse				29(8)		2(9.5)	4(10)	46(6)	6(10.5)
opaleye	3(8)								2(15)
halfmoon	16(6.5)	7(6)	2(13)	2(14)	36(5)	38(4)	11(6)	4(12.5)	19(6.5)
blacksmith		2(10)					2(11.5)		
garibaldi								4(12.5)	
giant kelpfish	24(5)	8(5)	7(6)	3(11)	21(6)	10(6.5)		4(12.5)	
cabezon				2(14)				2(16.5)	
California scorpionfish								2(16.5)	4(12.5)
rockfish spp.			3(10)	2(14)					6(10.5)
black croaker								2(16.5)	
salema								4(12.5)	
silversides	16(6.5)				19(7)				
jack mackerel	2(9.5)	3(7.5)	5(7.5)		17(8)	8(8)	2(11.5)		
Pacific barracuda					2(10.5)	2(9.5)			
leopard shark				2(14)					
thornback									2(15)
bat ray				2(14)				2(16.5)	
Pacific electric ray	2(9.5)	3(7.5)	2(13)						2(15)

TABLE 6.—Mean numerical and biomass densities (per 1,000 m³) of fishes observed in n daily samples per depth stratum at the SOK-U area in the San Onofre kelp bed during fall 1979. Values are the grand means (±1 standard error) of the daily means (adjusted for transect volume) over transects taken each sampling day.

Species	Numerical density (no./1,000 m³) 3 m (n=5) x̄	SE	7.6 m (n=5) x̄	SE	12 m (n=5) x̄	SE	Bottom (n=5) x̄	SE	Biomass density (kg/1,000 m³) 3 m (n=5) x̄	SE	7.6 m (n=5) x̄	SE	12 m (n=5) x̄	SE	Bottom (n=5) x̄	SE
kelp bass	1.57	0.87	2.67	1.19	2.48	0.93	4.76	1.20	0.091	0.071	0.416	0.171	0.664	0.270	1.372	0.372
barred sand bass	0		0.02	0.02	0.13	0.04	3.30	0.70	0		0.024	0.024	0.173	0.046	4.434	0.930
kelp perch	1.39	0.26	0.23	0.13	0.02	0.02	0		0.035	0.007	0.006	0.003	neg.		0	
black perch	0		0		0.12	0.07	2.25	0.65	0		0		0.046	0.028	0.717	0.209
white seaperch	1.91	1.21	3.16	1.20	2.33	0.86	3.07	0.59	0.319	0.210	0.491	0.209	0.287	0.105	0.376	0.108
pile perch	0		0.02	0.02	0.08	0.05	0.66	0.11	0		0.009	0.009	0.039	0.025	0.263	0.079
rubberlip seaperch	0		0		0.04	0.03	1.08	0.35	0		0		0.028	0.017	0.634	0.265
rainbow seaperch	0		0		0		2.02	0.92	0		0		0		0.167	0.068
señorita	26.95	6.53	24.45	5.78	4.66	2.22	14.16	5.95	0.950	0.223	1.103	0.225	0.241	0.110	0.566	0.237
California sheephead	0		0		0.13	0.06	4.87	1.16	0		0		0.058	0.040	1.561	0.338
rock wrasse	0		0		0		1.20	1.24	0		0		0		0.237	0.022
opaleye	0.03	0.03	0		0		0		0.033	0.033	0		0		0	
halfmoon	0.27	0.20	0.08	0.05	0.02	0.02	0.06	0.06	0.068	0.050	0.020	0.012	0.006	0.006	0.015	0.015
blacksmith	0		002	0.02	0		0		0		neg.		0		0	
garibaldi	0		0		0		0		0		0		0		0	
giant kelpfish	0.35	0.08	0.09	0.04	0.08	0.04	0.18	0.12	0.018	0.007	0.004	0.003	0.015	0.008	0.014	0.012
cabezon	0		0		0		0.06	0.06	0		0		0		0.089	0.089
Calif. scorpionfish	0		0		0		0		0		0		0		0	
rockfish spp.	0		0		0.04	0.02	0.06	0.06	0		0		0.003	0.003	0.024	0.024
black croaker	0		0		0		0		0		0		0		0	
salema	0		0		0		0		0		0		0		0	
silversides	4.21	1.54	0		0		0		0.092	0.029	0		0		0	
jack mackerel	0.09	0.90	8.77	8.74	0.50	0.36	0		0.010	0.010	1.008	1.005	0.057	0.041	0	
Pacific barracuda	0		0		0		0		0		0		0		0	
leopard shark	0		0		0		0.06	0.06	0		0		0		0.119	0.119
thornback	0		0		0		0		0		0		0		0	
bat ray	0		0		0		0.06	0.06	0		0		0		0.397	0.397
Pacific electric ray	0.01	0.01	0.03	0.02	0.02	0.02	0		0.136	0.136	0.320	0.196	0.154	0.154	0	

TABLE 7.—Mean numerical and biomass densities (per 1,000 m³) of fishes observed in *n* daily samples per depth stratum at the SOK-D area in the San Onofre kelp bed during fall 1979. Values are the grand means (±1 standard error) of the daily means (adjusted for transect volume) over transects taken each sampling day.

	SOK-D							
	Numerical density (no./1,000 m³)				Biomass density (kg/1.000 m³)			
	3 m (n=4)	7.6 m (n=4)	12 m (n=4)	Bottom (n=5)	3 m (n=4)	7.6 m (n=4)	12 m (n=4)	Bottom (n=5)
Species	x̄ SE	x̄ SE	x̄ SE	x̄ SE	x̄ SE	x̄ SE	x̄ SE	x̄ SE
kelp bass	4.23 0.63	4.61 1.09	4.84 1.07	12.87 3.95	0.726 0.162	1.101 0.440	1.621 0.672	2.363 0.675
barred sand bass	0	0	0.12 0.02	3.14 0.29	0	0	0.178 0.029	3.446 0.577
kelp perch	0.83 0.20	0.19 0.09	0.11 0.08	0	0.021 0.005	0.005 0.002	0.003 0.002	0
black perch	0	0	0.18 0.11	4.77 0.63	0	0	0.040 0.017	1.401 0.089
white seaperch	3.50 2.38	4.15 1.52	4.83 0.94	3.64 1.48	0.582 0.407	0.681 0.269	0.693 0.180	0.399 0.137
pile perch	0.04 0.04	0	0.23 0.13	1.74 0.18	0.013 0.013	0	0.105 0.068	0.682 0.056
rubberlip seaperch	0	0	0	0.64 0.24	0	0	0	0.447 0.165
rainbow seaperch	0	0	0	2.49 0.71	0	0	0	0.238 0.053
señorita	19.46 2.82	21.04 3.57	5.68 1.82	13.31 7.77	0.569 0.078	1.039 0.158	0.312 0.100	0.435 0.205
California sheephead	0.02 0.02	0.60 0.23	1.52 0.42	13.66 1.29	0.017 0.017	0.181 0.119	0.770 0.386	4.990 0.322
rock wrasse	0	0.02 0.02	0.06 0.03	1.86 0.49	0	0.005 0.005	0.028 0.004	0.405 0.110
opaleye	0	0	0	0	0	0	0	0
halfmoon	1.09 0.44	2.92 1.83	0.35 0.19	0.12 0.12	0.237 0.110	0.730 0.457	0.087 0.047	0.030 0.030
blacksmith	0	0	0.03 0.04	0	0	0	neg.	0
garibaldi	0	0	0	0.12 0.07	0	0	0	0.014 0.009
giant kelpfish	0.28 0.06	0.10 0.02	0	0.12 0.07	0.024 0.007	0.008 0.004	0	0.012 0.010
cabezon	0	0	0	0.07 0.06	0	0	0	0.099 0.099
Calif. scorpionfish	0	0	0	0.06 0.06	0	0	0	0.033 0.033
rockfish spp.	0	0	0	0	0	0	0	0
black croaker	0	0	0	11.85 11.85	0	0	0	2.667 2.667
salema	0	0	0	8.89 5.93	0	0	0	0.667 0.444
silversides	5.99 3.96	0	0	0	0.120 0.079	0	0	0
jack mackerel	20.96 9.05	19.34 17.69	3.32 3.32	0	2.410 1.040	2.224 2.035	0.381 0.381	0
Pacific barracuda	0.13 0.13	0.61 0.61	0	0	0.019 0.019	0.092 0.092	0	0
leopard shark	0	0	0	0	0	0	0	0
thornback	0	0	0	0	0	0	0	0
bat ray	0	0	0	0.12 0.12	0	0	0	0.794 0.794
Pacific electric ray	0	0	0	0	0	0	0	0

TABLE 8.—Mean numerical densities (per 1,000 m³) of young-of-the-year (yoy), all juveniles (including yoy), subadult, and adult kelp bass in *n* daily samples per depth stratum at SOK-U and SOK-D during fall 1979. Grand means calculated as in Tables 6 and 7.

	Numerical density (no./1.000 m³)			
	3 m (n = 5)	7.6 m (n = 5)	12 m (n = 5)	Bottom (n = 5)
SOK-U	x̄ SE	x̄ SE	x̄ SE	x̄ SE
yoy	0.65 0.20	0.36 0.12	0.10 0.05	0.24 0.24
all juvs.	1.23 0.62	0.85 0.34	0.90 0.38	1.36 0.76
subadults	0.32 0.25	1.76 0.94	1.18 0.52	2.59 0.69
adults	0.02 0.01	0.05 0.04	0.40 0.24	0.80 0.26

	3 m (n = 4)	7.6 m (n = 4)	12 m (n = 4)	Bottom (n = 5)
SOK-D	x̄ SE	x̄ SE	x̄ SE	x̄ SE
yoy	0.88 0.42	0.33 0.13	0.20 0.09	0.12 0.12
all juvs.	1.50 0.62	1.24 0.19	1.37 0.50	5.21 3.26
subadults	2.52 0.98	2.88 0.87	2.39 0.84	6.72 3.05
adults	0.20 0.12	0.49 0.28	1.08 0.49	0.94 0.18

kelp beds off northern San Diego County (DeMartini et al.[6]).

Seven of the 13 common species were most abundant near the bottom (Tables 5, 6, 7). Rainbow seaperch and rock wrasse rarely, if ever, strayed above the bottom. Black perch and rubberlip seaperch were recorded occasionally at 12 m, but

were much more abundant on the bottom. Pile perch were seen, at one site or the other, in all strata, but were most abundant on the bottom and at 12 m. Barred sand bass also concentrated on the bottom and, to a lesser degree, at 12 m. California sheephead were observed as shallow as 3 m at SOK-D, but no shallower than 12 m at SOK-U.

Species composition and relative abundance in each stratum reflected the distributional patterns of the species (Tables 9, 10). The three cosmopolitan species were among the three to five most abundant species in every stratum, particularly above the bottom. At 3 and 7.6 m, they made up 89-99% of total numerical density. The remaining fish in these strata were mainly upper water-column species, with a few of the more errant bottom species (such as California sheephead and pile perch) entering at 7.6 m. The three cosmopolites again dominated the assemblage at 12 m, forming 86-94% of fish numbers. A few individuals of canopy species were present at 12 m, however, and a greater number of bottom species were observed. The bottom stratum contained the greatest number of recorded species, and individuals were distributed more evenly among these species. The cosmopolites were still among the most abundant species on the bottom, but several of the bottom-zone species (such as California sheephead, black perch, and barred sand bass) were also abun-

TABLE 9.—Percent contribution of species to total numerical and biomass density at the SOK-U area of the San Onofre kelp bed during fall 1979. Percentages are given by stratum and for abundance integrated throughout the water column. Only those species contributing 1% or more are listed. Stratum values are based on data in Tables 6 and 7; integrated abundances on Table 11.

3 m		7.6 m		12 m		Bottom		Integrated	
Species	%	Species	%	Species	%	Species	%	Species	%
SOK-U Numbers									
señorita	83.0	señorita	79.5	señorita	48.0	señorita	37.5	señorita	72.0
white seaperch	5.9	white seaperch	10.3	kelp bass	24.5	Calif. sheephead	12.9	white seaperch	9.3
kelp bass	4.8	kelp bass	8.7	white seaperch	23.0	kelp bass	12.6	kelp bass	9.1
kelp perch	4.3			barred sand bass	1.3	barred sand bass	8.7	kelp perch	2.1
giant kelpfish	1.1			Calif. sheephead	1.3	white seaperch	8.1	Calif. sheephead	2.0
				black perch	1.2	black perch	6.0	barred sand bass	1.4
						rainbow seaperch	5.4		
						rock wrasse	3.2		
						rubberlip seaperch	2.9		
						pile perch	1.7		
SOK-U Biomass									
señorita	62.7	señorita	53.2	kelp bass	42.6	barred sand bass	42.4	señorita	30.2
white seaperch	21.1	white seaperch	23.7	white seaperch	18.4	Calif. sheephead	14.9	barred sand bass	19.1
kelp bass	6.0	kelp bass	20.1	señorita	15.4	kelp bass	13.1	kelp bass	17.7
halfmoon	4.5	barred sand bass	1.2	barred sand bass	11.1	black perch	6.8	white seaperch	14.2
kelp perch	2.3	halfmoon	1.0	Calif. sheephead	3.7	rubberlip seaperch	6.1	Calif. sheephead	6.6
opal	2.2			black perch	2.9	señorita	5.4	black perch	3.2
giant kelpfish	1.2			pile perch	2.5	white seaperch	3.6	rubberlip seaperch	2.7
				rubberlip seaperch	1.8	pile perch	2.5	pile perch	1.5
				giant kelpfish	1.0	rock wrasse	2.3	halfmoon	1.2
						rainbow seaperch	1.6		

TABLE 10.—Percent contribution of species to total numerical and biomass density at the SOK-D area of the San Onofre kelp bed during fall 1979. Percentages are given by stratum and for abundance integrated throughout the water column. Only those species contributing 1% or more are listed. Stratum values are based on data in Tables 6 and 7; integrated abundances on Table 11.

3 m		7.6 m		12 m		Bottom		Integrated	
Species	%	Species	%	Species	%	Species	%	Species	%
SOK-D Numbers									
señorita	66.1	señorita	62.6	señorita	31.6	Calif. sheephead	23.3	señorita	51.7
kelp bass	14.4	kelp bass	13.7	kelp bass	27.0	señorita	22.7	kelp bass	17.4
white seaperch	11.9	white seaperch	12.3	white seaperch	27.0	kelp bass	22.0	white seaperch	13.1
halfmoon	3.7	halfmoon	8.7	Calif. sheephead	8.5	black perch	8.1	Calif. sheephead	6.3
kelp perch	2.8	Calif. sheephead	1.8	halfmoon	1.9	white seaperch	6.2	halfmoon	4.4
				pile perch	1.3	barred sand bass	5.4	black perch	1.7
				black perch	1.0	rainbow seaperch	4.2	kelp perch	1.2
						rock wrasse	3.2	barred sand bass	1.1
						pile perch	3.0		
						rubberlip seaperch	1.1		
SOK-D Biomass									
kelp bass	32.6	kelp bass	29.4	kelp bass	42.2	Calif. sheephead	33.3	kelp bass	28.2
white seaperch	26.2	señorita	27.7	Calif. sheephead	20.1	barred sand bass	23.0	Calif. sheephead	17.2
señorita	25.6	halfmoon	19.5	white seaperch	18.1	kelp bass	15.8	señorita	14.5
halfmoon	12.3	white seaperch	18.2	señorita	8.1	black perch	9.3	white seaperch	14.3
giant kelpfish	1.1	Calif. sheephead	4.8	barred sand bass	4.6	pile perch	4.5	barred sand bass	8.9
				pile perch	2.7	rubberlip seaperch	3.0	halfmoon	7.8
				halfmoon	2.3	señorita	2.9	black perch	3.4
				black perch	1.0	rock wrasse	2.7	pile perch	2.3
						white seaperch	2.7	rock wrasse	1.1
						rainbow seaperch	1.6	rubberlip seaperch	1.0

dant. The gradual change in species composition that occurred between the water-column strata became more abrupt at the bottom.

The vertical profile of total numerical density reflected changes in the abundance of the most numerous species, señorita, and the increase in species number on the bottom. Numerical density was about the same at 3 and 7.6 m, dropped at 12 m, and peaked on the bottom (Fig. 4). Small differences in species composition at 3 and 7.6 m led to only small differences in the abundances of noncosmopolites, and the cosmopolites (particularly señorita) had similar densities in these strata (Tables 6, 7). Despite increased abundances of bottom species at 12 m, the loss of upper water-column species and the decline in abundance of señorita led to low overall numerical densities in this stratum (Tables 6, 7). Señorita became more abundant again in the bottom stratum, kelp bass reached peak density, and the bottom species became abundant (Tables 6, 7), leading to high numerical densities on the bottom (Fig. 4).

Biomass density did not differ among the water-column strata, but reached an exaggerated peak on the bottom (Fig. 5). At 12 m, the increase in size of kelp bass, and the addition of large-bodied species like California sheephead, barred sand bass, and
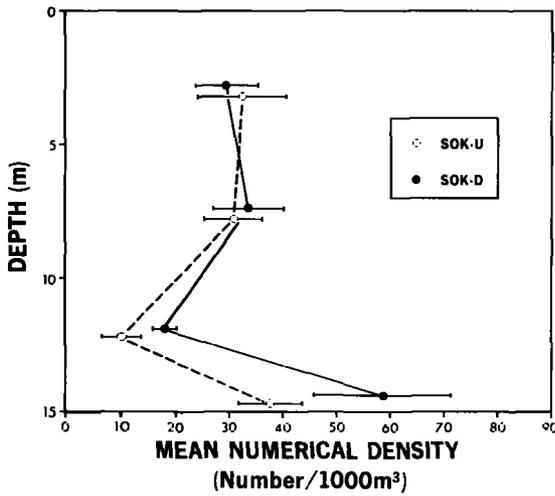
47

FIGURE 4.—Vertical distribution of the numerical densities of all resident teleosts in two areas within the San Onofre kelp bed during fall 1979. Points are mean densities over sampling dates at each site and stratum, and bars represent one standard error of the mean.
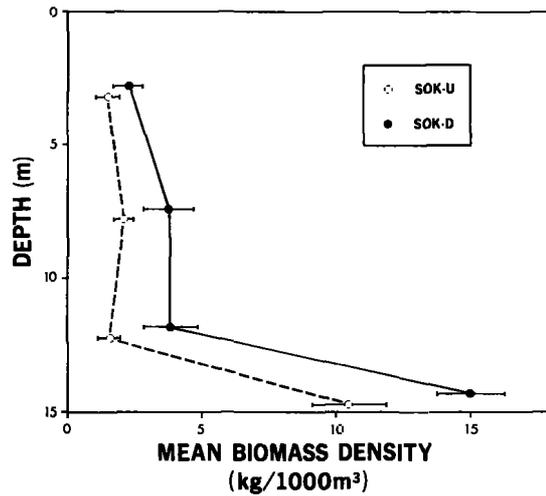

FIGURE 5.—Vertical distributions of the biomass density of all resident teleosts in two areas within the San Onofre kelp forest during fall 1979. Points are mean densities over sampling dates at each site and stratum, and bars represent one standard error of the mean.

various embiotocids compensated for the decline in abundance of señorita (Tables 6, 7). The higher numerical densities of these large fishes on the bottom contributed most to the peak biomass densities in this stratum.

Weighting densities for the size of stratum, we estimated that on average about 40 and 46 fish occurred over 100 m² at SOK-U and SOK-D, respectively, with corresponding biomass values of 3.9 and 6.5 kg/100 m² (Table 11). About 66% (SOK-D) to

77% (SOK-U) of all individuals occurred in the upper two strata, 9% (SOK-U) to 14% (SOK-D) at 12 m, and 14% (SOK-U) to 19% (SOK-D) on the bottom. The small vertical extent of the bottom stratum diminished its contribution to the abundance of fish integrated over the entire water column. About 44-45% of fish biomass occurred in the two upper strata, 15% (SOK-U) to 22% (SOK-D) occurred at 12 m, and 34% (SOK-D) to 40% (SOK-U) on the bottom. Thus much of biomass was near the bottom, but because of

TABLE 11.—Abundance of resident teleosts, based on densities integrated through the water column over 100 m² of bottom. The standing stock in numbers and biomass is given for each of two areas (SOK-U and SOK-D) within the San Onofre kelp bed, and for an adjacent area of cobble bottom with little kelp (Cobble), for samples taken in fall 1979.

| | Numbers per 100 m² | | | | | | Biomass (kg) per 100 m² | | | | | |
| | SOK-U | | SOK-D | | Cobble | | SOK-U | | SOK-D | | Cobble | |
Species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
kelp bass	3.66	1.02	8.04	0.80	0.25	0.14	0.67	0.15	1.83	0.41	0.12	0.04
barred sand bass	0.55	0.11	0.52	0.04	1.16	0.37	0.74	0.14	0.58	0.09	1.69	0.55
kelp perch	0.85	0.20	0.57	0.05	0		0.02	0.01	0.01	0.01	0	
black perch	0.38	0.10	0.78	0.10	0.54	0.32	0.13	0.03	0.23	0.02	0.19	0.11
white seaperch	3.76	1.43	6.05	1.54	0.46	0.31	0.55	0.24	0.93	0.30	0.07	0.06
pile perch	0.14	0.03	0.37	0.07	0.05	0.02	0.06	0.02	0.15	0.03	0.02	0.01
rubberlip seaperch	0.18	0.05	0.10	0.04	0.03	0.02	0.11	0.04	0.07	0.02	0.02	0.01
rainbow seaperch	0.30	0.14	0.37	0.11	0.01	0.12	0.03	0.01	0.04	0.01	0.01	0.01
señorita	28.86	4.63	23.88	2.06	2.16	0.77	1.17	0.21	0.95	0.05	0.06	0.04
Calif. sheephead	0.78	0.18	2.89	0.30	0.61	0.20	0.26	0.05	1.12	0.17	0.18	0.06
rock wrasse	0.18	0.04	0.31	0.08	0.03	0.01	0.04	0.01	0.07	0.02	0.01	0.01
opaleye	0.02	0.02	0		0.01	0.01	0.02	0.02	0		0.01	0.01
halfmoon	0.20	0.13	2.04	1.03	0.11	0.05	0.05	0.03	0.51	0.26	0.03	0.01
blacksmith	0.01	0.01	0.01	0.04	0		neg.		neg.		0	
garibaldi	0		0.02	0.01	0		0		neg.		0	
giant kelpfish	0.28	0.07	0.21	0.04	0		0.02	0.01	0.02	0.01	0	
cabezon	0.02	0.01	0.01	0.01	0		0.01	0.01	0.02	0.02	0	
Calif. scorpionfish	0		0.01	0.01	0.02	0.01	0		neg.		0.01	0.01
rockfish spp.	0.02	0.01	0		0.04	0.03	0.01	0.01	0		0.01	0.01
All residents	40.4	6.0	46.2	4.1	5.6	0.94	3.9	0.5	6.5	0.7	2.4	0.6

their more extensive bathymetric ranges, the low biomass-density upper strata still contributed nearly one-half of total biomass.

The most abundant species at SOK were the cosmopolites (Tables 9, 10, 11). Señorita, kelp bass, and white seaperch comprised 82 and 90% of all individuals in the kelp forests at SOK-D and SOK-U, respectively. These species also contributed strongly to overall integrated biomass, although large species like California sheephead, barred sand bass, and halfmoon were also important. As a result, the distribution of biomass among species was more even than the distribution of numbers (Tables 9, 10, 11).

Two relatively large fishes were more abundant at SOK-D than SOK-U during fall of 1979, contributing to the differences (see below) in our estimates of total biomass at each site (Table 11). The integrated abundance of kelp bass was significantly higher, or nearly so, at SOK-D (Numbers: $t = 3.37$, df = 7, $0.01 < P < 0.02$; Biomass: $t = 2.65$, df = 4, $0.05 < P < 0.1$). California sheephead were also more abundant at SOK-D, as tested with log-transformed bottom data (Numbers: $t = 4.81$, df = 6, $P < 0.01$; Biomass: $t = 3.35$, df = 5, $0.02 < P < 0.05$) and with integrated abundances (Numbers: $t = 6.03$, df = 5, $P < 0.01$; Biomass: $t = 4.92$, df = 4, $P < 0.01$). Halfmoon seemed to be more abundant at SOK-D, but the difference was not significant (Numbers: $t = 1.78$, df = 3, $P > 0.1$; Biomass: $t = 1.78$, df = 3, $P > 0.1$).

At the kelpless cobble site, most fish were bottom species and cosmopolites (Tables 5, 11). While barred sand bass, black perch, and California sheephead were fairly abundant in this area, the average abundances of other species were less than in the kelp-bed areas. The integrated numerical abundance of all fishes was significantly lower in the kelpless cobble area (cobble vs. SOK-U: $t = 5.71$, df = 4, $P < 0.01$; cobble vs. SOK-D: $t = 9.42$, df = 3, $P < 0.01$; SOK-U vs. SOK-D: $t = 0.79$, df = 7, $P > 0.4$). A one-way ANOVA of log-transformed counts on the bottom showed significant differences among the three areas ($F_{2, 12} = 9.42$, $P < 0.01$), but an a priori comparison of SOK-U and SOK-D versus the cobble area was not significant ($F_{1, 12} = 1.207$, $P > 0.25$). Thus, the lower overall numerical abundance at the kelpless cobble area was due largely to the presence of fish above the bottom at SOK. The integrated total biomass of fish did not differ significantly among the three areas ($F_{2, 11} = 0.25$, $P > 0.75$), even though the point estimate of 2.4 kg/100 m² at the cobble area was lower than both values at SOK. However, barred sand bass made up over 70% of fish biomass in the cobble area, so most other species were much less abundant there.

We estimated the density of *Macrocystis* plants >1 m tall to be 7.51 ± 0.71 (1 SE) plants/100 m² at the "kelpless" cobble area, 23.11 ± 1.47 plants/100 m² at SOK-U, and 30.18 ± 1.69 plants/100 m²at SOK-D. Thus, some kelp was present at the cobble area, but the density of subadult-adult plants there was 25-32% of density in our kelp-bed areas.

DISCUSSION

Sampling

Regardless of water clarity, our camera and film were unable to resolve fish beyond 3-4 m; this set an upper limit of just over 1,000 m³ to cinetransect volume. Alevizon and Brooks (1975) noted that in very clear, shallow waters, fish seemed difficult to distinguish on film beyond 5 m. Ebeling et al. (1980b) found camera range to be 3-3.5 m at horizontal visibilities of 4 and 15 m, and concluded that there was essentially no relation between camera range and horizontal visibility. Our data show this to be true at visibilities >7-9 m. The fixed focal length of the camera, shallow depth of field at maximum aperture, and quality of film account for the limited camera range, as discussed by Ebeling et al. (1980b). However, our data show that camera range decreases when visibility decreases to values that approach maximum camera range. Corrections for visibility are common in terrestrial line transects, whether the area of a given transect is taken as fixed throughout or as variable (Caughley 1977; Burnham et al. 1980). We regarded the volume of a given cinetransect to be fixed, its width determined by visibility.

The relatively low upper limit to camera range may help to make cinetransects in the water column more accurate than visual censuses. Searching efficiency would likely be poorer for broad visual transects made to the limits of visibility. Furthermore, it is difficult to judge arbitrary smaller distances in open water, unless they are only a meter or two on either side of the diver. Cinetransects provide an almost automatic upper limit to transect width, and this limit is wide enough (about 3 m to either side in moderately clear water) that a substantial volume of water is censused.

We have not verified the exact volume sampled in each of our cinetransects, nor are we able to compare densities measured in cinetransects with actual densities (Brock 1982), since the latter have not been measured by any method. To our knowledge, only Keast and Harker (1977) have actually marked the outside boundaries of visual underwater transects. However, Terry and Stephens (1976) and Stephens

and Zerba (1981) utilized two divers, swimming parallel, unmarked courses and counting fish between each other, to sample rocky-reef fishes. Perhaps such a method could be used to evaluate densities estimated in cinetransects.

Species Composition, Distribution, and Abundance

The species observed in the San Onofre kelp forest were a subset of the species found in other nearshore areas of hard substrate and vegetation off southern California. Many reef-dependent fishes that are very common in other kelp forests were either rare or unrecorded at San Onofre. Species such as blacksmith and opaleye (Ebeling and Bray 1976; Hobson and Chess 1976), garibaldi (Clarke 1970), painted greenling (DeMartini and Anderson 1979), and some species of *Sebastes* (Larson 1980) depend on rugose reefs for shelter or spawning sites. Some turf-grazing and otherwise bottom-feeding species of embiotocids also appeared to be less abundant at San Onofre than in other areas. Our estimates of 14-37 kg/ha of pile perch, 38-78 kg/ha of black perch, and 10-18 kg/ha of rubberlip seaperch were mostly smaller than the estimates of Ebeling et al. (1980b) off Santa Barbara and Santa Cruz Island. The rarity and low abundance of all these species markedly alters the character of the fish assemblage at San Onofre.

The abundant species at San Onofre kelp forest either are less dependent on rock reefs (at least, if kelp is present) or associate preferentially with low-relief substrates. The former group might include the canopy species, the cosmopolitan kelp bass and señorita, and perhaps the epibenthic California sheephead. The latter group might include barred sand bass and white seaperch. These two species (and perhaps señorita) were more common at San Onofre than others (Ebeling et al. 1980a, b) have reported in kelp forest anchored on high-relief substrates. Barred sand bass occurred in over half of the bottom transects at SOK, but in no more than 12% of bottom transects near Santa Barbara (Ebeling et al. 1980a). We found white seaperch in 40-60% of our transects, while Ebeling et al. (1980a) saw them on 7-42% of all transects (but 20-42% of "sandy margin" transects). Both of these species have been reported as associating with sand or the sand-rock interface (Quast 1968a; Feder et al. 1974; Ebeling et al. 1980a). Moreover, barred sand bass have a warmwater affinity (Frey 1971) and on average should be more abundant farther south in the Southern California Bight. The abundance of white seaperch at SOK may be unusually high during the

fall. At this time, white seaperch appear to use the SOK habitat for mating as well as feeding. While some individuals of white seaperch are found in kelp forests all year, much of their populations in kelp beds off northern San Diego County move offshore after fall (authors' observations).

The vertical distributions of species present at the San Onofre kelp bed were similar to patterns described in other kelp forests. Kelp perch, giant kelpfish, and, to a lesser extent, halfmoon have been recognized as water-column and canopy species (Quast 1968a; Feder et al. 1974; Bray and Ebeling 1975; Ebeling and Bray 1976; Hobson and Chess 1976; Coyer 1979; Ebeling et al. 1980a, b). Kelp bass and white seaperch have been described as members of a vertical "commuter" group of fishes in kelp forests near Santa Barbara (Ebeling et al. 1980a). The term "cosmopolite" better describes the habits of these two fishes. Señorita also fell into Ebeling et al.'s "canopy" group, but its occurrence throughout the water column was recognized by Hobson (1971), Ebeling and Bray (1975), Bernstein and Jung (1979), and others. We feel that it too should be considered a cosmopolite. Pile perch and rubberlip seaperch were also assigned to the commuter group of Ebeling et al. (1980a) and did appear above the bottom at San Onofre. However, the dense midwater aggregations of these species observed elsewhere were not present at San Onofre. Perhaps the relatively low density of these species at San Onofre was responsible for the absence of these aggregations. On the other hand, our fairly frequent observation of California sheephead well above the bottom is apparently new. Quast (1968a), in fact, noted that sheephead seem "reluctant" to leave the bottom. Barred sand bass, black perch, rainbow seaperch, and rock wrasse occurred almost exclusively on the bottom, and have been generally recognized as bottom dwellers.

Our estimates of vertically integrated standing stock were surprisingly high. Most estimates of fish biomass on tropical and temperate reefs fall into the range of a few to several hundred kg/ha (Brock 1954; Bardach 1959; Randall 1963; Quast 1968b; Talbot and Goldman 1972; Miller and Geibel 1973; Jones and Chase 1975; Russell 1977). It is encouraging that our estimates of 3.88-6.53 kg/100 m^2 (388-653 kg/ha) fell within this range. Furthermore, our density estimates for fall 1979 are generally similar to subsequent estimates made for canopy and bottom strata during the fall periods of 1980 and 1981 (E. DeMartini[7] Unpubl. data). In particular, the densities of resi-

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[7] E. DeMartini, Marine Science Institute, University of California, Santa Barbara, CA 93106.

dent species (kelp bass and California sheephead) that contributed most to biomass estimates for fall 1979 were not consistently larger or smaller, if different at all, at SOK during fall 1980 and 1981. Hence we feel that our estimates for fall 1979 are typical for SOK during this season. Furthermore, while species such as kelp bass and sheephead were most abundant at SOK-D during fall 1979, this was not always true in 1980 and 1981; the site of greater abundance switched between SOK-U and SOK-D for many species over the period of 1979-81 (DeMartini et al. footnote 6). Thus we also conclude that apparent differences between SOK-U and SOK-D during fall 1979, although perhaps statistically real, are not meaningful for our general characterization of standing stock at SOK. For this reason, we have provided data for the areas separately as brackets for our estimates of conditions in the San Onofre kelp bed in general, and do not specifically attribute the greater abundance of fishes at SOK-D to greater numerical density of giant kelp plants >1 m tall.

The surprising aspect of our standing-stock estimates is that they are as large or larger than those of Quast (1968b) in nearshore areas of greater bottom relief. Subtracting elasmobranchs, "nonresident" teleosts, and cryptic bottom species, his estimates of standing stock at two sites near San Diego were about 366 kg/ha for Del Mar and 299 kg/ha for Bathtub Rock. Thus, even though our areas at San Onofre lacked many individuals of such great contributors to biomass at Quast's sites as opaleye, blacksmith, kelp rockfish, and garibaldi, our bracketed values of biomass were of the same order to nearly twice Quast's estimates. Below, we examine three possible reasons for this perceived disparity: Bias due to sampling methods, bias due to the times and places sampled, and the possibility that there really was a relatively large standing stock of fishes at San Onofre.

Our sampling methods may have led to overestimates, or Quast's (1968b) to underestimates, of standing stock. Quast's quantitative collection at Del Mar lacked a wall net, so some fish may have escaped. Although he used transect densities for three of the abundant species in his corrected estimates, his transect method of counting fish to the limits of visibility may have led to reduced searching efficiency (as discussed above). It is less likely that we counted fish in a larger volume than we think. We may have inflated our estimates of integrated abundance by sampling the bottom stratum on different days than the water-column strata, so that the same individuals could have figured into average density in more than one stratum as distributions changed from day to day.

Such errors would have been most serious in the cosmopolitan species, and perhaps in large bottom species (like California sheephead) that also occurred in the water column. However, even in our 3 m stratum, the average numbers of señorita and white seaperch per transect (uncorrected for visibility) were greater than similar averages obtained by Ebeling et al. (1980a, b) in cinetransects off Santa Barbara, implying that these species really were abundant during the fall at San Onofre. For kelp bass, the average standing stock above the bottom was 48 ± 13 (SE) kg/ha at SOK-U and 148 ± 40 at SOK-D. These values are large fractions of our total respective estimates of about 69 and 183 kg/ha. Similarly, our estimates of sheephead biomass on the bottom alone were 23 ± 5 kg/ha at SOK-U and 75 ± 5 kg/ha at SOK-D, compared with our total estimates of about 26 and 112 kg/ha at the respective areas. We conclude that, while sampling problems may have contributed some bias to both our estimates and those of Quast's, much of the difference between Quast's estimates and ours is real, and fish really were relatively more abundant in the areas we sampled at SOK during the fall.

Our selection of sampling times and places could have led to estimates that are somewhat unrepresentative of conditions in general at San Onofre. Seasonal factors might be involved for some of our "resident" species. Dense concentrations of some fishes (notably white seaperch) may be atypically high at SOK and perhaps other kelp beds during the fall, when these areas are used for breeding. Many species of fish can be found in kelp beds all year, but their abundances might nevertheless fluctuate greatly as individuals move among areas within kelp beds, between different kelp beds, and perhaps between different nearshore habitats. We feel that our samples accurately characterize the standing stock of fishes at San Onofre kelp in the fall, but cannot extend our observations to other seasons.

Horizontal patchiness in the distribution of fish may also have affected our estimates. Our kelp-forest sampling areas were near the offshore edge of a large area of surface canopy, and fish often were quite dense at the actual edge of the kelp forest. Limbaugh (1955), Quast (1968a), Feder et al. (1974), Hobson and Chess (1976), Bray (1981), and others have discussed this "edge effect". Although many of our transects did not (by chance) sample the edge of the bed, the averages we calculated nonetheless may have overestimated the density of some species throughout the entire bed. However, our estimates of fish density at the particular study areas should be relatively unbiased. Quast's (1968b) Del Mar collec-

tion was also made at the edge of a kelp forest, so comparison with our areas is warranted.

The comparatively large standing stock of fishes at SOK in part reflects the nature of the kelp forest off San Onofre. This kelp forest was located in relatively deep (15 m) water, and was of moderate (0.1 adult plant/m²; Dean footnote 4) kelp density, with a surface canopy. Both of Quast's (1968b) sites were located in relatively shallow (7.6-10.7 m) water. Furthermore, Quast's Bathtub Rock site lacked a surface kelp canopy. A substantial part of the fish biomass we observed at San Onofre was in the extensive canopy and midwater zones. Nearly half of the biomass occurred in the upper two strata at each site, and about one-quarter occurred in the midwater (7.6 m) stratum alone. The contribution of the upper water column to overall standing stock is also illustrated by the relative importance of the cosmopolitan species. Ranging throughout the water column, kelp bass, white seaperch, and señorita comprised about 60% of total biomass at the San Onofre kelp bed. The relative contribution of water-column species to overall standing stock would be lower in kelp forests anchored on high-relief rock, because reef-dependent species would be more abundant than at San Onofre. However, the presence of an extensive bathymetric zone from the canopy into midwaters provided space, forage, and orientation for a substantial standing stock of fishes in the San Onofre kelp bed. The lack of such an extensive midwater zone may have limited the abundance of canopy and cosmopolitan species at Bathtub Rock and Del Mar, accounting, in part, for the relatively low estimates of standing stock in these areas.

Our study, then, suggests that kelp per se can enhance the potential standing stock of fishes in an area. Our kelp-forest areas lacked a high-relief bottom and the species of fish that depend on it. The remaining fish were those that either tolerate or are not influenced by a cobble bottom, and those that depend intimately on kelp. Yet the standing stock of fishes at the San Onofre kelp bed was substantial. The reduced numerical abundance of fishes and smaller biomass (excluding barred sand bass) in our kelp-depauperate area further indicates the importance of kelp at San Onofre. Experimental manipulation of kelp density is probably the best test of the influence of kelp on fish abundance (Miller and Geibel 1973; Bray 1981; M. Carr footnote 3). We also recognize that large-scale oceanographic factors may strongly affect survivorship of planktonic larvae and the subsequent abundance of juvenile and adult fishes (Stephens and Zerba 1981; Parrish et al. 1981). However, our comparisons indicate that giant kelp, even in only moderate density, was necessary for the existence of a large standing stock of diverse fishes in cobble-bottom areas. We conclude that, while rock reefs enhance the fish fuana of an area whether or not there is kelp, the presence of kelp in an area of low-relief bottom also augments the abundance of juvenile and adult fish on a local scale. Kelp may also contribute strongly to the standing stock of fish in areas of high-relief bottom, but no one to date has adequately evaluated this hypothesis. We predict that the densities of canopy species and cosmopolites like kelp bass and señorita will also prove to be related to the density of giant kelp on high-relief bottoms.

ACKNOWLEDGMENTS

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