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SPATIAL AND TEMPORAL PATTERNS OF RECRUITMENT OF YOUNG-OF-THE-YEAR ROCKFISHES (GENUS SEBASTES) INTO A CENTRAL CALIFORNIA KELP FOREST

A thesis submitted to the faculty of
San Francisco State University
in partial fulfillment of the
requirements for the
degree
Master of Arts

Mike/Judy –
Hope you'll find some of this useful.
I sure appreciate the many conversations we've
had discussing little rockfishies, ets.
Good luck and Thanks – Mark

by

MARK HARRISON CARR

San Francisco, California

December 1983

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INTRODUCTION

The ecological requirements of fishes often differ greatly between ontogenetic stages. These differences in the ecological requirements of young-of-the-year fishes versus older age classes often reflect size-related differences in the ability to consume prey and the ability to avoid predation. Because of their small size and consequent vulnerability to predation, young fishes may associate more strongly with structural cover than do adults (Hobson 1972, 1979, Olla *et al*. 1974, Keast 1977, Werner *et al*. 1977, Helfman 1978, Bray 1980). Similarly, the young of many macro-carnivorous fishes often prey mainly on plankton because of their smaller mouth size. Thus the early life stages may be subject to an array of competitors and predator-prey interactions that differ greatly from those of adults.

Most reef-associated marine fishes possess a pelagic larval stage (Breder and Rosen 1966, Johannes 1978, Barlow 1981, Sale 1980a, Thresher 1982). The transition from the planktonic stage to the reef-dwelling post-larval or juvenile stage is critical in the life history of such species. The importance of this transition is that subsequent occupation of a reef by a species may depend on the survival of new recruits in the face of high vulnerability to predation and high dependence on prey availability. Settlement and the subsequent spatial and temporal patterns of recruitment rely on a variety of interacting factors, including (1) the seasonal reproductive cycle of adults, (2) patterns of pelagic dispersal (Johannes 1978, Barlow 1981, Bakun and Parrish 1980), (3) habitat preferences (e.g. topographical heterogeneity, algal structure, etc.) (Sale 1968, Leaman 1972, Marliave 1977, Williams 1980), (4) interactions with the resident fish community (Sale 1976), and (5) differential mortality of the newly settled fishes.

Along the coast of central California, ten or more species of rockfish (genus Sebastes) constitute a major portion of the resident ichthyofauna and sport fishery of shallow rocky reefs (Burge and Schultz 1973, Miller and Giebel 1973, Hallacher 1977). In Sebastes, females release pelagic larvae which eventually return to nearshore reefs as recently-metamorphosed juveniles (Harada 1962, Carlson and Haight 1976, Moser 1967, Boehlert 1977, Richardson and Laroche 1979, Laroche and Richardson 1980). Recent studies of the home ranges of adult reef-dwelling rockfishes indicate that individual movements are restricted to portions of a reef or to isolated reef systems (see review by Love 1980). Hence, Love (1980) suggested that adults may not play an effective role in the recolonization of depopulated reefs.

As a consequence of the limited movement of adult reef fishes, areas available for the establishment of new territories or home sites may be most often colonized by newly immigrated post-larvae or juveniles. This, and the apparent persistence with which newly settled young fish maintain territories has led many observers of tropical reef fish communities to conclude that young-of-the-year fishes play a major role in determining the species composition of tropical reefs (Randall 1963, Russell et al 1974, Gundermann and Popper 1975, Nolan 1975, Smith and Tyler 1975, Sale and Dybdahl 1975, 1978, Sale 1978, Talbot *et al*. 1978, Williams 1980, Williams and Sale 1981). Likewise, the recruitment of juvenile *Sebastes* may strongly influence the subsequent species composition of a temperate rocky reef (Gascon and Miller 1981, 1982). Though numerous authors have observed the influx of post-larvae or juveniles onto temperate rocky reefs, assessment of the habitat features required by recruits and the factors influencing their utilization has been predominantly anecdotal and qualitative (Limbaugh 1955, Quast 1968, Burge and Schultz 1973, Miller and Giebel 1973, Feder *et al*. 1974).

The present study describes the spatial and temporal patterns of recruitment of young-of-the-year *Sebastes* which seasonally occupy a central California kelp forest. The patterns addressed include (1) the seasonal occurrence of young-of-the-year *Sebastes*, (2) their vertical distribution throughout the water column, (3) the influence of substratum relief and composition on fish distributions, (4) the relative influence of the giant kelp, *Macrocystis pyrifera*, and the rocky substratum on the distributions of young-of-the-year *Sebastes* and (5) daily and seasonal changes in their distributions within the kelp forest habitat.

METHODS

I. Study Area

From May 1980 to July 1981, observations were made at a shallow rocky reef extending subtidally from Arrowhead Point, at the northern end of Carmel Bay (36° 33.6'N, 121° 56.3'W), south of the Monterey Peninsula along the coast of central California (Figure 1). Arrowhead Point is protected from the northwest swells and winds typical throughout the year, but is highly exposed to the more severe southerly winds and waves which occur during fall and winter.

The reef substratum is composed of mixed low and high relief conglomerate, sandstone and basaltic rock interspersed with coarse granitic sand (Simpson 1972). On all but the nearshore side, the reef is surrounded by sand. The reef surface varies in depth between 9 m and 13 m and is characterized by an extensive cover of encrusting coralline algae and sessile invertebrates. Understory algae are usually sparse and composed of <u>Pterygophora</u> <u>californica</u>, <u>Cystoseira</u> <u>osmundacea</u>, and a seasonally dense cover of <u>Desmerestia</u> <u>ligulata</u> var. <u>ligulata</u>. The reef supports a dense stand of the giant kelp <u>Macrocystis</u> <u>pyrifera</u> which usually increases in numbers and biomass during spring (May to July), reaches highest abundance through the summer (August to September), and diminishes rapidly with the onset of southerly storms in fall (October to December) (Gerard 1976 and pers. obs.).

II. Species Descriptions

Species distinction during the present study was based on gross morphometrics (ie. head size to body length proportions, body depth to length proportions) and on such features of color pattern as general body pigmentation, barring, dorsal fin spots and clearing of the lateral line. These characters, in conjunction with meristic measurements and grow-out studies, have been used to identify young-of-the-year of 16 species of *Sebastes* from central California kelp forests (Anderson 1983).

Data were combined for certain species whose distinction is difficult based on coloration alone. Observations described for *S. serranoides* may also have included individuals of *S. flavidus* and early recruits of *S. atrovirens*, *S. carnatus* and *S. caurinus* were initially combined until they reached sizes which were distinguishable. At night, observations of *S. melanops* and *S. entomelas* were combined.

III. Seasonal Occurrence and Water Column Distribution

To determine the vertical distribution of each species, five randomly-located 10 m transects were sampled at three depths (surface, mid-depth and bottom). Transects originated at random points along the edge of the kelp forest, and extended perpendicularly into the forest. Surface transects covered an area 1 m wide by 1 m deep below the water surface. Transects at mid-depth (5 m to 7 m) included an area 1 m wide by 2 m deep. Transects along the bottom were 1 m wide and extended 1 m above the bottom. Fishes occupying the water column at depths other than these discrete levels were not sampled. Transects were sampled in order of increasing depth so as not to disturb fishes with the ascending bubbles of the observer's SCUBA.

Monthly samples during the period of May 1980 to March 1981 included one day of transect observations per month. Monthly samples from April 1981 to July 1981 consisted of two days of sampling per month. Distributions of the transect values were highly skewed due to the aggregated spatial distributions of all nine species sampled. Therefore the data were log-transformed ($Y = \log_{10}(X+1)$) and the means and 95 percent confidence intervals presented were back-transformed (Sokal and Rohlf 1969).

On each census date, sea surface conditions were recorded along with water temperature and horizontal visibility at each depth. Underwater visibility was estimated by measuring the greatest distance along a meter tape at which a 22 cm diameter, white plastic disc was distinguishable. Sampling was conducted only on days when horizontal visibility was 3 m or greater. The possible influence of horizontal visibility on sampling efficiency was tested by comparing the rank order of fish abundances versus visibility of each sample with the Spearman rank correlation test (Siegel 1956).

Seasonal trends of coastal upwelling and the occurrence of young *Sebastes* at Arrowhead Point were compared.

Estimates of mean monthly upwelling intensity were measured by the NOAA/NMFS Pacific Environmental Group (Monterey, California, at a site 63 km south of Arrowhead Point (A. Bakun; unpublished data). Timing of the occurrence of upwelling within the kelp forest at Arrowhead Point was measured by recording water temperature at the three transect depths on days of monthly censuses. Arrowhead Point surface temperatures were compared with surface temperatures collected by the California Department of Fish and Game at the Granite Canyon Mariculture Laboratory located 9.3 km south of Carmel Bay. Because the Granite Canyon data were more frequently and routinely collected, these data were ranked and compared with the ranked monthly upwelling estimates using a Spearman rank correlation test. Monthly upwelling estimates were then compared with monthly abundances of young-of-the-year Sebastes with the same test.

IV. Influence of Macrocystis pyrifera on Fish Distributions.

The influence of the vertical fronds of M. pyrifera on the distributions of fish within the water column was assessed by recording the proximity of observerved fish to the nearest M. pyrifera frond. As fish were encountered along surface and mid-depth transects, the proximity of each fish to the nearest vertical frond was classified as either (1) > 0.5 m from fronds, (2) between 0.25 m and 0.5 m from fronds, (3) < 0.25 m but not in contact with fronds, or (4) in contact with fronds.

Within the surface portion of the water column the overlapping fronds of M. pyrifera form a canopy of greater density than the vertically-ascending fronds. To assess the influence of the canopy on fish distributions, fishes were censused at a nearby kelp forest where the canopy was artificially removed by a commercial kelp harvester. Kelp harvesting conducted on July 24,1981 removed all of the M. pyrifera from the upper 2 m of the water column within a swath approximately 20 m wide. Transects 1 m x 1 m x 10 m were swum along random compass bearings through the upper 1 m of the water column and individuals of each species were visually censused. Transects were made before and after cutting, in the harvested area and in an inshore non-harvested (control) area. Mean abundances (all species combined) from transects in the harvested and control areas before harvesting and the control area after harvesting were compared with the Kruskal-Wallis non-parametric analysis of variance (Sokal and Rohlf 1969). The two areas were to be resampled later in October, but by this time the control canopy had been cleared by a storm, and no fish were present at either site.

VI. Substratum Utilization

I categorized microhabitats on the bottom with regard to algal occurrence (M. pyrifera and drift algae) and bottom relief, (high relief rock (> 1 m), low relief rock (< 1 m) and sand). In assessing habitat availability and habitat utilization, each microhabitat category was evaluated independently, by presence or absence. Availability of substratum types and drift algae was determined from 103 random 1 m^2 quadrats within the 250 m^2 area sampled. These data were collected once, during August 1981. Though the abundance of drift algae changed seasonally, its distribution was limited to similar low relief habitats throughout the year. Availability data for _M. pyrifera_ were not collected in the same manner. Instead, the kelp transplant experiment (section VII) was conducted to assess fish associations with _M. pyrifera_.

Utilization of each habitat component was determined by recording the presence or absence of that component within a 1 m^2 area projected around each fish encountered during transects. Utilization data for the periods June-September and October-May are presented seperately due to the observed shifts in microhabitat associations subsequent to the removal of much of the _M. pyrifera_ during October storms. Quadrats of mixed relief (i.e. low/high rock or sand/low/high rock) were divided into and apportioned evenly between their contributing categories in order to simplify the presentation of data. This procedure had little effect on the values for utilization, availability, and electivity of microhabitats.

The presence of a species in a microhabitat category was compared with the number of individuals observed. This was done to offset the possible bias of making a few observations of large aggregations transiently occupying a habitat. A Spearman rank correlation coefficient (Sokal and Rohlf 1969) was used to compare the rank order of habitat usage by percent number of individuals versus percent number of observations. Significant differences in orders would suggest that disproportionally few observations were made of large numbers of individuals within a particular habitat type.

The degree to which each species was distributed randomly among the various substratum categories was assessed using a two-way (single classification) goodness of fit test (Sokal and Rohlf 1969). The expected utilization of each substratum type by a species was calculated from the percent availability of that substratum type times the total number of individuals of the species observed.

To assess electivity toward particular substrata, Strauss' (1979) Linear Food Selection Index (L) was calculated. This index, originally designed to determine prey preference, compares the availability of a resource with the utilization of that resource by a species or individual. In this case, substratum types were substituted for prey items in the following equation:

$$L = r_i - p_i$$

where L is the measure of selection, r the relative utilization of substratum type i (expressed as the proportion of individuals of a species occupying that substratum type), and p is the proportionate availability of substratum type

i. The index ranges from -1 to 1 with negative values indicating avoidance or inaccessibility of a substratum type, zero indicating random distribution among substratum types, and positive values indicating utilization greater than that expected from random. The index has an approximately normal distribution (Strauss 1979) and the variance can be calculated, allowing the statistical comparison of a calculated selection value (L) and a standard value (in this case zero) with the t-test (Sokal and Rohlf 1969).

Similarities in habitat utilization among bottom species was measured with the Percent Similarity Index (PSI) (Whittaker 1952). Cailliet and Barry (1978), Bloom (1981), and Feinsinger, et. al. (1981) independently concluded that PSI was the least biased similarity (overlap) index, accommodating the widest range of sampling distributions. PSI is calculated by summing the minimum of the paired utilization values of each substratum type:

$$PS = \min(p_{ij}, p_{ik})$$

where p is the proportion to which species j and species k utilize substratum type i. Using this equation the values range between 0 and 1.00 with increasing values representing a greater degree of similarity (overlap) in utilization of substrates. Species groups based on similar utilization of substratum types were calculated from matrices of PSI values with the unweighted pair-group method using arithmetic averages (Sneath and Sokal 1973).

VII. Relative Importance of _Macrocystis_ _pyrifera_ Versus Rock Substratum

The relative importance of _M_. _pyrifera_ versus the rock reef substratum on recruiting _Sebastes_ was assessed by experimentally isolating the _M_. _pyrifera_ and rock components. During the first week of May 1981 all of the _M_. _pyrifera_ was removed from a 112 m^2 reef near Arrowhead Point that was 10 m to 13 m deep. Eighteen of the removed plants were transplanted to an area of sand bottom located between the denuded reef and the non-manipulated reef at Arrowhead Point (Figure 2). The holdfasts of the transplants were sewn to a 1.6 cm (5/8") polypropylene line with 0.32 cm (1/8") nylon cord. The polypropylene line was secured to the bottom by an equilateral triangular pattern of sand anchors (Figure 3). The total area of the triangle was 62 m.

The kelp-transplanted area was sampled once in May (20), twice in June (8, 9), twice in July (1, 11) and once in August (19). The surface canopy was sampled by counting all rockfishes occurring in 1 m x 11 m transects along random bearings originating from the offshore apex of the triangle. The number of transects sampled each day varied (June n=6/day, July n=5/day, August n=4/day) as increased numbers of individuals and species greatly increased the time spent on each transect. Mean abundance and 95 percent confidence intervals for each species were calculated from $\log_{10}$-transformed counts and then extrapolated to densities per total canopy area (mean number of fish per 11.0 m transect multiplyed by 5.67 to estimate the number of fish per total 62.35 m^2 area). Total abundances at mid-depth were determined by sampling the entire length (from 1 m below the surface to 1 m above the holdfast) and within 1 m of each *M. pyrifera* plant and counting the few individuals not adjacent to the *M. pyrifera* fronds. Abundances at the bottom were determined by censusing each holdfast (including 1 m around and above the holdfast) and any individuals not in close proximity to holdfasts within 1 m of the sand bottom.

The denuded reef was sampled by partitioning the water column directly above the reef into three sections (surface, mid-depth, and bottom) similar to the transplant site and censusing the entire area within each section. The seasonal occurrence data from the non-manipulated site were used for comparison. The denuded reef and the non-manipulated reef were sampled within a day of the kelp transplant site.

VII. Distributional Changes Associated with Diel Activity

Based on movement patterns of fishes observed during four sunrise and four sunset periods of August 1980, permanent transects 1 m wide x 1 m deep x 20 m long were established at three depths (surface = 0 m, mid-depth = 9 m, bottom = 13.5 m) within three locations parallel to the edge of the kelp forest (3 m inside, along the kelp-sand interface, and 3m outside). Sampling was conducted during ten nights from 10 July to 26 August 1981. All nine transects were censused before, during and after the dusk transitional period of the same day. The crepuscular period was subjectively determined since heavy and variable fog altered ambient light intensity relative to the time of actual sunset. The mean number of individuals of each species at each location, depth and time was calculated from censuses on different nights. Means and 95 percent confidence intervals were calculated from $\log_{10}(X+1)$ transformed data.

RESULTS

The results are presented by combining species into three groups based on similarities of adult distributions (onshore versus offshore) and the observed distributional patterns of recruiting young-of-the-year (species aggregating in the water column, versus benthic solitary species). Young of ten *Sebastes* species were recorded from the Arrowhead Point kelp forest during the 1980 and 1981 recruitment periods. Adults of three species (*S. miniatus*, *S. paucispinis* and *S. pinniger*) occur more commonly in deeper offshore waters (Miller and Lea 1973). Adults of the other six species (*S. atrovirens*, *S. carnatus*, *S. caurinus*, *S. melanops*, *S. mystinus*, and *S. serranoides*) all occur commonly in central California kelp forests (Hallacher 1977).

I. Seasonal Occurrence and Water-Column Distribution of Young *Sebastes*

Sea conditions during days used in monthly censuses were similar, almost always characterized by clear sunny skies with 0.0 m to 0.3 m surface swell. Underwater horizontal visibility varied between 3 m and 10 m (surface), 3 m and 11 m (mid-depth) and 5 m to 11 m (bottom). Reduced water clarity was usually due to one of three factors: (1) phytoplankton (2) bottom sediments suspended by wave surge, or (3) particulate matter derived from the degradation of the *M. pyrifera* canopy in late summer.

There was no significant correlation between visibility and fish counts as measured with the rank correlation coefficient (r_s) (fish abundance of all species combined versus horizontal visibility at each depth; surface $r_s = -0.22$; mid-depth $r_s = -0.24$; bottom $r_s = 0.15$). Clearest days occurred during winter and early fall when young-of-the-year were least abundant.

The immigration of newly recruited *Sebastes* to Arrowhead Point was associated with seasonal trends of coastal upwelling. The local occurrence of upwelling at Arrowhead Point was indicated by abrupt decreases in water temperature. Seasonal water temperatures at Arrowhead Point were similar to monthly temperatures recorded at Granite Canyon Mariculture Laboratory (Figure 4), which in turn exhibited an inverse correlation with monthly estimates of upwelling ($r_s = -0.80$) (Figure 5).

Initial recruitment of many of the young-of-the-year *Sebastes* occurred just after the month of strongest upwelling (May) during 1980 and 1981 (Figure 5). Monthly upwelling estimates and young-of-the-year abundance were positively correlated ($r_s = 0.76$) when adjusted for a one month delay for fish abundance.

During 1980, young-of-the-year *S. melanops*, *S. mystinus* and *S. serranoides* arrived in late May and occurred throughout the water column in small numbers. During the remainder of the summer, all three species occured in much larger aggregations within the lower portion of the water column (Figure 6). Numbers of *S. mystinus* and *S. serranoides* reached peak abundance during late spring-early summer, while *S. melanops* seemed to be most abundant during late summer. The rapid decrease of all three species during October coincided with the onset of southerly storms. Few young-of-the-year *S. serranoides* and *S. melanops* were observed again in the kelp forest until the recruitment in spring of 1981. *S. mystinus* was slightly more abundant than the other two species through the winter period.

All three species recruited much more strongly in 1981 and seemed to occur more widely throughout the water column (Figure 6). Again, *S. mystinus* occurred in greatest numbers near the bottom, though many fish also occurred at mid-depth. Unlike the apparent concentration of *S. serranoides* near the bottom in 1980, greatest numbers occurred at mid-depth in 1981. As in 1980, all three species initially recruited in late May with the majority of *S. melanops* not appearing until after censusing was terminated in July.

S. atrovirens, *S. caurinus*, and *S. carnatus* are more benthic and solitary as adults, and exhibit similar patterns of recruitment. All three species initially occurred in the *M. pyrifera* canopy at different but overlapping times (Figure 7). During 1980 I was not able to distinguish between the small individuals of *S. carnatus* and *S. caurinus* occupying the kelp canopy. Therefore data for these two species at the surface are combined. Individuals occurring at mid-depth and the bottom were usually larger, and more easily distinguished, so data for the two species at these levels are presented separately. The combined species initially occurred in the canopy in late May and increased in numbers through July. As numbers decreased in the canopy, they increased at mid-depths and near the bottom, indicating a gradual movement of each species from the surface to the bottom over separate one-month periods. Individuals of *S. caurinus* at all three levels of the water column were generally larger than those of *S. carnatus*, suggesting either earlier recruitment or faster growth rates for *S. caurinus*.

Like the water-column aggregating species, recruited abundances of *S. carnatus* and *S. caurinus* were greater in 1981 than in 1980 (Figure 7). During 1981 I was able to distinguish between the two species at the surface as well as at mid-depth and on the bottom. *S. caurinus* initially occurred in April, as opposed to May in 1980, and increased dramatically by June. This early recruitment preceded the annual reestablishment of the kelp canopy that year. Individuals of *S. caurinus* were first seen in aggregations over drift *M. pyrifera* on the bottom. Later, with subsequent development of the kelp canopy, highest abundances again occurred in the canopy, though relatively large numbers simultaneously inhabited the mid-depth and bottom portions of the water column. As numbers of *S. caurinus* decreased in the canopy in late June and July, numbers of *S. carnatus* increased. Though the trend of surface to benthic migration was not as evident in data for *S. caurinus*, it was repeated by *S. carnatus*.

S. atrovirens also occurred first in the upper water column, though later in the summer than S. caurinus and S. carnatus. S. atrovirens recruited in much higher numbers than S. carnatus and S. caurinus during 1980, and the surface to benthic migration was more clearly indicated (Figure 7). In 1981, censusing was terminated before the period of highest recruitment of S. atrovirens. During subsequent qualitative observations from August to September, I witnessed a large increase of early recruits similar to that described for 1980.

Of the three species whose adults occur offshore, S. paucispinis recruited within the surface portion of the water column while S. miniatus and S. pinniger remained on or near the bottom (Figure 8). S. paucispinis and S. pinniger first appeared in the kelp forest in May, increased in abundance through June, and gradually decreased over the remainder of the summer. This pattern of seasonal abundance was repeated by both species during 1981. S. miniatus recruited in much smaller numbers than the other two offshore species and was rarely observed during the May to July period of highest abundances for S. paucispinis and S. pinniger. S. miniatus occurred sporadically during the winter months (Figure 8).

II. Influence of Macroysitis pyrifera on Fish Distributions

The kelp forest in which microhabitat associations were determined was characterized by a few aggregations of large

M. pyrifera plants with numerous fronds. These aggregations were separated by extensive areas of open water. I estimated that kelp fronds below the canopy comprised only 30 percent of the planar area in the kelp forest.

At the surface, a number of species exhibited a tendency to aggregate in close proximity to the ascending fronds. Random distribution of fishes at the surface would result in encounters with fish near vertical fronds in proportion to the availibility of fronds (estimated at 30%). However, nearly 50% of all the *S. atrovirens*, *S. melanops*, and *S. caurinus* observed were within 0.25 m of the vertical fronds (Table 1). Approximately 58% of the *S. carnatus* occurred within 0.5 m of vertical fronds, suggesting a similar affinity to the cover developed by these fronds as opposed to the canopy-forming horizontal fronds. *S. paucispinis* and *S. serranoides* exhibited little affinity for vertical fronds. Only 34% and 21%, respectively, occurred within 0.5 m of vertical fronds.

At mid-depth, several species were more strongly associated with the vertical fronds of *M. pyrifera* (Table 1). Of the three solitary benthic species, all of the *S. atrovirens* and *S. caurinus* encountered occurred within 0.25 m of fronds and *S. carnatus* was always observed in contact with fronds. The shift toward stronger affinity with the *M. pyrifera* fronds at mid-depth reflects the absence of the kelp canopy refuge present at the surface. This affinity for fronds at mid-depth is further reflected by the lack of observations of *S. carnatus* and *S. caurinus* at mid-depth during 1981 when both species were actually more abundant but *M. pyrifera* fronds were less frequently encountered by transects than in 1980.

At all three depths, the three water-column aggregating species were less strongly associated with *M. pyrifera* fronds than the solitary benthic species (Table 1). In 1980, when fish occurred singly or in small aggregations, 98% of the *S. melanops* occurred within 0.25 m of the *M. pyrifera* stipes. In contrast, during the higher recruitment of this species in 1981, few individuals were observed near the stipes, but were seen more frequently in large aggregations at the edge of the kelp forest. *S. mystinus* rarely occurred at mid-depth when the stipe affinity data were collected. Large numbers were observed at this depth during the following year (1981) and individuals observed during that period exhibited a stipe affinity very similar to *S. melanops* (during 1980) in which many individuals aggregated close to, but not in contact with the *M. pyrifera* stipes. Only 12% of the *S. serranoides* encountered were within 0.5 m of the *M. pyrifera* stipes. This species exhibited the least affinity toward vertical fronds of the water column aggregators. *S. paucispinis* occurred frequently (80%) within 0.5 m of the stipes, but rarely closer than 0.25 m. Encounters with this species were primarily of solitary individuals. Aggregating individuals exhibited a greater tendency to avoid stipes in the water column, similar to aggregations of

S. serranoides.

The high degree of frond affinity exhibited by species occupying the surface portion of the water column, suggested that the kelp canopy constituted an important form of cover. Therefore the canopy was experimentally removed to assess its affect on fish distributions. The canopy removal experiment indicates that at least five species may be influenced by the presence of the canopy microhabitat. Three species, S. atrovirens, S. carnatus, and S. caurinus comprised 87.5% of the total number of inidivduals (n = 454) censused prior to kelp-canopy removal. Of this proportion, numbers were not attributed to each species because they could not be reliably distinguished from each other at the time of sampling. The remaining 12.5% consisted of S. melanops (6%), S. paucispinis (4%), and S. serranoides (2%).

For all species combined, the mean numbers (and 95% confidence intervals) of individuals per transect in the control and harvest areas before harvesting were 10.1 (±2.4) and 7.1 (±1.9), respectively. Five days after harvesting, the mean number of individuals per transect in the control and harvest areas were 10.3 (±2.8) and 0.0, respectively (Table 2). The rank order of transect means of the control area before harvesting, the harvested area before harvesting and the control area after harvesting did not differ significantly (Kruskal-Wallis $p < 0.05$, $H/D = 4.43$). In contrast, the dramatic reduction of newly recruited rockfish numbers in the post-harvest area negated the need for statistical testing.

Upon harvesting, no M. pyrifera fronds were encountered on any of the surface transects sampled in the harvested area. Cursory observations lower in the water column of the harvested area detected no obvious increase in abundances of the canopy-associated species. Displaced fishes may have moved horizontally to areas of undisturbed canopy.

III. Substratum Utilization

Occurrence (availability) of the five substratum types varied as follows; sand/low rock (32%), high rock (29%), sand/high rock (22%), low rock (15%), and sand (1%) (Figure 9a). Drift algae occurred predominantly with sand/low rock and sand/high rock. These two habitats are characteristic of the reef-sand interface, where drift algae accumulates. Though only qualitatively assessed, M. pyrifera plants occurred predominantly on low rock and high rock. Availability of the algal components was not quantitatively reassessed after the fall storm period. The abundance of M. pyrifera and drift algae diminished during fall storms but the remaining plants and drift material were dispersed among the same substratum categories as before the storm.

With the onset of fall storms and the removal of much of the drift algae and M. pyrifera plants, many young-of-the-year Sebastes either left the kelp forest entirely or shifted microhabitat types. For those species which exhibited noticeable habitat shifts the substratum utilization data are presented separately for periods before and during the storm season (June to September versus October to May).

The two offshore benthic species, S. miniatus and S. pinniger, exhibited similar patterns of substratum utilization (Figure 9a). Young-of-the-year S. miniatus exhibited positive electivity toward the sand/low rock substratum type (82%) and was also frequently observed over the sand only substratum type (15%). The utilization of the sand habitat by S. miniatus was probably underestimated due to the few samples taken there. Young S. pinniger occurred primarily over sand/low rock (56%), sand/high rock (17%) and sand (12%) with significant positive electivity for the sand and sand/low rock habitats (Figure 9a; Table 3). Both species were rarely observed associated with any algal component (Figure 9a).

Disributions of the three solitary benthic species differed from one another (Figure 9b). Young of S. caurinus occurred predominantly in the sand/low rock (50%), sand (28%) and low rock (15.5%) substratum types and were almost always associated with drift algae (88%) (Figure 9b). The high co-occurrence with drift algae suggests that young S. caurinus were attracted to the substrata where drift M. pyrifera accumulated. However, with the onset of fall storms and the removal of most of the drift material, the few remaining young-of-the-year still occcupied the sand/low rock substratum type. This continued association with the sand/rock habitat after removal of the drift material suggests an underlying affinity toward the reef-sand interface. Significantly high electivity was exhibited toward the sand and sand/low rock habitats prior to the storms and to the sand/low rock habitat during and after the storm period ($p < 0.05$; Table 3).

Young-of-the-year S. carnatus predominantly occupied the sand/low rock (40%) and low rock (39%) substratum types and exhibited an algal affinity divided between drift algae and M. pyrifera plants (Figure 9b). Later, during and after the fall storms, individuals were most frequently observed in cracks and crevices within the high rock relief (71%). Electivity toward these substratum types was significantly positive ($p < 0.05$; Table 3).

The majority of S. atrovirens young-of-the-year occurred in the low rock (59%) and high rock (38%) substratum types and were almost always associated with M. pyrifera plants (Figure 9b). With the onset of fall storms, many (63%) of the young fish observed had abandoned the M. pyrifera plants to take cover in low rock (36%), high rock (27%) and high rock/sand (22.5%) habitats. Electivity toward all but the latter two of these substratum types was significantly positive ($p < 0.05$; Table 3).

Young of the three species which constitute the water column aggregating group exhibited high overlap of substratum type utilization, yet their affinity toward M. pyrifera differed distinctly. Young S. mystinus displayed significantly positive electivity toward the high rock (35%) and low rock (28%) substratum types ($p < 0.05$; Table 3). This species occurred predominantly over bare substratum and rarely associated with any algal component within the bottom portion of the water column (Figure 9c).

Young-of-the-year *S. melanops* exhibited patterns of substratum utilization which were very similar to that of *S. mystinus*. Significant positive electivity was calculated for the high rock (44%) and low rock (30%) substratum types (table 3). However, the majority (70%) of the *S. melanops* observed were aggregated closely around the lower portions of *M. pyrifera* plants (Figure 9c). The few *S. melanops* encountered during and after the fall storms had shifted to bare substratum habitats and were no longer associated with *M. pyrifera*.

S. serranoides young-of-the-year occurred in similar proportions over all four substratum categories which contained a rocky component; low rock (35%), sand/high rock (26%), high rock (22%) and sand/low rock (21%) (Figure 9c). The high utilization and proportionally low availability of the low rock habitat resulted in significantly positive electivity ($p < 0.05$) toward this substratum type (Table 3). Electivity toward the sand/high rock substratum was also significantly positive ($p < 0.05$; Table 3) as a result of this species' tendency to aggregate amid high relief rocks in areas of reduced water movement where sand and drift algae accumulated.

Species with the highest percent similarity (overalap) values for substratum utilization also displayed relatively lower fidelity toward the reef surface and/or differences in affinity for algal components. The three water column aggregators frequently utilized other portions of the water column (Section I) and differed by their affinity for *M. pyrifera* (Figure 9c). Percent Similarity values for these three species were the highest calculated (Table 4). Likewise, the next highest P. S. value was calculated for two species (*S. caurinus* and *S. pinniger*) which occupied similar substratum types but differed strongly in their affinity toward drift algae. The three solitary benthic species (*S. atrovirens*, *S. carnatus* and *S. caurinus*) were similarly attracted toward some type of algal cover and exhibited the least overlap of substratum utilization (Table 4).

Comparison of species similarities based on substratum utilization produced groups which correspond with the previously-described groupings based on adult and young-of-the-year distributions (Figure 10). The three water column aggregators were clustered closest together. The two offshore species clustered together with *S. caurinus*, indicative of their co-occurrence along the reef-sand interface. *S. atrovirens* and *S. carnatus* remained separate from the other species and were most closely associated with *S. melanops* due to their like associations with *M. pyrifera*.

IV. Relative Importance of *Macrocystis pyrifera* Versus Rock Substratum

Kelp Only Habitat

Young-of-the-year of seven _Sebastes_ species were recorded during the twelve weeks of observation in the transplanted kelp habitat (Table 5). Two species, _S. mystinus_ and _S. serranoides_, occurred infrequently and in very low numbers. The other five species, _S. atrovirens_, _S. carnatus_, _S. caurinus_, _S. melanops_ and _S. paucispinis_ were attracted in greater numbers and occurred there consistently.

The three solitary benthic species displayed similar patterns of seasonal abundance and water column distribution in the manipulated (kelp only) and unmanipulated (kelp/rock) sites (see Section I). Data for _S. carnatus_ and _S. caurinus_ at the surface and the first three months at mid-depth are again combined due to my inability to distinguish them at that time. Initial recruits of _S. atrovirens_ at the surface in July are also combined with the other two for the same reason. By early August, _S. atrovirens_ was distinguishable from the others at all three depths. It was then apparent that _S. atrovirens_ was responsible for the majority of the high combined-species densities at the surface during the previous sample (late July). _S. caurinus_ contributed little to the numbers in the canopy then, but increased at mid-depth and the bottom. By early August, no _S. carnatus_ or _S. caurinus_ were observed in the canopy. Numbers of _S. caurinus_ had also decreased at mid-depth and increased dramatically at the bottom. Hence, the gradual surface-to-bottom migration was more easily discernible at this site than the non-manipulated site. Sampling was terminated before inidividuals of S. carnatus migrated to the bottom.

Sebastes melanops recruited at similar depths as observed at the kelp-rock site, with the majority of individuals aggregating around kelp holdfasts near the bottom. This algal affinity supports the observed high utilization of M. pyrifera by this species during the substratum utilization study. As observed at the kelp-rock site, S. paucispinis recruited into and remained in the surface portion of the water column with fewer numbers occurring at mid-depth.

Rock Only Habitat

Of the six species observed at the rock only site, only two were also observed at the kelp only site. The two species which also occurred at the kelp only site (S. carnatus-caurinus type) were observed inconsistently at the rock only site and were always strongly associated with drift algae at the reef-sand interface. The other four species, S. miniatus, S. mystinus, S. pinniger and S. serranoides, displayed stronger affinity with the bare rock substratum and occurred there more consistenly (Table 5). These four species exhibited little algal association during the substratum utilization study (Table 6). S. pinniger was the only species to recruit to the rock only habitat in relatively high numbers (Table 4). Young-of-the-year S. miniatus were observed during February and March, though no observations were made during November through January, at which time they may have also occurred there.

Rock and Kelp Habitat

Relative abundances of those species which recruited to the kelp-rock habitat is represented by the seasonal occurrence data (Section I) collected in the non-manipulated site concurrently with the sampling of the two manipulated sites. All nine species of youn-of-the-year were observed in relatively high numbers in this habitat and remained there through the duration of biweekly observations at the three sites. Their occurrence at the non-manipulated site indicates that recruits of each species were available in the general area, so the recruitment patterns in the manipulated sites can not be explained by lack of potential recruits.

Results from the kelp transplant experiment support the previously-described affinities of some *Sebastes* species toward *M. pyrifera* and/or drift algae (Table 6; see Sections II and III). Each of these species displayed associations with an algal component during frond affinity and/or substratum utilization observations. Species which occurred at the rock only site exhibited little algal affinity during previous observations.

VI. Distributional Changes Associated With Diel Activity

Young-of-the-year of eight *Sebastes* species exhibited some change of spatial distribution at dawn and dusk (Figure 11). Those species which moved least were the solitary benthic species. With the onset of darkness these three species gradually moved closer to the structural cover nearest them, often becoming concealed among M. pyrifera fronds or the rock substratum. This resulted in lower abundances recorded during the transition period and especially afterwards (nocturnal period) (Table 7). Such reductions within the same locations throughtout the water column were not indicative of large scale movements through the water column or outside the kelp forest. Unlike the other two benthic species, large numbers of S. caurinus remained exposed along the reef interface through the crepuscular period.

As ambient light decreased through the crepuscular period, the three water-column aggregating species gradually vacated the mid-depth portion of the water column and increased numerically along the bottom (Table 7). Young-of-the-year S. mystinus restricted their vertical descent to the rocky reef below. S. serranoides and S. melanops descended to the reef surface but some individuals also aggregated along the reef interface at dusk and eventually moved on to the adjacent sand bottom at night. Abundances recorded for S. melanops over the sand at night are overestimated due to the inclusion of another species (apparently S. entomelas; Todd Anderson pers. comm.) in these counts (Table 6). Apparently S. entomelas, which was never observed in the Arrowhead Point kelp forest, settles over the sand bottom adjacent to the reef interface at night. The large number of S. serranoides observed at the surface along the margin of the kelp canopy at night were larger (1 year old) individuals and were not young-of-the-year recruits.

Only one of the three offshore species was numerous enough to quantitatively describe changes of distribution. S. pinniger exhibited a marked nightly migration from the rock reef out onto the adjacent sand bottom (Figure 11a). Though individuals of S. paucispinis were occasionally observed actively moving below the kelp canopy at night, their numbers were too few to quantify. Similarly, S. miniatus was only rarely encountered along the reef-sand interface at night.

With the gradual increase of ambient light at dawn, all eight species exhibited a direct reversal of the movement patterns described for the evening transition. The crepuscular period was the time of greatest movement and individuals were usually in their new locations by the beginning of the subsequent diurnal/nocturnal period.

DISCUSSION

Seasonal Occurrence

The seasonal recruitment of young-of-the-year *Sebastes* into shallow kelp-forest habitats appears to be strongly influenced by coastal hydrographic conditions, particularly upwelling. Parturition for most rockfishes, including those studied here, occurs during late winter and early spring (Table 8). At this time, offshore surface transport is reduced and surface currents are predominantly shoreward (Bakun and Parrish 1980, Parrish *et al*. 1981). Bakun and Parrish (1980) noted a possible inverse relationship of young-of-the-year *Sebastes* abundance with upwelling intensity along the California coast. Years of increased upwelling were characterized by poor nearshore recruitment, and years of reduced upwelling corresponded with times of high recruitment. Hence, Bakun and Parrish (1980) have suggested that the reproductive seasonality of *Sebastes* may be in response to the "problem" of maintaining larvae within close proximity to the shore.

Other hydrographic phenomena, such as shifts of water masses of different temperature, may influence the local occurrence and abundance of recruits to an area. This relationship may explain annual changes in numerical dominance between the recruiting young of *Sebastes dalli* and *S. saxicola* off southern California (Mearns *et al*. 1980). Probably also important to small scale patterns of recruitment of young-of-the-year are localized nearshore currents (ie. eddies and local upwelling).

In the present study the initial recruitment of some of the young Sebastes to shallow reefs corresponded with the initiation of coastal upwelling. However, annual recruitment at Arrowhead Point did not vary predictably with differences in upwelling duration or intensity in 1980 and 1981. Both years were characterized by similar degrees of upwelling, but in 1981 recruitment of all nine species was much stronger than the previous year. Also, a one month delay between the peak upwelling period and the initial occurrence of young was observed in both years. Within the seasonal restrictions presumably established by net on-offshore transport of pelagic larvae, other factors may be important in defining the timing of parturition and nearshore recruitment of the different Sebastes species.

Interspecific differences in the seasonal occurrence of the Sebastes recruits and the observed specificity for particular microhabitats suggests that microhabitat availability may be an ultimate influence on the temporal patterns of parturition and recruitment. Young of the deeper offshore species (S. paucispinis, S. pinniger, and S. miniatus) recruit, attain peak abundance and leave the shallow reefs earlier than the reef-dwelling species (S. atrovirens, S. carnatus and S. caurinus). Young of the reef-dwelling species exhibit the strongest affinity for the kelp forest habitat and parturate (Table 8) and recruit (Table 9) later than the offshore species. Such a trend would seem to contradict the strategy of early parturition and recruitment for avoidance of offshore transport. The late parturition characteristic of the shallow reef species would risk the loss of larvae to offshore transport more than the offshore species.

Among the kelp forest-dwelling species, those which exhibit the greatest affinity toward an algal structure recruit latest in the summer. Of the three water column aggregating species, *S. melanops* displayed the strongest affinity for *M. pyrifera* and also reached peak abundance later than the other two species. Leaman (1972) noted that *S. melanops* young did not recruit in large numbers to a *Macrocystis integrifolia* forest in Barkely Sound until the canopy reached near maximum (75%) cover. Of the three solitary benthic species, *S. atrovirens* exhibited the strongest affinity for *M. pyrifera* and also recruited latest. Gerard (1976) has described the gradual increase of plant density, plant size and canopy cover of a central California *M. pyrifera* forest over the spring-summer period. Both *S. melanops* and *S. atrovirens* may have evolved reproductive strategies which delay parturition and/or recruitment relative to the other members of their distributional group thereby increasing the probability of algal availability when recruits encounter the reef. Unfortunately, data for seasonal parturition of *S. melanops* are lacking for the central California area.

It is possible, but not certain, that the successive peak abundances of the three solitary benthic species within the kelp canopy are a means of temporally partitioning the utilization of that habitat. Observations of large areas of kelp canopy vacant of fish suggest that the canopy cover was never saturated. It is conceivable, however, that years of low recruitment and growth of *M. pyrifera* may have at some time resulted in the limited availability of this habitat. Keast (1978) has described the temporal segregation of juvenile fishes in the weedbeds and adjacent nearshore waters of a temperate lake. This sequence of species occurrence is maintained by the different spawning periods of those species (Amundrud *et al*. 1974).

The seasonal periodicity of parturition and nearshore recruitment of rockfish may be influenced by the seasonal availability of food within the nearshore environment. The nine species of young-of-the-year rockfish observed at Arrowhead Point fed predominantly on harpacticoid and calanoid copepods (Singer 1982). However, changes in the relative abundance of copepods and other zooplankters on shallow rocky reefs over the spring upwelling and subsequent summer period is not well documented. Consequently, the possible influence of zooplankton compostion and abundance on the temporal occurrence of young of the different species of rockfish cannot be discussed. The staggered peak abundances of the different species may also be a mechanism by which utilization of a common prey (zooplankton) is partitioned temporally.

The differential influence of algal availability on the period of residency of the various Sebastes young may also be evident by comparison of the timing of the habitat shifts and emigration from the kelp forest in some species. Apparent reduction in the numbers of the two abundant offshore species (S. paucispinis and S. pinniger) was evident by the beginning of August, whereas the shallow reef-dwelling species did not exhibit greatly reduced abundances until the onset of fall storms (October). For all but S. atrovirens and S. carnatus, these reductions appear to be the result of the emigration of individuals to deeper reefs.

By the end of their first year, young-of-the-year rockfish occupy habitats typical of adult conspecifics. Timing of the transition from the algal habitats occupied by young recruits to those habitats typical of adults appears to be prompted by storm disruption of the algae. It is difficult to distinguish the relative effects of increased water motion versus the removal of large quantities of M. pyrifera and drift material on the subsequent emigration and/or habitat shifts of the reef-dwelling species during the storm season. Though seasonal changes of water motion may not significantly alter the seasonal distributions of fishes associated with kelp forests south of Pt. Conception (Ebeling et al. 1979), many of the Sebastes species inhabiting more northerly reefs appear to be influenced by seasonal increases of water turbulence (Burge and Schultz 1973, Miller and Giebel 1973, Patten 1973, Moulton 1975, 1977, Carlson and Barr 1977).

Water Column Distribution

Those species which aggregate in the water column (S. melanops, S. mystinus and S. serranoides) recruit earlier than the solitary benthic species (excepting S. melanops vs. S. caurinus). Their habit of forming large aggregations may function as an alternative form of refuge from predators, reducing the need to seek cover. The formation of aggregations is common among nearshore fishes and is an effective defense mechanism against predators (Hobson 1978). The behavior is especially pronounced among juveniles during their size-related period of high vulnerability to predators. The development of aggregations of juvenile fishes is often enhanced by interspecific associations (Keenleyside 1955, Ehrlich and Ehrlich 1973, Ogden and Ehrlich 1977). The common occurrence of mixed-species aggregations of young rockfish has been mentioned in this study and others (Burge and Schultz 1973, Miller and Giebel 1973, Hallacher 1977).

The reduced vulnerability to predation upon formation of aggregations may also explain the wider occupation of the water column by aggregating species during years of increased abundance (1980 vs. 1981). As numbers of young S. mystinus, S. melanops and S. serranoides increased over the spring these species exhibited more relaxed affinities for substratum or algal cover and occupied open areas of the kelp forest. This same trend was also observed for individuals of S. paucispinis. Those species which displayed the most cohesive aggregating behavior (S. paucispinis and S. serranoides) also exhibited the least affinity toward the vertical fronds of M. pyrifera and the reef surface.

Seasonal transect data in this study probably underestimates mean abundances of the three water column aggregators. Mid-depth transects included the water column above the depth at which many of these individuals aggregated (2-4 m above the reef surface) and bottom transects sampled below them. S. mystinus was usually the most abundant of the three species. Past studies have described S. mystinus as the most abundant of the young-of-the-year rockfishes occupying central California kelp forests during the summer season (Burge and Schultz 1973, Miller and Giebel 1973, Hallacher 1977). However, at Arrowhead Point mean abundances of two benthic species (S. atrovirens 1980, and S. caurinus, 1981) were comparable with or exceeded values of S. mystinus at particular times of the recruitment season. Hence, S. mystinus may not always be the most abundant young Sebastes inhabiting a particular reef; this depends on the time of year, relative strength of recruitment of each species and the availability of microhabitats to which each species is attracted.

Occupation of the lower portion of the water column by the majority of newly recruited rockfishes was also observed by Miller and Giebel (1973) and Hallacher (1977). Limbaugh

(1955) noticed that juvenile S. mystinus in southern California kelp beds occupy deeper, colder water than the juveniles of other rockfishes. This may be due to a thermal preference based on a physiological temperature optima for this species (Helley 1976). However, young of S. mystinus in central California are commonly encountered in tidal pools (Limbaugh 1955, Burge and Schultz 1973). Water temperatures measured during the spring-summer period rarely varied more than 1.0-2.0° C throughout the water column. It is more likely that young-of-the-year rockfish inhabiting central California waters remain near the bottom due to an attraction to the reef substratum. This "thigmotaxic" behavior mentioned by Burge and Schultz (1973) also describes the behavior of the three water column aggregators, who gathered about higher rock relief and near the ascending fronds of M. pyrifera.

Size/Age-related Differences of Spatial Distribution

All nine species of young-of-the-year Sebastes exhibit distributions which differ from their adult conspecifics by depth, position in the water column, or proximity to physical structures. Post-planktonic S. miniatus, S. paucispinis, and S. pinniger occupy shallower reefs than of adult conspecifics (Miller and Lea 1972). Previous records of young-of-the-year S. miniatus associated with shallow rocky reefs have been made by Limbaugh (1955) (depth= 7.5 m and 30.5 m) and Burge and Schultz (1973) (depth= 18 m). Burge and

Schultz also observed large numbers of young S. pinniger (43-87 mm SL) at depths of 7.5 m and 18 m during their subtidal surveys off Diablo Cove, central California. Miller and Giebel (1973) mentioned the occurrence of first year S. pinniger in a kelp forest off Cabrillo Pt. on Monterey Bay. Follett and Ainley (1976) collected young-of-the-year S. pinniger (38-45 mm TL) from tidal pools in northern California. Young-of-the-year S. paucispinis have been previously observed within the canopy region of shallow kelp forests off southern (Limbaugh 1955, Carlisle et al. 1964, Moser 1967) and central California (Burge and Schultz 1973, Miller and Giebel 1973).

Similarly, adult S. caurinus are not common inhabitants of shallow central California kelp forests (Hallacher 1977), but typically occupy deeper reefs offshore. The occurrence of young-of-the-year S. caurinus in shallow kelp forests along central California has been previously reported by Miller and Giebel (1973) (70 mm TL) and Burge and Schultz (1973) (28.5-40.5 mm SL).

The occurrence of young-of-the-year at depths much shallower than adults has been recorded for other Sebastes species as well. Harada (1962) described the occupation of shallow sea grass beds by young-of-the-year Sebastes inermis along the coast of Japan. Carlson and Haight (1976) collected younger Sebastes alutus at progessively shallower depths off the coast of Alaska. The shallower occurrence of newly recruited young of other reef-associated species is not uncommon (Clarke 1977, Helfman 1978). The relative importance of shallow reefs versus deeper offshore reefs to the young of these deeper-dwelling Sebastes is not known, due to the lack of abundance data from deeper reefs.

Newly recruited young of the reef-dwelling Sebastes species (the three water column aggregators and the three solitary benthic species) also exhibit markedly different spatial distributions from those of conspecific adults. Hallacher (1977) and Larson (1980) have illustrated the depth and water column distributions of adult rockfishes which typically occupy kelp forests. Hallacher based his description on observations made at nearby kelp forests within Carmel Bay. Generally, the young of the water column aggregators (S. melanops, S. mystinus and S. serranoides) occupy lower portions of the water column than conspecific adults. Young of the solitary benthic species (S. atrovirens, S. carnatus and S. caurinus) display much stronger affinities toward algal structure, which in turn allows them to occupy a wider portion of the water column.

Dissimilarities of spatial distributions between different size/age classes of reef fishes are common and are usually due to the restriction of young to areas providing protection from predators. The tendency of juveniles to occupy lower portions of the water column and remain closer to the reef surface than adult conspecifics has been recorded for other reef-dwelling species (Hobson 1972, 1979, Bray 1980). Olla et al. (1974) observed restricted movements of young Tautoga onitis (Labridae) relative to adult conspecifics.

During their occupation of the kelp forest, young-of-the-year Sebastes are a major prey source for a variety of piscivorous reef fishes. Piscivores such as Paralabrax clathratus (Young 1963), Ophiodon elongatus (Miller and Giebel 1973) and the adults of all the reef associated Sebastes species (Larson 1972, Burge and Schultz 1973, Hallacher 1977, Roberts 1979, Love and Westphal 1981) are the most significant predators of young rockfish.

Probably the second most significant predators are the piscivorous seabirds, including pigeon guillemots (Follett and Ainley 1976), Brandt's cormorants (Hubbs et al. 1970, Ainely et al. 1981), common murres, tufted puffins, rhinocerus auklets (D. Ainley, pers. comm.) and western gulls (R. Pierotti, pers. comm.). At the Arrowhead Point kelp forest, great blue herons and snowy egrets were observed to feed successfully on young-of-the-year rockfishes during dusk and dawn. These two species perched on the M. pyrifera fronds at the surface and removed young rockfish from the kelp canopy (pers. obs.). Otoliths collected from Pescadero Rocks (0.2 km from Arrowhead Point), where cormorants and gulls frequently roosted, were primarily from young Sebastes (J. Fitch, pers. comm.).

Influence of Substratum Heterogeneity on Distribution of Recruits

As a consequence of predatory influences, the availability of structural cover appears to play a paramount role in the distributions and habitat selection of other newly recruiting reef fishes. Sale (1968, 1969a, 1969b) has demonstrated experimentally the modifying affect structural cover has on the depth and spatial distribution of newly settled juvenile manini (Acanthuridae). However, the literature is comprised of conflicting results which support or discount the importance of size and type of structures during the settlement process of recruiting fishes.

The majority of studies assessing the influence of structural specificity on the settlement of pelagic recruiting post-larvae has involved observations of tropical species colonizing artificially constructed substrates or isolated coral structures. Russel _et_ _al_. (1974) observed recruitment to small (1.6 m X 0.6 m X 0.6 m) cement structures of four different hole sizes (including one structure with no holes). They hypothesized that habitat selectivity (as a function of structural relief) would restrict the occurrence of a species to one of the four structural types and differences of habitat selectivity would be reflected in differences of species composition and diversity of the assemblage of recruits occupying each structure. They found little difference in relative abundance and diversity of the species recruited to each of the treatments and concluded that selectivity for the type of structural cover (hole size) was not important in establishing the species composition of a reef. Talbot et al. (1978) extended these same experiments and concluded that less than half of the 105 recruited species may have been influenced by the differing heterogeneity of the structures. Molles (1978) arrived at similar conclusions based on a study employing small (1.2 m x 0.6 m x 0.4 m) artificial structures in the Gulf of California, Mexico.

Sale and Dybdahl (1975, 1978) monitored recruitment to small (25-30 cm dia.) isolated pieces of live and dead corals. Of the 56 species observed to recruit to these structures, only five appeared to display a marked preference for the "live" units. Among the live and dead types seperately, no smaller scale structural specificity was apparent. Likewise, Itzkowitz (1977) concluded that habitat specificities of juvenile pomacentrids inhabiting Jamaican coral reefs were not as well defined as those of the adults. Such observations have led Sale (1977, 1978, 1980b) to explain the subsequent diversity and composition of recruited reef fishes occupying coral reefs as a stochastic rather than deterministic (e.g. habitat specificity) phenomenon.

In their studies employing artificial structures similar to those of Talbot et al., Gascon and Miller (1981, 1982) observed little effect of differences in topographical relief on the subsequent species composition of temperate reef-dwelling fishes in Barkley Sound, Canada. Included among the post-larval and juvenile fishes which recruited to their reefs, and which exhibited indifference to variations of relief, were *Sebastes caurinus* and *S. maliger*.

In contrast to those studies demonstrating a lack of structural discrimination by recruiting young-of-the-year, other studies have concluded that microhabitat specificity can strongly influence the distribution of settlement of new recruits. Marliave (1977) observed significant preferences for different substratum types (rocks vs. pebbles vs. sand) and algal structures by settling larvae of five different temperate intertidal species. In contrast to Itzkowitz's (1977) observations, Sale (1971) observed a greater discrimination between available coral species occupied by juvenile *Dascyllus aruanus* (Pomacentridae) than that observed for adults. Contrary to those previously-mentioned studies addressing the species composition of post-larvae recruited to coral isolates, some recent studies indicate that habitat specificity may strongly influence the distribution of settlement of newly colonizing recruits (Sale *et al*. 1980, Williams 1980, Williams and Sale 1981).

The significant electivities toward particular substratum types observed for the eight species of young-of-the-year *Sebastes* in this study reflect distributional patterns strongly influenced by differences of structural relief (*S. mystinus*, *S. serranoides*), proximity to the reef-sand interface (*S. pinniger*, *S. miniatus*, *S. caurinus*) and, perhaps most importantly, the presence of algal structure (*S. atrovirens*, *S. carnatus*, *S. caurinus*, *S. melanops*).

Young *Sebastes* exhibited significantly different abundances among larger-scale features of habitat relief and type than the scale of habitat heterogeneity examined by the previously-mentioned studies. The results of this study suggest that possible partioning of structural cover between the young *Sebastes* could occur at spatial scales greater than that examined by Gascon and Miller (1981, 1982) and similar studies conducted in the tropics.

Influence of Algal Cover on Distributions of Newly Recruited Fishes

It is apparent from the results of each of the different phases of this study that *Macrocystis pyrifera* plays an important role in determining the distribution of young-of-the-year of at least six of the species observed. The influence differs among the species. Though *S. paucispinis* and *S. serranoides* exhibited little affinity for vertical fronds, they typically aggregated below the *M. pyrifera* canopy. *S. melanops* and *S. mystinus* often associated closely with the vertical fronds at mid-depth. However only *S. melanops* displayed strong affinity toward *M. pyrifera* while in the bottom portion of the water column.

The utilization of surface and mid-depth portions of the water column by the three solitary benthic species closely corresponded with the occurrence of *M. pyrifera* canopy and vertical fronds as indicated by the canopy removal and kelp transplant experiments. Occupation of the kelp canopy by young-of-the-year *S. caurinus* and *S.*

atrovirens has been previously mentioned by Miller and Giebel (1973). In the lower portion of the water column the affinities of the three solitary benthic species toward *M. pyrifera* diverge. *S. atrovirens* maintains a strong association with the *M. pyrifera* plants on the reef surface, while *S. carnatus* divides its algal affinity between the intact *M. pyrifera* plants and drift material. *S. caurinus* primarily associates with the drift *M. pyrifera* which accumulates along the rock-sand interface at the edge of the kelp forest.

The close association of young *Sebastes* with *M. pyrifera* is probably due to protection from predation, in a manner similar to that suggested for young fishes that associate with shallow lake vegetation (Keast 1978, Werner *et al*. 1977) and shallow seagrass beds (Adams 1976, Weinstein and Heck 1979, Blaber and Blaber 1980). Hubbs *et al*. (1970) concluded that Brandt's cormorants while feeding in shallow nearshore waters, were less successful at feeding on the more cryptic fish species and those which associated closely with the fronds of *M. pyrifera*. Mitchell and Hunter (1970) noted that small fishes (including young-of-the-year rockfishes) were more frequently preyed upon by piscivorous fish when removed from the cover of drift *M. pyrifera*. Helfman (1981) has discussed the benefit to potential prey species of hovering in the shade of physical structures. Fishes hidden by shade are not only less conspicuous to their predators but also perceive approaching predators better. Gibson and Keenleyside (1966) have demonstrated a preference for shaded habitats by juvenile salmon (Salmo salar) and brook trout (Salvelinus fontinalis). Young-of-the-year Sebastes which accumulate under the kelp canopy probably benefit from this shading effect and the ability to quickly retract into the interstices of the overlapping kelp fronds.

The strong affinity for M. pyrifera is underscored by the disappearance of young rockfishes within the surface portion of the water column upon removal of the kelp canopy and the absence of subsequent recruitment into the water column upon removal of entire M. pyrifera plants from the "denuded" reef. Miller and Giebel (1973) concluded that juvenile Sebastes migrated from the surface to the bottom portion of the water column upon artificial removal of the canopy of a M. pyrifera forest in Monterey Bay, central California. Leaman (1980) however, has observed differing affects of canopy removal on fish densities within the water column of a Nereocystis lutkeana forest in Barkley Sound, British Columbia. Removal of the kelp canopy within the inner and middle portion of the forest resulted in increased densities of neritic species whereas canopy removed along the outer edge of the bed caused decreased densities. It is not clear however as to what portion of the fish observed by Leaman included young-of-the-year Sebastes.

Juveniles of other fishes common to California kelp forests exhibit strong algal affinities. Coyer (1979) described the close association of juvenile Heterostichus rostratus (Clinidae), Brachyistius frenatus (Embiotocidae), Paralabrax clathratus (Serranidae) and Sebastes atrovirens (Scorpaenidae) with M. pyrifera. Among all these species juveniles exhibit comparable or stronger affinity toward the structure of M. pyrifera than do conspecific adults. Young-of-the-year of some reef dwelling embiotocids exhibit a similar pattern of abundance and survivorship in relation to the presence of understory algal species (esp. Pterygophora californica) (A.W. Ebeling and D. Laur, pers. comm.). Experimental clearing of Pterygophora californica resulted in habitat shifts and depressed densities of young-of-the-year while adults were less affected.

Marliave (1977) observed significant differences in the frequency of settlement of two intertidal species on artificial algal structures of different form. He observed larval Pholis laeta (Pholididae) to settle more frequently on narrow elongate plastic strips similar to the form of the surf grass Phyllospadix scouleri (Zosteraceae) than on wider plastic strips. In contrast, Gobiesox meandricus (Gobiesocidae) displayed a greater tendency to settle on wider plastic strips more representative of broader-bladed plant species. The differences in forms selected by P. laeta and G. maeandricus reflect differences in the plant forms characteristically inhabited by the adults of these two species. Both species preferentially settled on plants rather than bare rock substrata of various rugosities and showed little discrimination between the artificial structures and the actual plants. Leaman (1972) observed a similar attraction of young-of-the-year S. melanops to plastic strips employed as a facsimile of M. integrifolia fronds. This lack of discrimination between artificial and actual algal forms supports the contention that the physical structure is the major cue by which recruiting young fish are attracted to the plants.

The high fidelity of species associated with the kelp canopy habitat is indicated by the high similarity of species composition within this habitat between island and mainland fish assemblages off Santa Barbara, California (Ebeling et al. 1980). The fish assemblages associated with the kelp canopy habitat exhibited less interlocality variability than did the assemblages associated with the reef surface at the same sites. Further, changes in M. pyrifera availability (density) appear to influence the densities (Ebeling et al. 1979) and distributions (Bray 1980) of kelp-associated species on a reef. Likewise, Adams (1976) found significant correlations between fish biomass, temperature and biomass of the sea grass Zostera marina (Linnaeus). The importance of this additional structure for some temperate reef fishes is emphasized by the number of species which have developed strong affinities for a habitat characterized by marked differences of seasonal abundance. Feder et al. (1974) and Gerard (1976) describe the ephemeral quality of the kelp canopy habitat.

Other Factors Which Influence Young Fish Distributions

The interspecific differences in microhabitat utilization described here may lead to dietary differences among the planktivorous young-of-the-year Sebastes species. All nine species feed predominantly on calanoid and harpacticoid copepods (Singer 1982). Whether these zooplankters are ever a limiting resource to young Sebastes during the spring to fall period is not known. Food availability may be important in promoting the accumulation of the water column aggregators along the offshore edge of the kelp forest (Bray 1980).

The relative influence of prior residents (adults or previously settled young) on the distribution of new recruits seems to vary according to the species addressed. Some studies indicate that prior residence of conspecifics alters the occurrence and spatial distribution of settling young (Russel et al. 1974, Sale 1976, 1980a, Nursall 1977, DeMartini 1976). Early agonistic behavior among juveniles has been observed for a variety of fishes (Keenleysde and Yamamoto 1962, Hartman 1965, Gibson 1968, Itzkowitz 1977, see review by Helfman 1978).

Other studies however, suggest that adult-young interactions (other than predation) cause little effect on the patterns of settlement of pelagic recruits to reefs (Talbot et al. 1978, Sale et al. 1980, Williams 1980). Larson (1980) concluded that adult S. chrysomelas usually tolerated young conspecifics less than 100 mm SL and displayed no aggressive behavior toward them. Also, densities of recruiting young did not appear to be limited by adult densities since settlement did not noticeably increase in areas which had been cleared of adults. Larger juveniles however, eventually began to elicit aggressive behavior from adults and consequently developed "floater" ranges restricted by adult territories. No intraspecific or interspecific interactions (other than predation) were noticed during this study, although aggressive behavior seems to develop between young of the benthic species within their first year (G. Hoelzer, pers. comm.). Whether adults recognize and avoid or selectively prey upon conspecific young is not known.

Spatial Distributions Associated With Diel Activity

Changes of activity and spatial distribution associated with the transition from diurnal to nocturnal light conditions are common among reef associated fishes. The replacement of diurnally active fish assemblages with nocturnally adapted species is characteristic of tropical coral reefs (Hobson 1965, 1972, 1973). These shifts of habitat and activity correspond closely with and are most apparent during the dawn and dusk crepuscular periods. Fishes indigenous to California rocky reefs exhibit similar patterns of activity, especially among those species whose families are of tropical derivation (Ebeling and Bray 1976, Hobson and Chess 1976, Bray 1980, Hobson *et al*. 1981). Hobson has inferred that the evening migration of diurnal planktivores toward the structural cover of the reef substratum reflects their increased vulnerability to predation during their nocturnal period of inactivity.

The crepuscular migrations toward the reef surface at dusk and back into the water column at dawn by the three water column aggregators seems to lend support to Hobson's inferences regarding changes in diel distributions. Young *S. melanops*, *S. mystinus* and *S. serranoides* all feed on microcrustacea during the day and not at night (Singer 1982) and are subjected to heavy predation by resident piscivores. Consequently, all three species may seek cover from predation upon the reef surface during their period of nocturnal inactivity. Similarly, the three solitary benthic species drew closer to the cover of *M. pyrifera* and the reef substratum when inactive throughout the night.

The nocturnal migration of young *S. pinniger* from the rock substratum to the adjacent sand bottom and the settlement of young *S. melanops* and *S. serranoides* over the sand bottom seems incongruous with Hobson's refuge-seeking hypothesis. The movement of young *S. pinniger* onto the open sand bottom would appear to remove this species from the reef cover and increase exposure to predators. Data are insufficient to determine whether young *S. pinniger* feed over the sand at night. The movement of some *S. melanops* and *S. serranoides* onto the adjacent sand bottom at night may have been influenced by the large aggregation of another young-of-the-year *Sebastes* (probably *S. entomelas*; T.

Anderson pers. comm.) which settled near the sand-reef interface at night but was not seen within the kelp forest during the day.

Relative to tropical reef fish communities, temperate kelp forests lack many conspicuous nocturnally active piscivores. Many of those species which may feed on fish at night are primarily benthic species (e.g. _Ophiodon elongatus_, _Scorpaenichthys marmoratus_ and adult _Sebastes_ spp.), most active in the lower portion of the water column. Consequently, it is possible that species which vacate the water column at night to settle on the reef may actually increase the probability of encountering predators. Young _Sebates_ were often observed laying exposed on the reef surface at night.

An alternative hypothesis for the nightly movement of young _Sebastes_ from the water column to the reef surface might be that settlement is a more energetically efficient means of maintaining position within the kelp forest (i.e. in proximity to structural cover) relative to actively swimming against surge or currents. Settlement may prevent fish from being swept from the protection of the reef during periods in which they are unable to feed.

SUMMARY

Young-of-the-year of nine species of *Sebastes* were observed within the Arrowhead Point kelp forest during the spring-summer period of recruitment (1980 and 1981). The nine species constituted three groups, based on their distributional patterns as young-of-the-year; water column aggregators (*S. melanops*, *S. mystinus* and *S. serranoides*) vs. solitary benthic species (*S. atrovirens*, *S. carnatus* and *S. caurinus*); and a third group of species who, as adults, inhabit deeper offshore waters (*S. miniatus*, *S. paucispinis* and *S. pinniger*). Timing of recruitment differed between groups (offshore species recruited earlier than kelp forest-dwelling species) and within groups (species exhibiting the strongest affinity for *Macrocystis pyrifera* recruited latest). The onset of the recruitment season was correlated with the development of the upwelling period along the central California coast.

All nine species of young-of-the-year *Sebastes* were distributed contagiously within the kelp forest. Distributions of the three species which aggregated in the water column were influenced by rock relief and displayed interspecific differences of attraction toward *M. pyrifera*. Affinities for substratum and algal structures seemed to decrease as the size of aggregations increased and all three species occassionaly formed mixed-species aggregations. The distributions of species which temporarily occupied the surface portion of the water column were strongly influenced by the presence of the M. pyrifera canopy. Species which occupied the bottom portion of the water column exhibited interspecific differences of distribution which corresponded with differences of affinities for substratum type (sand vs. low relief rock vs. high relief rock) and algal structure (Macrocystis pyrifera and drift algal material). Though no understory algal species such as Pterygophora californica occurred at Arrowhead Point, observations in nearby kelp forests suggest that those algal species also strongly influence some young Sebastes distributions. The strong affinity for M. pyrifera exhibited by some newly recruited Sebastes appears to be in response to heavy predation pressure. However, this was not tested experimentally.

Changes in distribution of young-of-the-year Sebastes were observed during the dawn-dusk crepuscular periods. All three water column aggregators vacated the water column during the evening crepuscular period and assumed inactive positions in contact with the bottom. At dawn, these three species reaggregated and reoccupied the lower portion of the water column. The solitary benthic species showed no marked changes of vertical distribution but came in closer contact with nearby physical structures with the onset of darkness. One species, S. pinniger, underwent daily migrations from the rock reef to the adjacent sand bottom each evening and returned to the reef at dawn.

In conclusion, young-of-the-year Sebastes exhibit patterns of spatial distribution which differ markedly from those of adult conspecifics, probably as a result of attraction for structural cover in avoidance of predation. The role of macro-algae appears especially important as a refuge from predation. These results suggest that assessment of factors influencing the patterns of settlement of temperate reef fishes warrants consideraton of algal structure as well as substratum heterogeneity and other factors previously addressed in tropical studies.

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Appendix I.

Percent number of individuals and percent frequency of occurrence (number of observations) of juvenile rockfish species occupying the different substratum types. Rank order of percent number and percent frequency (in parentheses) were compared with the Spearman rank correlation coefficient (r_s).

			Substratum Types						
Species	Months	r_s	sand	low rock	high rock	sand/lo rock	sand/hi rock	lo/hi rock	sand/ lo/hi rock
S. atrovirens	Aug-Dec	.63*	0(0)	43(37)	23(37)	3(8)	0(0)	31(17)	0(0)
	Feb-May	1.0	0(0)	36(36)	27(27)	9(9)	18(18)	0(0)	9(9)
S. carnatus	Jun-Sep	1.0	6(4)	30(25)	8(8)	40(43)	0(0)	18(17)	0(0)
	Oct-May	.87	0(0)	10(14)	68(62)	3(5)	13(9)	6(5)	0(0)
S. caurinus	Jun-Sep	.94	28(14)	14(21)	2(7)	46(39)	0(0)	3(10)	7(7)
	Oct-May	1.0	0(0)	14(20)	14(20)	71(59)	0(0)	0(0)	0(0)
S. melanops	Jun-Sep	1.0	1(4)	30(30)	44(39)	19(17)	3(9)	0(0)	0(0)
	Oct-May	.6*	0(0)	13(5)	23(32)	33(26)	26(32)	3(5)	0(0)
S. miniatus	Jun-May	1.0	15(33)	3(17)	0(0)	82(50)	0(0)	0(0)	0(0)
S. mystinus	Jun-May	.85	0(1)	20(18)	27(41)	16(20)	18(9)	16(8)	1(2)
S. pinniger	Jun-May	.95	13(9)	11(13)	2(7)	55(45)	16(22)	1(2)	2.5(3)
S. serranoides	Jun-May	.19*	0(1)	20(29)	10(28)	14(15)	18(10)	21(6)	14(7)

*($p < .05$; not significantly correlated)

Figure 1. Location of study site at Arrowhead Point, Carmel Bay, central California.

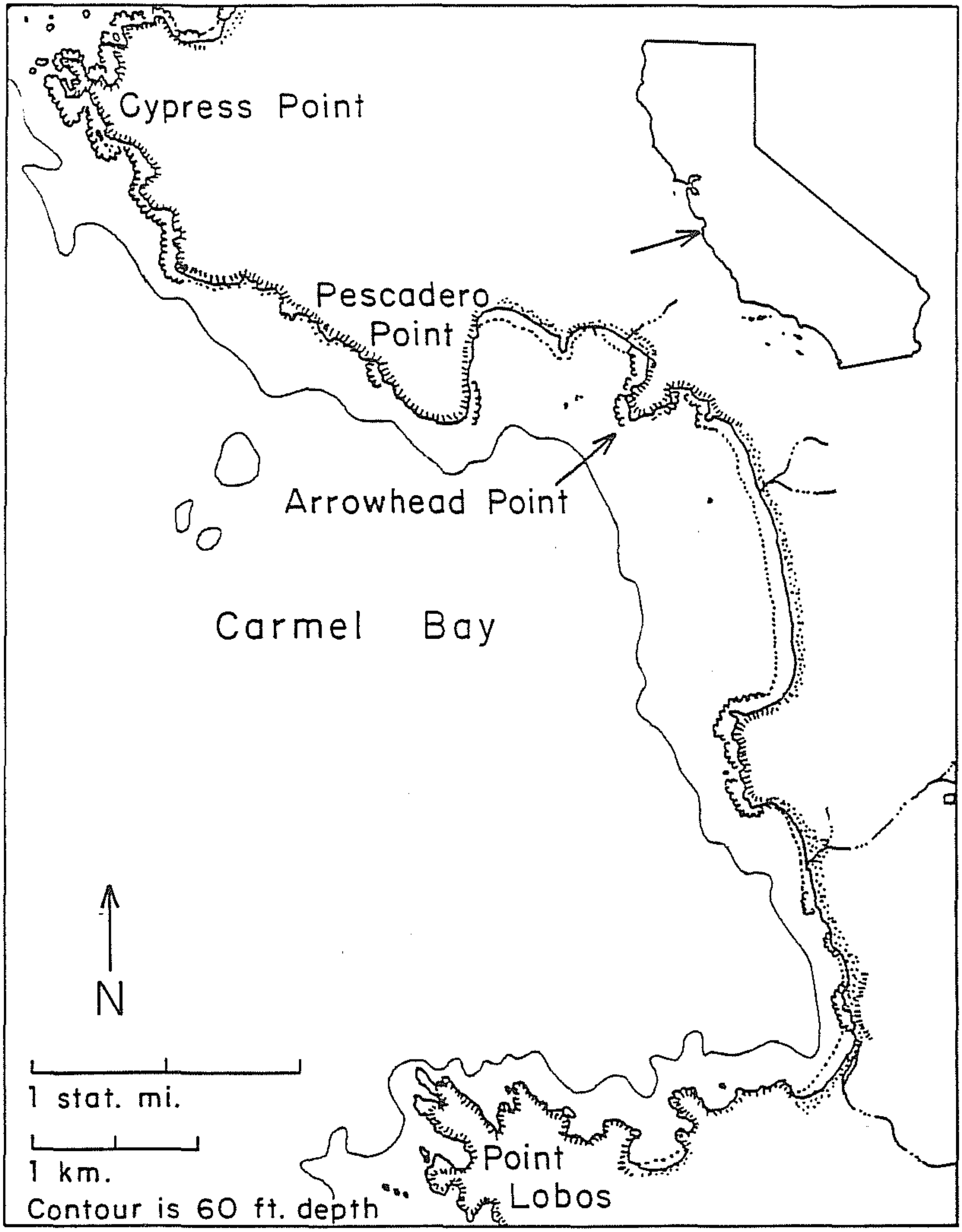

Cypress Point
Pescadero Point
Arrowhead Point
Carmel Bay
N
1 stat. mi.
1 km.
Contour is 60 ft. depth
Point Lobos

Figure 2. Locations of the kelp only, rock only and non-manipulated kelp-rock sites. Hash marked area includes high relief rock reef (< 7 m deep). Stippled contour indicates hard-soft bottom interface.

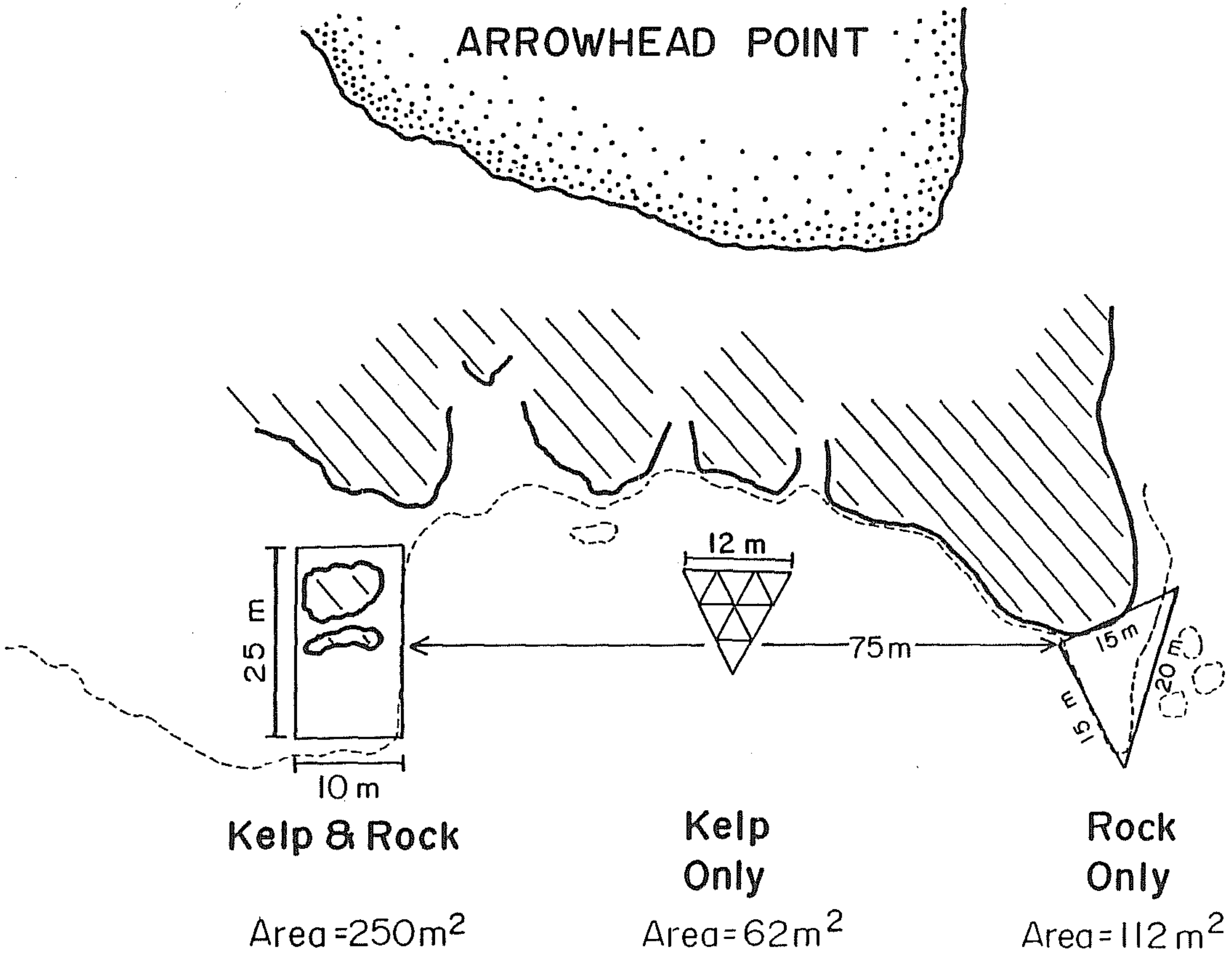

ARROWHEAD POINT
12 m
75m
15m
20 m
15 m
25 m
10 m
Kelp & Rock
Area =250m²
Kelp Only
Area = 62m²
Rock Only
Area = 112 m²

Figure 3. Configuration of the transplanted *Macrocystis pyrifera* plants at the kelp only site.

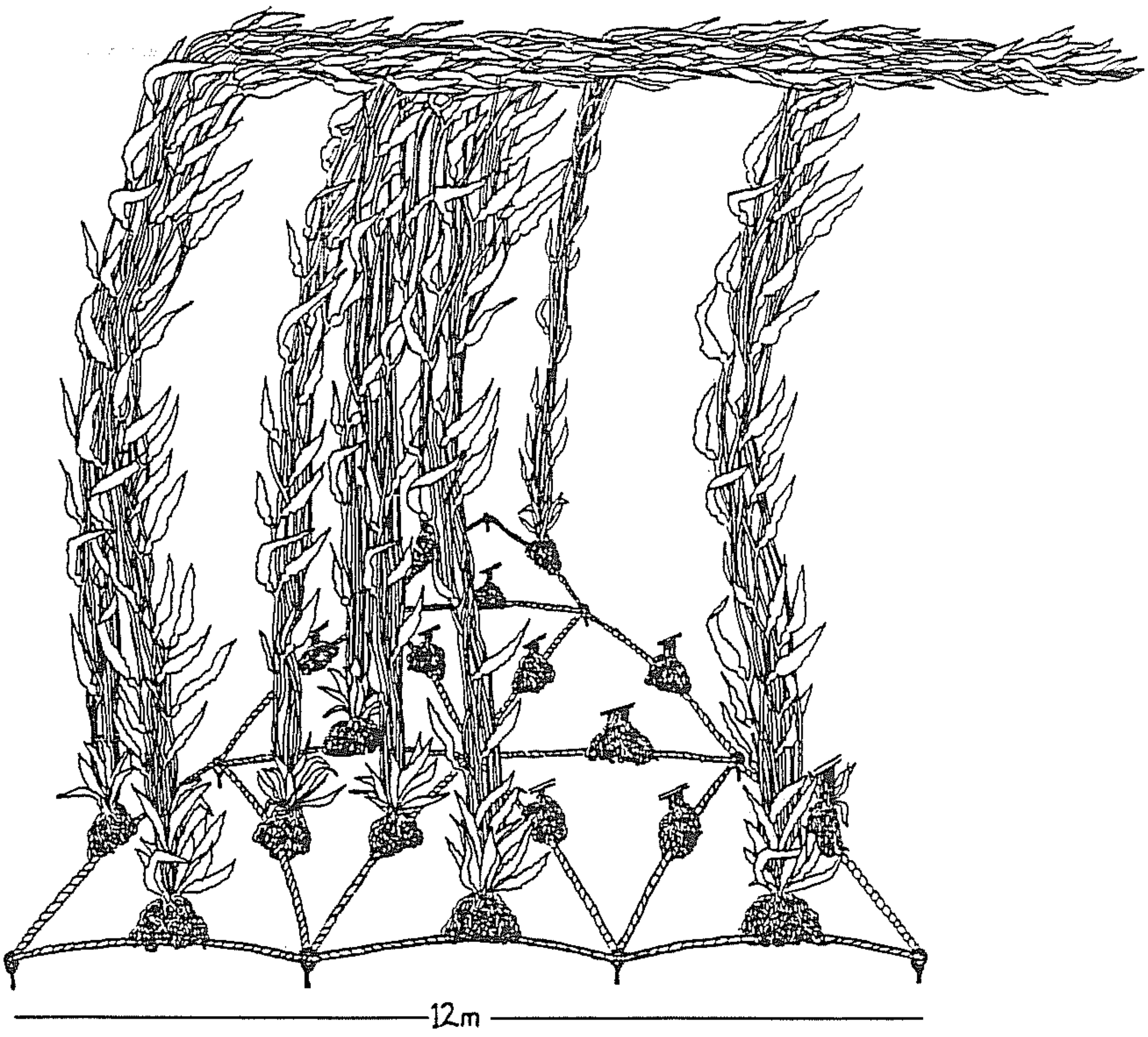

12m

Figure 4. Water temperatures at three depths within the water column at Arrowhead Point and surface water temperatures at Granite Canyon Mariculture Station during 1980-1981.

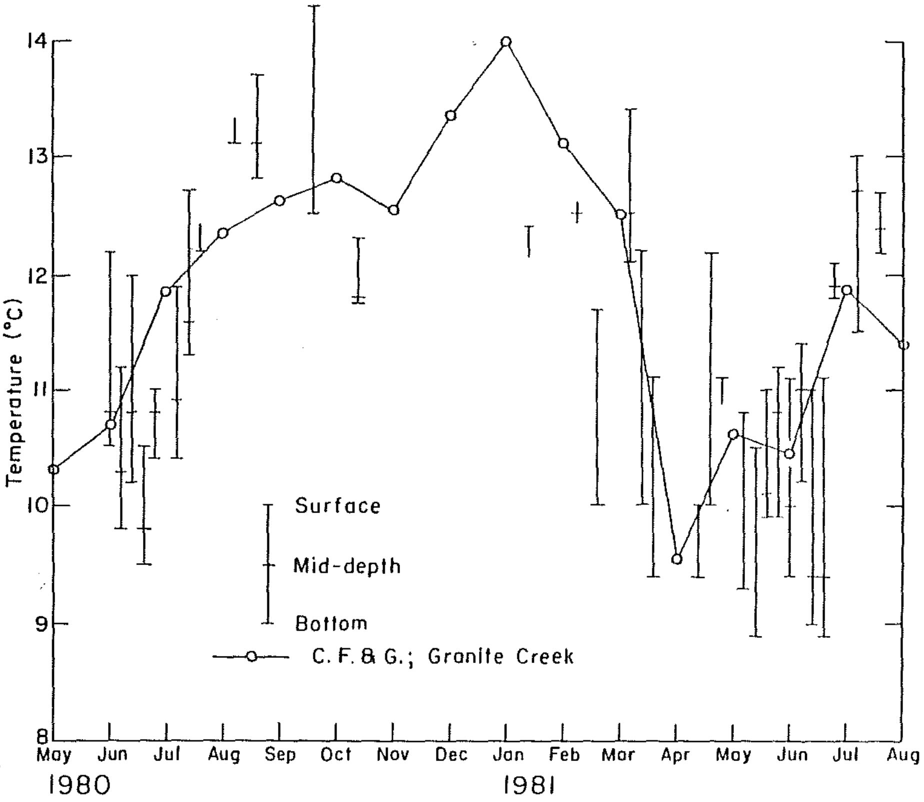

Temperature (°C)
14
13
12
11
10
9
8
Surface
Mid-depth
Bottom
C. F. & G.; Granite Creek
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
1980
1981

Figure 5. Monthly total number of young-of-the-year *Sebastes* at Arrowhead Point (all species combined), mean coastal upwelling estimates (NOAA/NMFS Monterey, California) and mean surface water temperatures (Granite Canyon Mariculture Station) during 1980 and 1981.

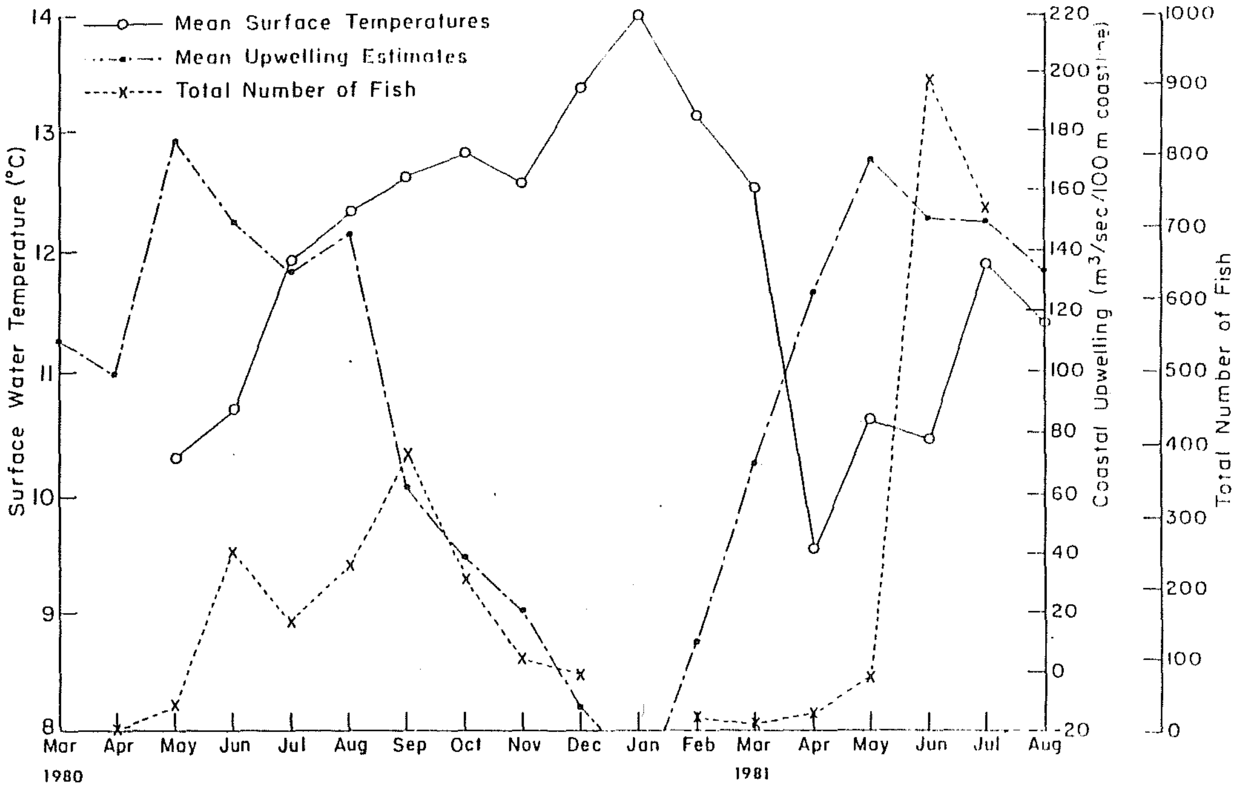

Mean Surface Temperatures
Mean Upwelling Estimates
Total Number of Fish
Surface Water Temperature (°C)
14
13
12
11
10
9
8
Coastal Upwelling (m^3/sec/100 m coastline)
220
200
180
160
140
120
100
80
60
40
20
0
-20
Total Number of Fish
1000
900
800
700
600
500
400
300
200
100
0
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
1980
1981

Figure 6. Seasonal occurrence of the three water-column aggregating species at three vertical levels within the Arrowhead Point kelp forest. Values represent back-transformed $\log_{10}(X+1)$ means and 95% confidence intervals ($n = 5$).

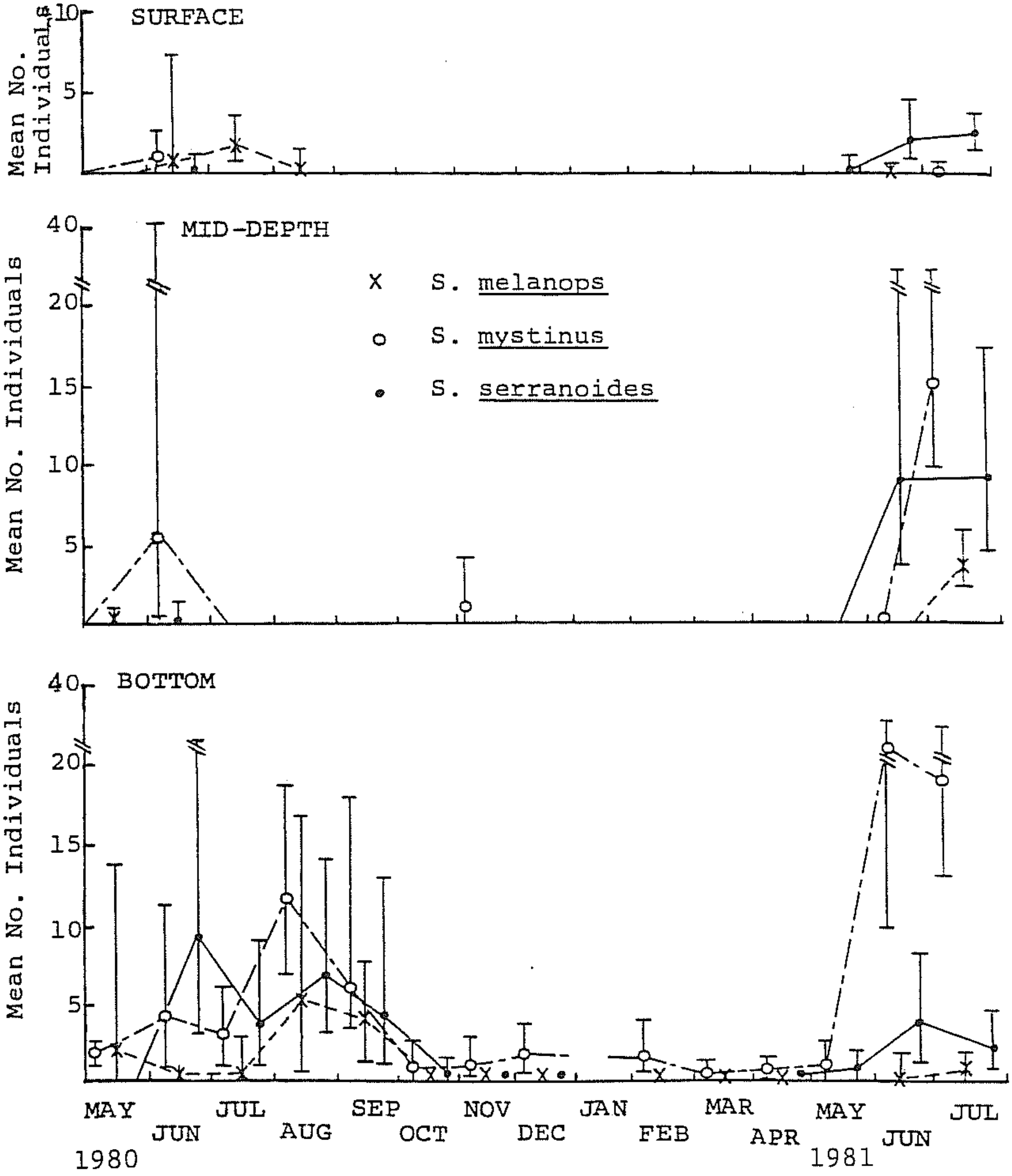

SURFACE
Mean No. Individuals
10
5
MID-DEPTH
Mean No. Individuals
40
20
15
10
5
X S. melanops
o S. mystinus
• S. serranoides
BOTTOM
Mean No. Individuals
40
20
15
10
5
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
1980
1981

Figure 7. Seasonal occurrence of the three solitary benthic species at three vertical levels within the Arrowhead Point kelp forest. Values represent back-transformed $\log_{10}(X+1)$ means and 95% confidence intervals (n = 5).

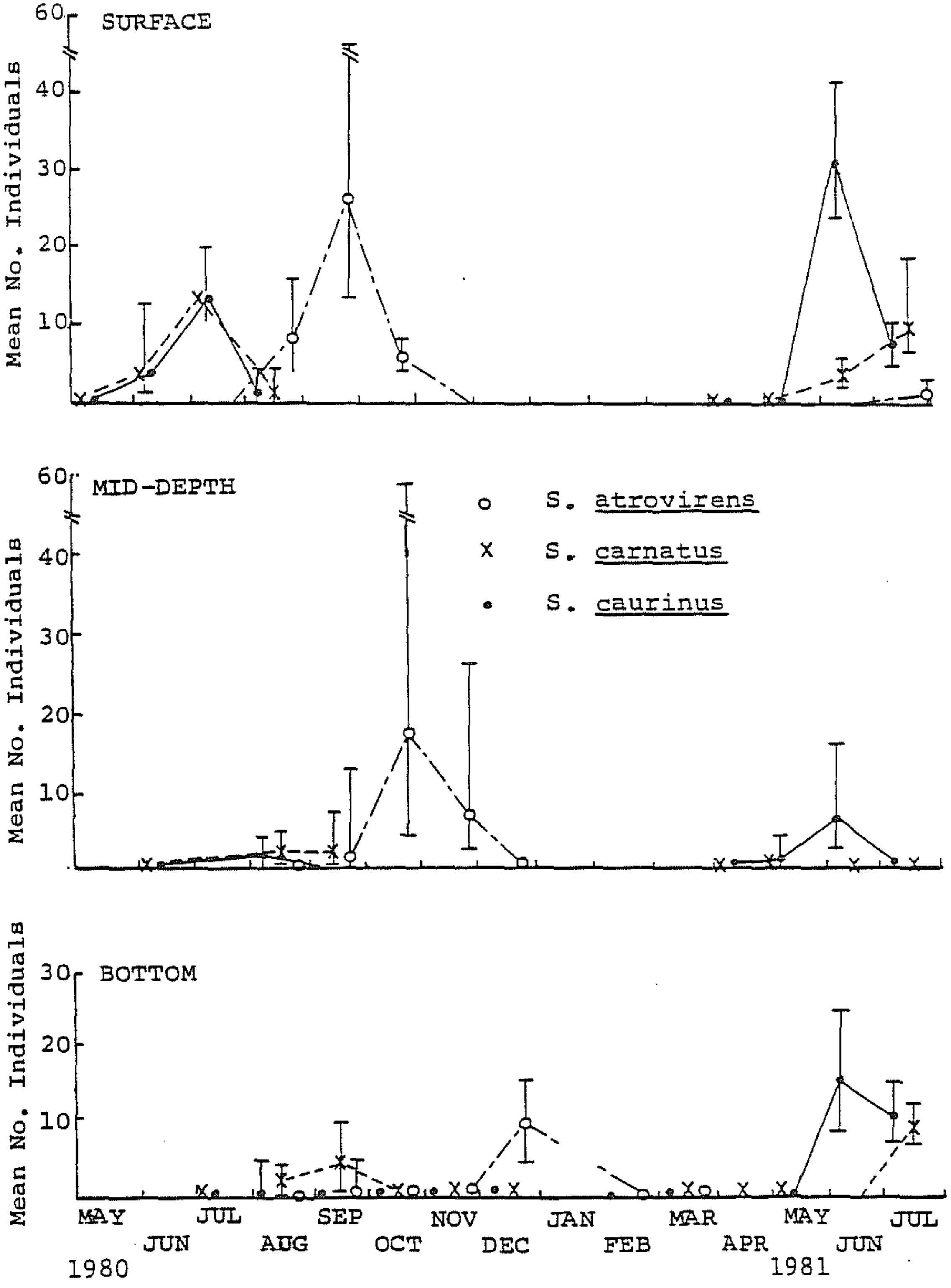

SURFACE
MID-DEPTH
BOTTOM
Mean No. Individuals
60
40
30
20
10
○ S. atrovirens
X S. carnatus
• S. caurinus
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
1980
1981

Figure 8. Seasonal occurrence of the three offshore species at three vertical levels within the Arrowhead Point kelp forest. Values represent back-transformed $\log_{10}(X+1)$ means and 95% confidence intervals ($n = 5$).

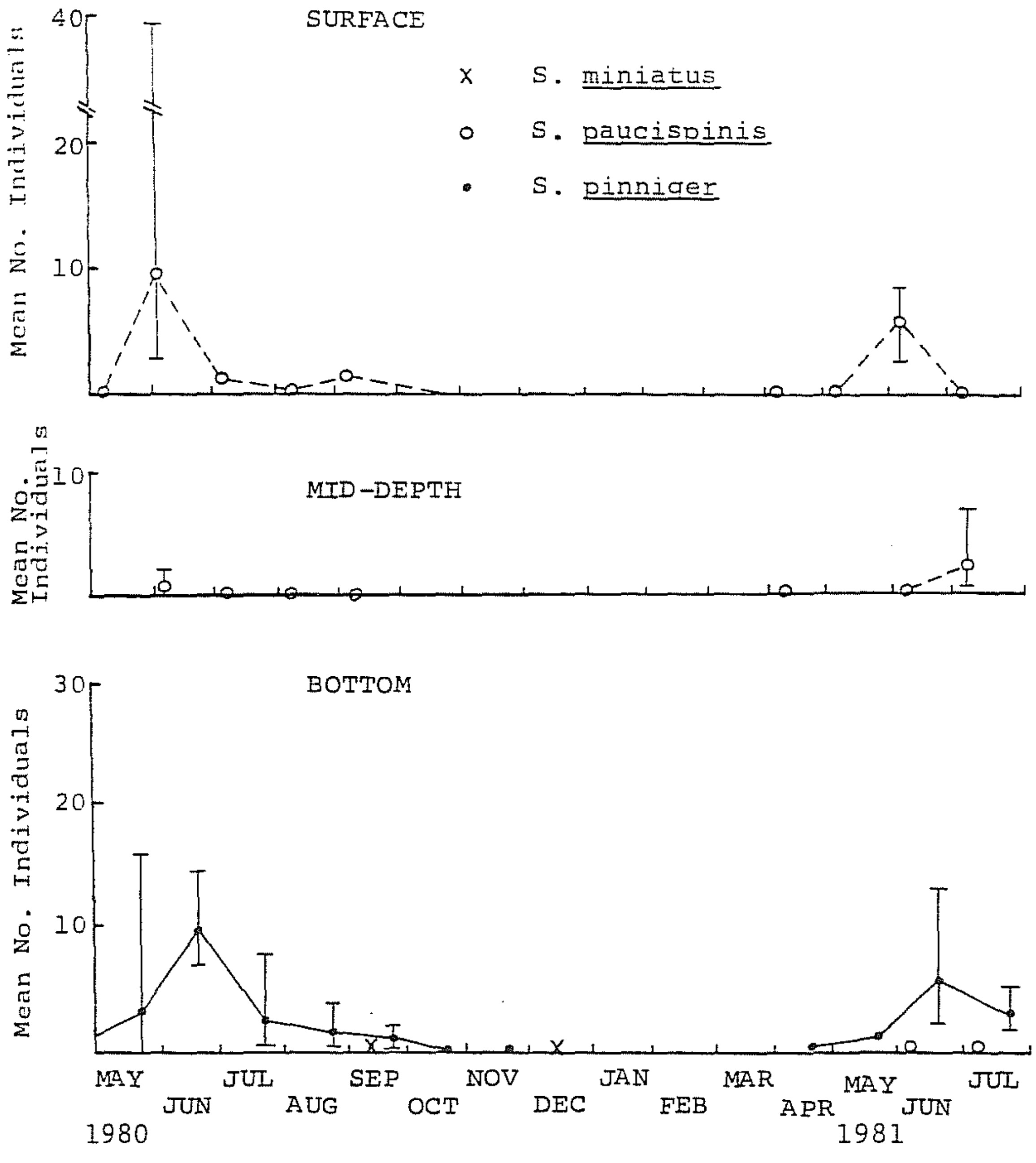
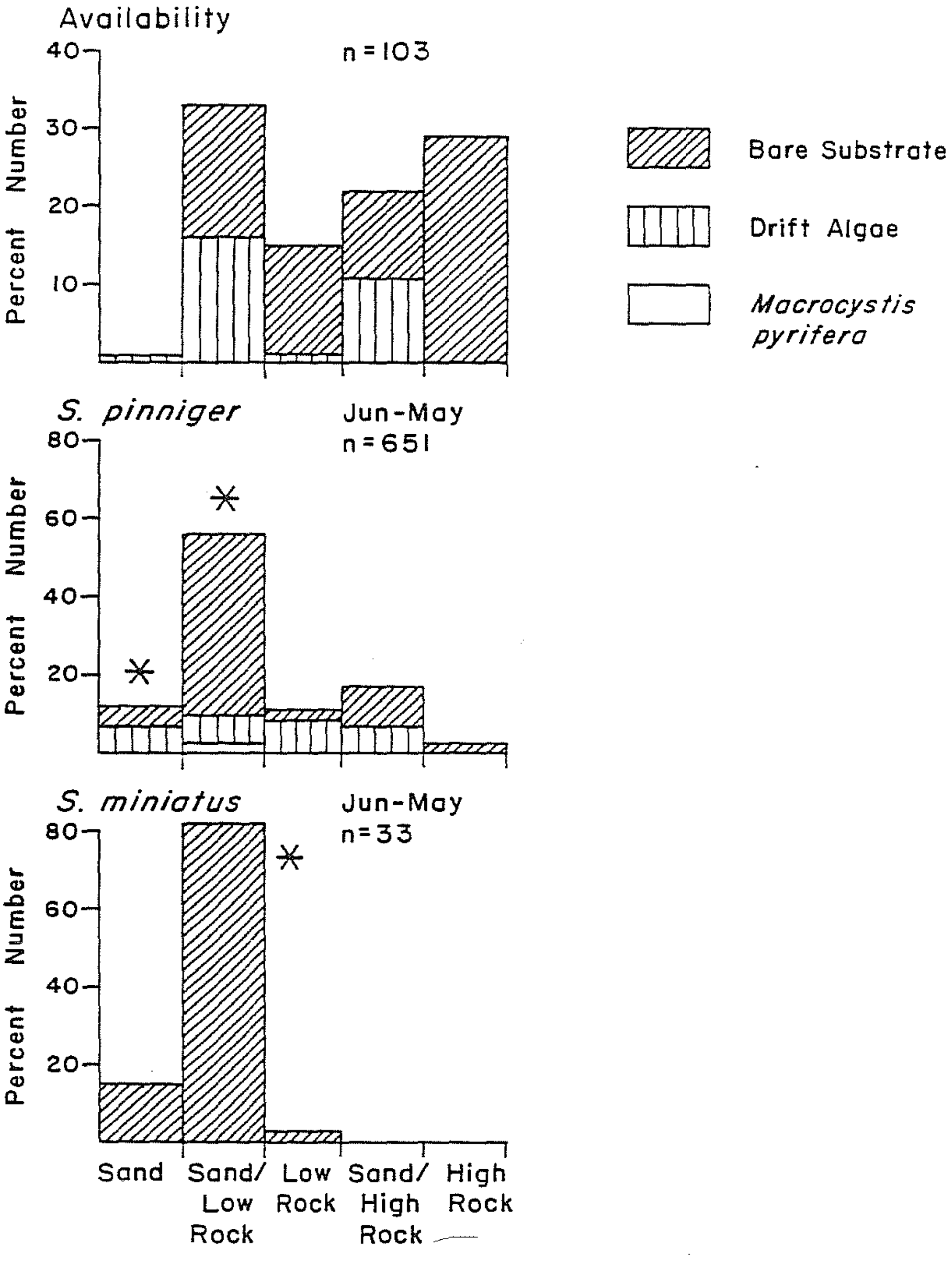

SURFACE
X S. miniatus
o S. paucispinis
• S. pinniger
Mean No. Individuals
40
20
10
MID-DEPTH
Mean No. Individuals
10
BOTTOM
Mean No. Individuals
30
20
10
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
1980
1981

Figure 9a. Percent cover (availability) of each of five substratum types and the occurrence of bare substratum and drift algae. Availability of _M. pyrifera_ was not assessed. Percent number of the two offshore, bottom-dwelling _Sebastes_ species within each substratum category and co-occurrence of bare substrate, drift algae and _M. pyrifera_ with fish. Asterisks indicate significant electivity ($P < 0.05$) for a substratum category.


Availability
n=103
Percent Number
40
30
20
10
Bare Substrate
Drift Algae
Macrocystis pyrifera
S. pinniger
Jun-May
n=651
80
60
40
20
S. miniatus
Jun-May
n=33
Sand
Sand/ Low Rock
Low Rock
Sand/ High Rock
High Rock

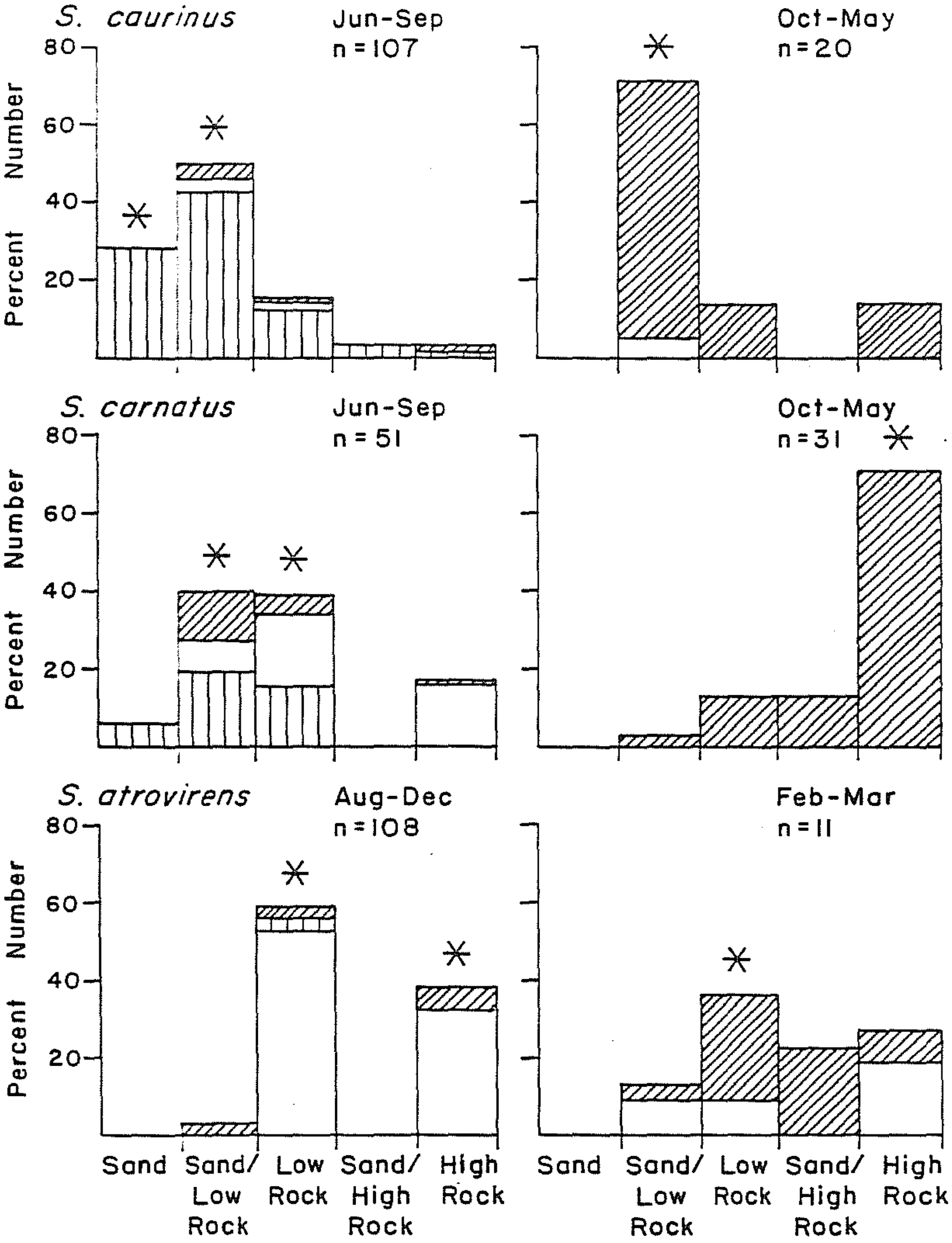

S. caurinus
Jun-Sep
n=107
Oct-May
n=20
S. carnatus
Jun-Sep
n=51
Oct-May
n=31
S. atrovirens
Aug-Dec
n=108
Feb-Mar
n=11
Percent Number
80
60
40
20
Sand
Sand/ Low Rock
Low Rock
Sand/ High Rock
High Rock
*

Figure 9c. Percent number of individuals of the three water-column aggregating _Sebastes_ species within each substratum category and the co-occurrence of bare substratum, drift algae and _M. pyrifera_ with fish. Asterisks indicate significant electivity ($P < 0.05$) for substratum category.

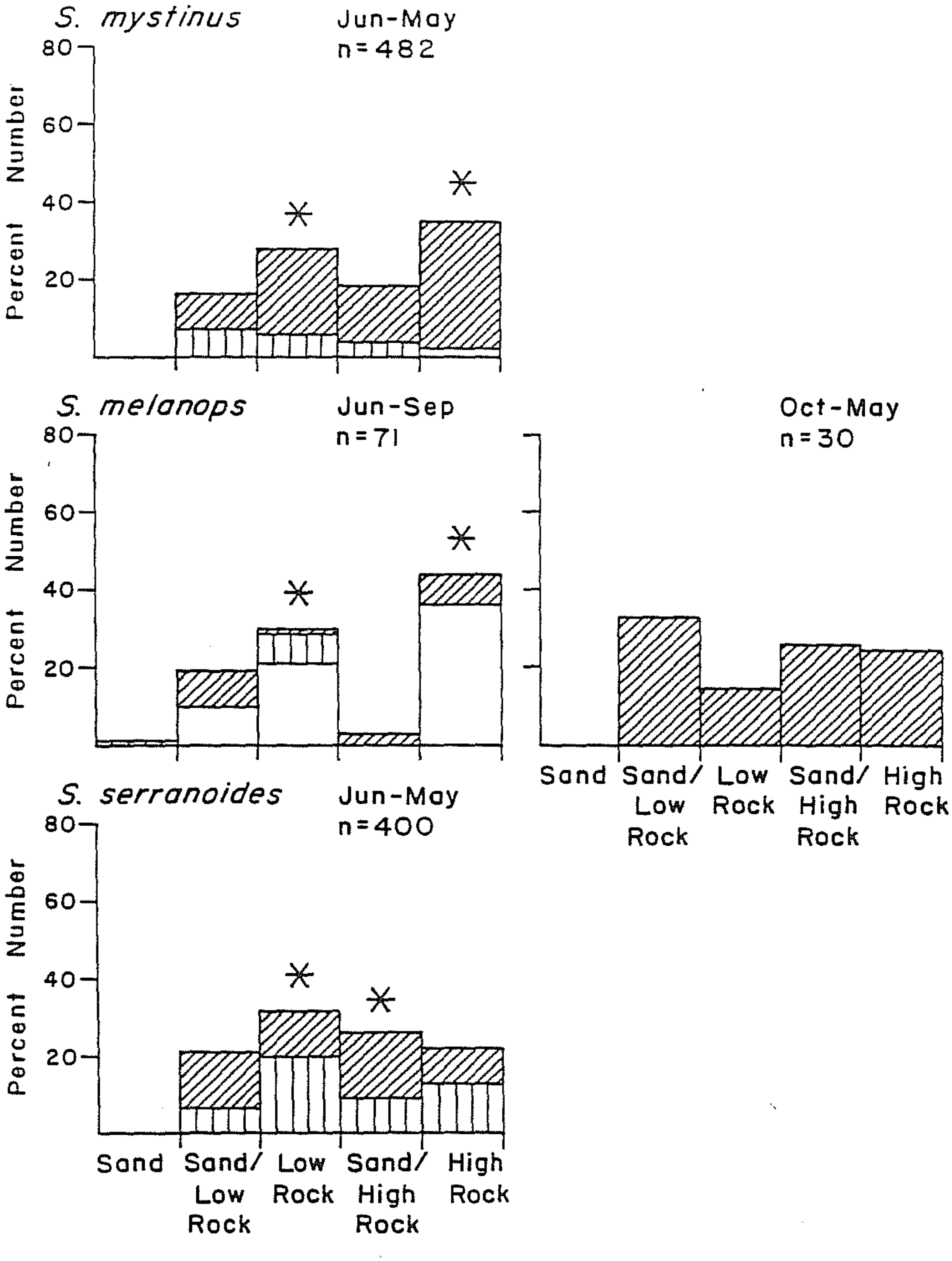

S. mystinus
Jun-May
n=482
Percent Number
80
60
40
20
S. melanops
Jun-Sep
n=71
Oct-May
n=30
Sand
Sand/ Low Rock
Low Rock
Sand/ High Rock
High Rock
S. serranoides
Jun-May
n=400
*

Figure 10. Clustering dendrogram of the eight young-of-the-year *Sebastes* species based on percent similarity values (PSI) of substratum type utilization.

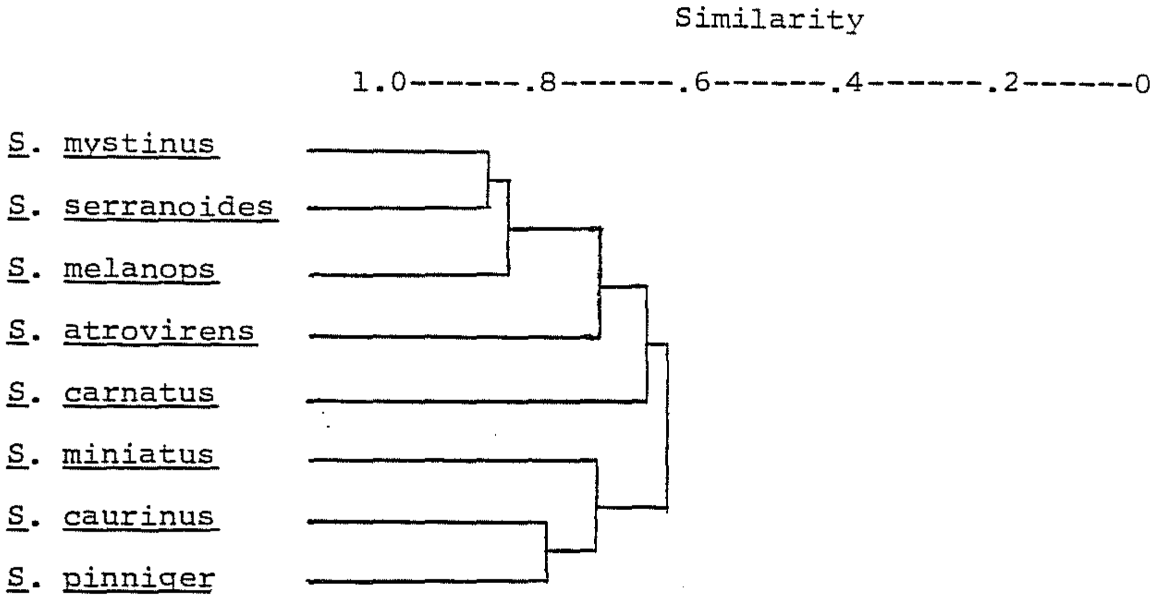

Similarity
1.0------.8------.6------.4------.2------0
S. mystinus
S. serranoides
S. melanops
S. atrovirens
S. carnatus
S. miniatus
S. caurinus
S. pinniger

Figure 11. Diagrammatic representation of the distributions of young-of-the-year of nine Sebastes species before and after the evening crepuscular period within the Arrowhead Point kelp forest.

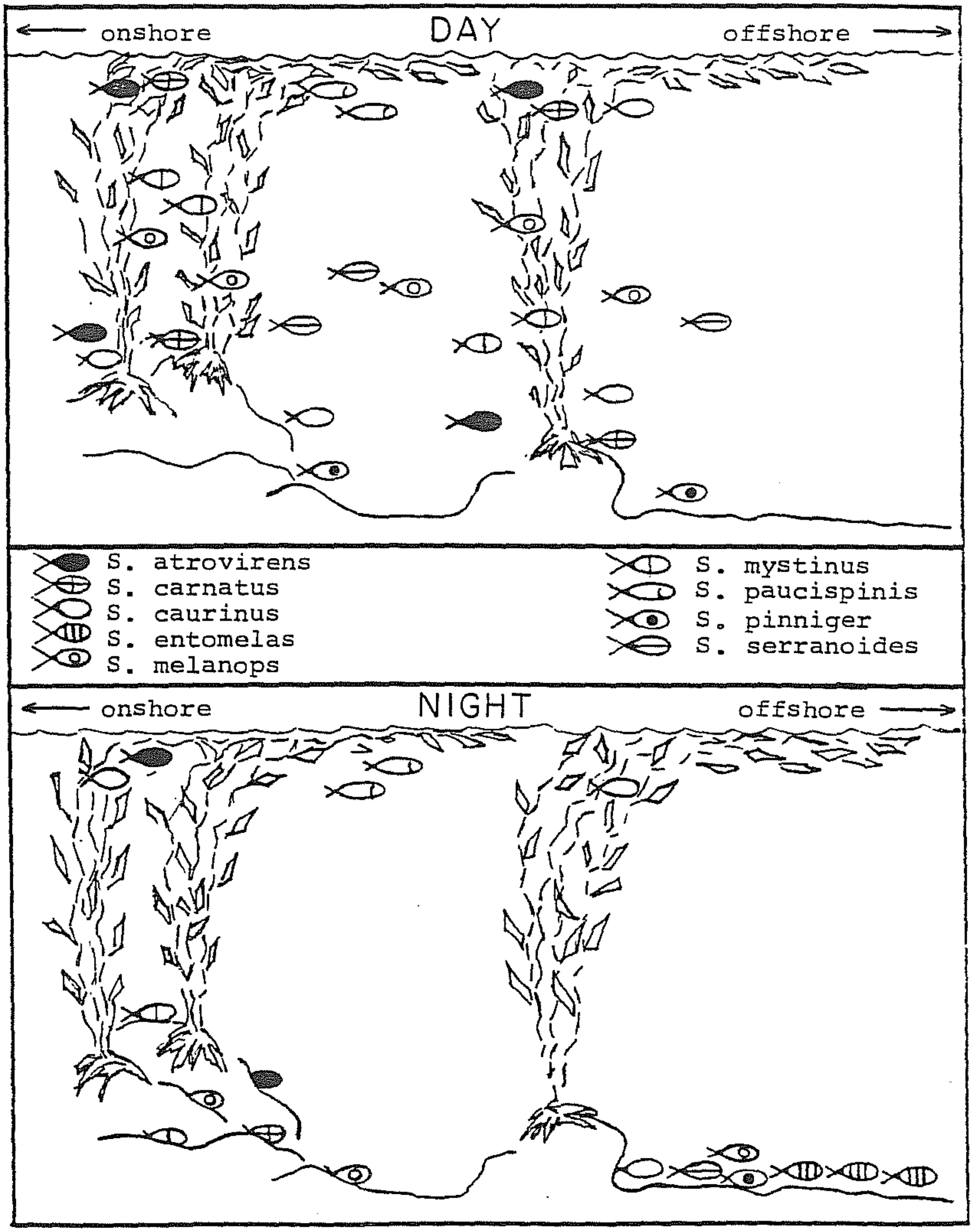

← onshore
DAY
offshore →
S. atrovirens
S. carnatus
S. caurinus
S. entomelas
S. melanops
S. mystinus
S. paucispinis
S. pinniger
S. serranoides
← onshore
NIGHT
offshore →

Table 1. Percent number of individuals of young-of-the-year *Sebastes* species within each of four categories of proximity to the vertical fronds of *Macrocystis pyrifera* at the surface and mid depth portions of the water column during 1980. I= fish > 0.5 m from fronds, II= 0.5 m > fish > 0.25 m, III= 0.25 m > fish > contact with fronds, IV= fish in contact with fronds. n= number of individuals observed.

	Surface					Mid-Depth				
		Proximity Categories					Proximity Categories			
Species	n	I	II	III	IV	n	I	II	III	IV
S. atrovirens	380	26.5	19	48.5	6	259	0	0	31	69
S. carnatus	89	42	26	26	6	31	0	0	0	100
S. caurinus	240	38	16	43	2	127	0	0	91	9
S. melanops	106	27	27	34	11	72	0	0	98	2
S. paucispinis	238	66	24	7	3	41	5	78	2	14
S. serranoides	19	79	0	21	0	140	86	2	10	2

Table 2. Mean number of young-of-the-year *Sebastes* (all species combined) before and after canopy removal at the harvested and non-harvested sites. Mean values of the before and after non-harvested and the before harvested treatments were compared with the Kruskal-Wallis (H/D) nonparametric analysis of variance. n= number of transects, C. I.= 95% confidence intervals.

Treatment	n	$\overline{X}$	C. I.	Total number of fish
Before				
Non-harvest	20	10.1*	±2.4	202
Harvest	18	7.1*	±1.9	128
After				
Non-harvest	12	10.3*	±2.8	124
Harvest	15	0.0	0	0

*H/D= 4.43; not significant ($P < 0.05$).

Table 3. Chi square (X^2) results and electivity values for each of eight young-of-the-year *Sebastes* species toward the five substratum categories. Asterisks indicate significantly positive ($P < 0.05$) differences of observed from expected (i.e., random) utilization of each substratum category, and all categories combined. n= number of fish observed.

				Substratum Type				
Species	Period	n	X^2	Sand	Sand/ Low rock	Low rock	Sand/ High rock	High rock
S. atrovirens	Aug-Sep	108	(*)	-0.01	-0.30	0.44*	-0.22	0.09*
	Feb-May	11	(n.s.)	-0.01	-0.15	0.21*	-0.04	-0.02
S. carnatus	Jun-Sep	51	(*)	0.05	0.07*	0.22*	-0.22	-0.12
	Oct-May	31	(*)	-0.01	-0.30	-0.02	-0.09	0.42*
S. caurinus	Jun-Sep	107	(*)	0.27*	0.17*	0.00	-0.18	-0.26
	Oct-May	20	(*)	-0.01	0.38*	-0.01	-0.22	-0.15
S. melanops	Jun-Sep	71	(*)	0.00	-0.13	0.16*	-0.19	0.16*
	Oct-May	30	(n.s.)	-0.01	0.00	0.02	0.04	-0.04
S. miniatus	Jun-May	33	(*)	0.14	0.49*	-0.12	-0.22	-0.29
S. mystinus	Jun-May	482	(*)	-0.01	-0.16	0.14*	-0.03	0.06*
S. serranoides	Jun-May	400	(*)	-0.01	-0.11	0.16*	0.04*	-0.08
S. pinniger	Jun-May	651	(*)	0.11*	0.23*	-0.04	-0.05	-0.26

Table 4. Similarity matrix of substratum type utilization. Based on P. S. I. values derived from pairwise comparison between all species among all five substratum types.

Species	S. atrovirens	S. carnatus	S. caurinus	S. melanops	S. miniatus	S. mystinus	S. pinniger	S. serranoides
S. atrovirens	-							
S. carnatus	.59	-						
S. caurinus	.22	.65	-					
S. melanops	.71	.67	.42	-				
S. miniatus	.06	.49	.68	.23	-			
S. mystinus	.66	.61	.39	.82	.19	-		
S. pinniger	.17	.60	.79	.37	.71	.47	-	
S. serranoides	.56	.69	.43	.74	.24	.85	.52	-

Table 5. Numbers of juvenile *Sebastes* species observed at the kelp-only and rock-only treatments during summer census periods. Values are total number of each species per entire area at each depth. Species abundances within the surface (canopy) area are derived from 11.0m X 1.0m X 1.0m transects (log transformed mean and 95% confidence intervals) multiplied by 5.67.

Habitat	Species	Z	Census Periods					
			18 May	7 June	18 June	1 July	11 July	19 August
Kelp Only								
	S. *atrovirens*	surf.	0	0	0	0		$32(^{+48}_{-23.5})$
		mid.	0	0	0	0	0	38
		bott.	0	0	0	0	0	12
	S. *carnatus*	surf.	0*	$24(^{+36}_{-16})$*	$17(^{+33}_{-9})$*	$17(^{+31}_{-8.5})$*	$93(^{+248}_{-38})$**	0
		mid.	0*	6*	18*	32*	15	22
		bott.	0*	0*	1*	8*	0	0
	S. *caurinus*	surf.						0
		mid.					45	28
		bott.					21	114
	S. *melanops*	surf.	0	$16(^{+36}_{-6})$	$1(^{+1.5}_{-0})$	$5(^{+10}_{-2})$	$11(^{+34}_{-1})$	0
		mid.	0	1	36	20	5	3
		bott.	0	45	85	180	172	81
	S. *paucispinis*	surf.	0	$18(^{+40}_{-6})$	$15(^{+34}_{-5})$	$4(^{+11}_{-0})$	$12(^{+35}_{-2})$	0
		mid.	0	2	15	6	0	0
		bott.	0	0	0	0	0	0
Rock Only								
	S. *mystinus*	surf.	0	0	0	0	0	0
		mid.	0	0	0	0	0	0
		bott.	4	4	3	9	2	0
	S. *pinniger*	surf.	0	0	0	0	0	0
		mid.	0	0	0	0	0	0
		bott.	8	47	50	77	51	19
	S. *serranoides*	surf.	0	0	0	0	0	0
		mid.	0	0	0	0	0	0
		bott.	0	1	20	12	6	3

* Value represents combined numbers of S. *carnatus* and S. *caurinus*.

** Value represents combined numbers of S. *atrovirens*, S. *carnatus* and S. *caurinus*.

Table 6. Comparison of microhabitat utilization of fishes recruited to the rock only and kelp only treatments. Data are given as percent of individuals. Algae includes drift and _Macrocystis pyrifera_ combined.

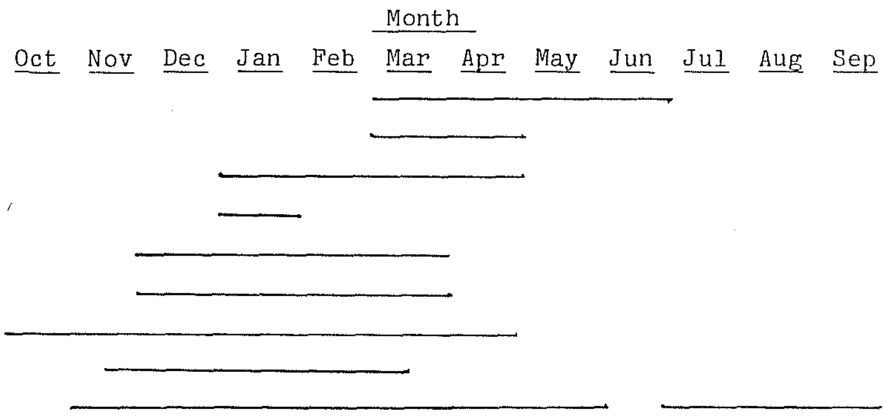
Habitat	Species	Bottom Microhabitat Utilization	
		Bare Rock	Algae
Rock Only			
	S. miniatus	100	0
	S. mystinus	76	24
	S. pinniger	64.5	35.5
	S. serranoides	47	53
Kelp Only			
	S. atrovirens	12	88
	S. carnatus	14	86
	S. caurinus	8	92
	S. melanops	20	80
	S. paucispinis	-	-

Table 7. Mean number of individuals within each of nine locations of the kelp forest before, during and after the evening crepuscular period. Data presented are back-transformed after log(X+1) transformation: (+ and −) represent upper and lower limits respectively, of 95% confidence interval.

Species	Depth	Before			During			After		
		Inside $\bar{x}$ (C.I.)	Interface $\bar{x}$ (C.I.)	Outside $\bar{x}$ (C.I.)	Inside $\bar{x}$ (C.I.)	Interface $\bar{x}$ (C.I.)	Outside $\bar{x}$ (C.I.)	Inside $\bar{x}$ (C.I.)	Interface $\bar{x}$ (C.I.)	Outside $\bar{x}$ (C.I.)
S. atrovirens			(n=6)			(n=5)			(n=7)	
	surface	$4.1(^{+8.7}_{-1.7})$	$5.8(^{+9.5}_{-3.4})$	0	$3.0(^{+9.0}_{-.6})$	$1.6(^{+5.0}_{-.1})$	0	$0.4(^{+1.0}_{-0})$	0	0
	mid	0	0	0	0	0	0	0	0	0
	bottom	0	0	0	0	0	0	0	0	0
S. carnatus			(n=8)			(n=4)			(n=7)	
	surface	$4.9(^{+8.6}_{-2.6})$	$5.0(^{+8.5}_{-2.8})$	0	$2.0(^{+5.2}_{-1.0})$	$2.0(^{+8.0}_{-0})$	0	$.6(^{+1.6}_{-0})$	$.2(^{+.5}_{-0})$	0
	mid	$.1(^{+.4}_{-0})$	$1.4(^{+2.8}_{-.5})$	0	$.2(^{+.6}_{-0})$	$1.2(^{+3.6}_{-0})$	0	0	0	0
	bottom	$6.4(^{+10.7}_{-3.7})$	$5.1(^{+6.7}_{-3.8})$	0	$2.0(^{+2.8}_{-1.3})$	$.9(^{+3.3}_{-0})$	0	$.1(^{+.4}_{-0})$	0	0
S. caurinus			(n=8)			(n=4)			(n=7)	
	surface	$1.4(^{+2.9}_{-.5})$	$3.5(^{+5.1}_{-2.3})$	0	$1.8(^{+4.6}_{-.4})$	$3.4(^{+6.0}_{-1.8})$	0	$1.2(^{+2.1}_{-.5})$	$.3(^{+.7}_{-0})$	0
	mid	$.2(^{+.5}_{-0})$	$6.4(^{+13.1}_{-2.9})$	0	0	$1.7(^{+5.2}_{-.2})$	0	0	$.1(^{+.3}_{-0})$	0
	bottom	$6.6(^{+8.6}_{-5.0})$	$29.0(^{+39.5}_{-21.0})$	0	$4.8(^{+7.6}_{-3.0})$	$32.0(^{+49.0}_{-21.0})$	0	0	$1.2(^{+3.4}_{-.1})$	$1.2(^{+2.2}_{-.5})$
S. pinniger			(n=8)			(n=4)			(n=7)	
	surface	0	0	0	0	0		0	0	0
	mid	0	0	0	0	0		0	0	0
	bottom	$9.3(^{+12.1}_{-7.7})$	$7.4(^{+10.6}_{-5.4})$	$.2(^{+.5}_{-0})$	$1.6(^{+3.0}_{-.6})$	$25.5(^{+46.0}_{-14.0})$	$2.0(^{+6.5}_{-.2})$	$.2(^{+.7}_{-0})$	$4.4(^{+7.5}_{-2.4})$	$5.2(^{+6.8}_{-3.9})$
S. melanops			(n=9)			(n=4)			(n=9)	
	surface	0	0	0	0	0	0	0	0	0
	mid	$3.9(^{+6.7}_{-2.2})$	$2.8(^{+7.3}_{-.7})$	0	0	0	0	0	0	0
	bottom	$1.8(^{+4.4}_{-.5})$	$.3(^{+.6}_{-0})$	0	$8.7(^{+20.0}_{-3.4})$	$7.8(^{+37.4}_{-1.0})$	$2.0(^{+11.0}_{-0})$	$7.4(^{+7.6}_{-7.2})$	$1.0(^{+2.5}_{-.1})$	$28.5(^{+45.8}_{-17.6})$
S. mystinus			(n=8)			(n=4)			(n=7)	
	surface	$.2(^{+.5}_{-0})$	$.1(^{+.3}_{-0})$	0	$.2(^{+.7}_{-0})$	0	0	0	0	0
	mid	$16.6(^{+24.0}_{-11.5})$	$16(^{+23.0}_{-11.0})$	0	0	0	0	0	0	0
	bottom	$16.1(^{+23.0}_{-11.0})$	$2.8(^{+5.1}_{-1.3})$	0	$29.0(^{+52.0}_{-16.0})$	$5.0(^{+9.4}_{-2.4})$	0	$12.3(^{+16.5}_{-9.0})$	$.3(^{+1.0}_{-0})$	0
S. paucispinis			(n=10)			(n=4)			(n=9)	
	surface	$.4(^{+.8}_{-0})$	$.8(^{+1.6}_{-.2})$	0	$.2(^{+.7}_{-0})$	$.4(^{+1.0}_{-0})$	0	$1.3(^{+3.2}_{-.3})$	$.2(^{+.7}_{-0})$	0
	mid	0	$.1(^{+.1}_{-0})$	0	0	$.2(^{+.7}_{-0})$	0	0	$.1(^{+.3}_{-0})$	0
	bottom	$.1(^{+.2}_{-0})$	$.4(^{+.9}_{-0})$	0	0	$.5(^{+1.5}_{-0})$	0	0	0	$.1(^{+2.6}_{-0})$
S. serranoides			(n=8)			(n=4)			(n=7)	
	surface	$2.5(^{+5.7}_{-1.0})$	$4.6(^{+11.0}_{-1.6})$	0	$1.9(^{+6.3}_{-0})$	$3.4(^{+13.0}_{-.4})$	0	$1.7(^{+3.6}_{-.6})$	$13.1(^{+27.0}_{-6.0})$	$1.2(^{+3.0}_{-.6})$
	mid	$9.9(^{+16.3}_{-5.9})$	$3.5(^{+8.0}_{-1.2})$	$.1(^{+.3}_{-0})$	$3.0(^{+10.5}_{-.4})$	$8.7(^{+17.0}_{-4.2})$	0	$.2(^{+.5}_{-0})$	$1.1(^{+3.0}_{-1.0})$	$.3(^{+.9}_{-0})$
	bottom	$2.8(^{+4.5}_{-1.6})$	$.3(^{+.6}_{-0})$	0	$5.9(^{+27.0}_{-.7})$	$25.0(^{+53.0}_{-11.4})$	$4.4(^{+16.0}_{-.4})$	$6.7(^{+10.0}_{-4.3})$	$2.0(^{+5.0}_{-.5})$	$21.0(^{+36.5}_{-12.3})$

Table 8. Periods of parturition of the nine species of Sebastes whose young-of-the-year occurred within the Arrowhead Point kelp forest.

Species	Source*
S. atrovirens	3, 8
S. carnatus	3, 8
S. caurinus	1, 3
S. melanops	7
S. mystinus	3, 4
S. serranoides	2
S. paucispinis	1, 5, 6
S. pinniger	6
S. miniatus	1, 3



*Source	Location
1. Eigenmann, 1891	southern California
2. Love and Westphal, 1981	central California
3. Love, pers. comm. 10 June 1982	southern and central California
4. Miller and Giebel, 1973	central California
5. Moser, 1967	southern California
6. Phillips, 1964	California
7. Westrheim, 1975	Oregon
8. pers. obs. (this study)	Carmel Bay, California

Table 9. Timing of the initial occurrence of young-of-the-year *Sebastes* species to nearshore shallow reefs.

Species	Season	Location	Source
S. atrovirens	April-August	central California	Limbaugh 1955
	late July-August	Arrowhead Pt.	this study
S. carnatus	mid-June	Santa Cruz Island	Larson 1980
	July	southern California	Limbaugh 1955
	late June-July	Arrowhead Pt.	this study
S. caurinus	October	Puget Sound	Patten 1973
	late April-May	Arrowhead Pt.	this study
S. melanops	mid-May, peak later	Barkely Sound	Leaman 1972
	May-June, peak later	Arrowhead Pt.	this study
S. miniatus	March-April	southern California	Limbaugh 1955
	May, Sept., Dec.	Arrowhead Pt.	this study
S. mystinus	October	southern California	Carlisle *et al* 1964
	April	Monterey, California	Miller and Giebel 1973
	April	Arrowhead Pt.	this study
S. paucispinis	May-June	southern California	Moser 1967
	July	" "	Carlisle *et al* 1964
	April	" "	Limbaugh 1955
	April	Monterey, California	Miller and Giebel 1973
	April-June	Arrowhead Pt.	this study
S. pinniger	June-August	central Oregon	Richardson & Laroche 1979
	April-May	Arrowhead Pt.	this study
S. serranoides	May-June	southern California	Carlisle *et al* 1964
	May	" "	Feder *et al* 1974
	mid-summer	Santa Catalina Is.	Hobson and Chess 1976
	March-April	Avila, central Calif.	Love 1981
	May-June	Arrowhead Pt.	this study