# THE INVERTEBRATE ASSEMBLAGE ASSOCIATED WITH THE GIANT KELP, *MACROCYSTIS PYRIFERA*, AT SANTA CATALINA ISLAND, CALIFORNIA: A GENERAL DESCRIPTION WITH EMPHASIS ON AMPHIPODS, COPEPODS, MYSIDS, AND SHRIMPS[1]

JAMES A. COYER[2]


## ABSTRACT

The motile invertebrate assemblage associated with the giant kelp, *Macrocystis pyrifera*, fronds was examined monthly from June 1975 through December 1976, at Santa Catalina Island, California. Replicate samples were collected from each of three vertical zones (canopy [C], middle [M], bottom [B]).

The number of species collected from all zones was 114 and ranged from 51 to 75 for any given month. Amphipods, copepods, mysids, and shrimps comprised the majority of invertebrate abundance (86 [C], 92 [M], 93% [B]) and biomass (90 [C], 89 [M], 86% [B]). Gammarid amphipods dominated the assemblage in numbers (34 [C], 60 [M], 51% [B]), biomass (34 [C], 68 [M], 67% [B]), and number of species (20).

The assemblage displayed three patterns of vertical stratification within the *Macrocystis* forest: 1) The mean number of species progressively decreased from the bottom to the canopy (several species displayed zone preferences); 2) more individuals and a greater total biomass were present in the lower zones than in the canopy; and 3) the mean lengths of gammarids, mysids, and shrimps were significantly larger and proportionately greater numbers of large individuals were present in the canopy than in either of the lower zones.


Subtidal forests of giant kelp have long attracted the interest of biologists, beginning with Darwin's (1860: 240) description of the organisms associated with the giant kelp forests off Tierra del Fuego. Since the advent of scuba techniques in the mid-1950's, several studies have examined in detail the attached and/or motile species of invertebrates associated with surfaces of the giant kelp, *Macrocystis pyrifera* (Limbaugh 1955; Clarke 1971; Ghelardi 1971; Jones 1971; Wing and Clendenning 1971; Miller and Geibel 1973; Lowry et al. 1974; Bernstein and Jung 1979; Yoshioka 1982 a, b). Few, however, have attempted a long-term and comprehensive examination of the entire assemblage of small and motile invertebrates found with the giant kelp. The assemblage is important for several reasons, notably as the major source of food for most fishes residing within the kelp forests (see fish diet studies by Quast 1968; Hobson 1971; Bray and Ebeling 1975; Hobson and Chess 1976).

The present report examines the composition, patterns of vertical stratification, and seasonal dynamics of the small and motile invertebrate assemblage associated with the fronds of *M. pyrifera*. A general overview of the assemblage and a detailed examination of the amphipods, copepods, mysids, and shrimps are presented.

## STUDY AREA

The study area was Habitat Reef, located in Big Fisherman Cove, Santa Catalina Island, Calif. (lat. 33°28'N, long. 118°29'W). Habitat Reef is a fingerlike extension of bedrock ranging in depth from 2 to 18 m and is bounded on the three outer margins by an expansive area of shelly debris substrate. The western and northern sides of the reef slope sharply to a depth of 20-25 m, whereas the eastern edge slopes gradually to a shallower area ranging from 8 to 19 m. Water temperatures at Habitat Reef ranged from 13.6° to 21.2°C during the study, warmest during July through September and coolest from December to February.

The algal community of the shoreward portion (<3 m depth) of Habitat Reef was dominated by *Phyllospadix torreyi*, *Eisenia arborea*, *Cystoseira neglecta*, and *Sargassum muticum* (seasonally). The outermost portion (>3 m depth) was dominated by *Macrocystis* and the understory algae in this area was sparse, although small patches of *Dictyopteris zonarioides* and *C. neglecta* were present in some areas.

[1]Contribution No. 37, from the Catalina Marine Science Center.

[2]Catalina Marine Science Center (University of Southern California), Avalon, Calif.; present address: Division of Science and Mathematics, Marymount Palos Verdes College, Rancho Palos Verdes, CA 90274.

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# MATERIALS AND METHODS

## Zonation and Kelp Density

The kelp forest at Habitat Reef was divided into three vertical zones: Canopy (C), middle (M), and bottom (B). The canopy extended from the water surface to a depth of 1 m, the bottom ranged from just above the kelp holdfasts to 2 m above the substrate, and the middle included the area between the canopy and the bottom. Holdfasts were not examined. Kelp density was measured by randomly establishing 25 circular 1 $m^2$ plots within the study area during November 1975 and October and December 1976. The number of enclosed plants and the number of fronds/plant were determined.

## Sampling Procedure

Samples were collected monthly from plants in the central portion of the kelp forest (7-9 m depth) during tidal heights ranging from +1.0 to +1.3 m mean lower low water. From June through September 1975, three replicate samples were collected from each zone; from October 1975 through December 1976, five replicates were collected. Only one sample was collected from any plant, and this sample consisted of the entire plant portion within the desired zone. The middle and bottom zones were collected by carefully severing the upper portions and allowing them to drift away. Disturbance to the lower zones during this procedure was negligible. Similar amounts of kelp were collected from each zone throughout the study ($n$ = 19; $\overline{kg}$ = 2.5[C] 2.1[M], 2.3 [B]).

The kelp-associated invertebrates were collected by scuba divers maneuvering a plankton net (1 m diameter, 3 m long, 0.33 mm mesh) over the desired portion of the plant. This procedure captured most motile invertebrates on the kelp, as well as within the surrounding water column (1 m diameter). The enclosed sample was placed in a large container filled with warm freshwater (providing a thermal and salinity shock), vigorously agitated, and removed. The remaining water was filtered through a 0.25 mm sieve and the residue preserved. Thus, the term "invertebrate" in this investigation refers to all motile individuals larger than 0.33 mm (excluding protozoans, cnidarians, and nematodes).

The efficiency of the agitation-freshwater method was tested by placing the processed kelp into another container of warm freshwater and allowing it to stand for 4 h. Subsequent agitation and filtering indicated that 96% of all motile invertebrates in each zone were removed by the initial agitation-freshwater treatment.

Organisms were identified to species (except for some juveniles). The wet weight of kelp from each sample was measured, and abundances of all taxa were expressed as the number of individuals per kilogram (wet weight) of kelp. The somewhat unconventional normalization of species abundance to unit biomass was selected for three reasons. First, structural complexity within the kelp forest habitat is created by interdigitating kelp blades and stipes and is a function (in part) of both kelp surface area and biomass. Many kelp-associated species, particularly the swarming mysids, may respond primarily to structural complexity of the habitat when seeking shelter and/or food. Secondly, biomass is much easier and faster to measure than is surface area (conversion ratios of kelp wet weight to surface area [both sides of blades + stipes] and kelp dry weight to wet weight are presented in Table 1). Thirdly, unit biomass will facilitate comparisons with invertebrate associations of other species of marine algae for which it is difficult to compute a unit area (i.e., bushy reds and browns).

TABLE 1.—Ratios of kelp wet weight (kg) to kelp surface area ($m^2$) and dry weight (kg) to wet weight (kg).

| | Wet weight/area | | | Dry weight/Wet weight | | |
|---|---|---|---|---|---|---|
| Zone | $\bar{x}$ | SD | $n$ | $\bar{x}$ | SD | $n$ |
| Canopy | 0.21 | 0.002 | 10 | 0.16 | 0.010 | 6 |
| Middle | 0.19 | 0.002 | 10 | 0.15 | 0.025 | 6 |
| Bottom | 0.42 | 0.040 | 10 | 0.13 | 0.042 | 6 |

## Determination of Invertebrate Lengths and Biomass

Growth series within the principal taxa were established. Individuals ($n$ = 30-94) were measured to the nearest 0.04 mm, using a dissecting microscope and occular micrometer, blotted dry, and weighed using an analytical balance to determine length-weight relationships. Smaller and/or minor taxa (copepods, ostracods, caprellids, molluscs, etc.) were assigned constant weights based on the mean weight of 20 individuals.

Vertical patterns of size-stratification were examined by measuring the lengths of principal taxa within each zone for each quarter from January 1975 through October 1976. Single samples were collected in January and April 1975; subsequent samples were replicated (3 or 5). For shrimps and mysids, all (January through July 1975) or up to 75 individuals of each major species were measured from each replicate of each zone; for gammarid amphipods, at least 50 individuals (comprising all species) were measured from one randomly selected replicate of each zone. Replicates were pooled and size-frequency distributions were determined for each taxon within each of the zones. The nonparametric Kolmogorov-Smirnov (K-S) two-sample test (one-tailed) was used to test whether the values from one distribution were stochastically larger than the values from another distribution (Siegel 1956).

The mean weight of an individual within a major taxon (shrimps, mysids, gammarids) was determined from the mean length and the appropriate length-weight formula. The mean weight then was multiplied by the mean monthly abundance of the taxon to determine the taxon biomass. Quarterly length measurements were applied to the month preceding and following the measuring month (i.e., April measurements were assigned to March and May) for biomass measurements. Monthly abundance values of the smaller taxa were multiplied by the assigned weight to estimate the biomass.

# RESULTS

## Kelp Density

*Macrocystis* density at Habitat Reef was high (4.7 plants/m$^2$) from November 1975 through August 1976 (Table 2). In late September 1976, density and canopy cover were reduced (1.5/m$^2$) and continued to decline over the next 4 mo.

TABLE 2.—*Macrocystis* density and the number of fronds/plant (± width of 95% C.I./2) at Habitat Reef. Sample size in parentheses.

| Date | Density/m$^2$ | No. of fronds/plant |
|---|---|---|
| Nov. 1975 | 4.7±2.3 (25) | 3.4±1.0 (118) |
| Oct. 1976 | 1.5±0.7 (29) | 6.7±1.6 (46) |
| Dec. 1976 | 0.7±0.3 (25) | 4.7±2.6 (17) |

## General Taxonomic Composition of the Invertebrate Assemblage

The invertebrate assemblage associated with the fronds of *Macrocystis* was composed primarily of amphipods, copepods, mysids, and shrimps (Tables 3, 4). Mysids and shrimps were among the largest

TABLE 4.—Mean abundance ($\overline{\text{no.}}$/kg kelp ± width of 95% C.I./2) for the major invertebrate taxa within each zone. Parenthetical values are the mean length and weight ($\overline{\text{mm}}$, $\overline{\text{mg}}$) of each taxon; an asterisk indicates that a constant length and weight was used for all zones. All values are averaged over the entire 19-mo study.

| Taxon | Canopy | Middle | Bottom |
|---|---|---|---|
| Gammarid amphipods | 882.4 ± 267.0 (2.8,0.6) | 4,123.0 ± 890.2 (1.8,0.4) | 3,117.8 ± 715.3 (2.0,0.4) |
| Copepods | 1,128.0 ± 370.2 | 1,977.0 ± 540.8 *(0.8,0.1) | 2,453.1 ± 441.0 |
| Ostracods | 188.2 ± 76.7 | 108.8 ± 51.1 *(0.9,0.1) | 65.7 ± 30.0 |
| Echinoids (juv.) | 13.9 ± 25.5 | 260.5 ± 375.4 *(0.5,0.1) | 83.0 ± 119.2 |
| Mysids | 91.4 ± 57.8 (6.2,3.5) | 151.8 ± 38.9 (4.7,1.3) | 108.0 ± 50.5 (4.4,1.2) |
| Molluscs ("shelled") | 14.8 ± 9.0 | 98.0 ± 21.8 *(1.3,0.7) | 168.4 ± 44.9 |
| Caridean shrimps | 136.5 ± 48.4 (7.1,3.8) | 65.2 ± 28.4 (6.0,2.7) | 51.4 ± 16.0 (5.4,2.3) |
| Platyhelminthes | 31.7 ± 17.1 | 36.8 ± 16.2 *(–,3.8) | 34.0 ± 17.0 |
| Cladocerans | 72.2 ± 93.4 | 9.2 ± 5.1 *(0.7,0.1) | 9.3 ± 6.9 |
| Polychaetes | 8.8 ± 11.3 | 28.0 ± 8.0 *(3.3,0.5) | 17.4 ± 7.2 |
| Cypris (barnacle) larvae | 13.4 ± 16.6 | 24.0 ± 22.1 *(0.7,0.1) | 14.3 ± 9.4 |
| Molluscs (nudibranchs) | 10.9 ± 11.3 | 13.4 ± 11.8 *(1.3,1.1) | 8.1 ± 7.5 |
| Sphaeromatid isopods | 0.1 ± 0.1 | 0.2 ± 0.1 *(2.4,1.1) | 19.7 ± 23.0 |
| Caprellid amphipods | 4.1 ± 2.0 | 2.7 ± 1.0 *(6.9,0.8) | 1.8 ± 1.3 |
| Idoteid isopods | 3.1 ± 3.2 | 0.1 ± 0.1 *(7.2,4.0) | 0.1 ± <0.1 |
| Asteroids (juv.) | 0 2 ± 0.1 | 1.1 ± 1.3 *(2.7,2.0) | 0.6 ± 0.8 |
| Jaeropsid isopods | 0.1 ± 0.1 | 0.2 ± 0.3 *(2.3,0.3) | 1.4 ± 0.9 |
| Cumaceans | 0 — | 0.2 ± 0.2 — | 0.3 ± 0.3 |
| Brachyurans (zoea) | 0 — | 0 — — | 0.1 ± <0.1 |
| Ophiuroids (juv.) | 0 — | <0.1 ± <0.1 — | <0.1 ± <0.1 |
| Tanaids | 0 — | <0.1 ± 0.1 — | 0.1 ± 0.1 |

TABLE 3.—The mean (± width of 95% C.I./2) monthly abundance ($\overline{\text{no.}}$ organisms/kg kelp) and biomass ($\overline{\text{mg}}$ organisms/kg kelp) for each major invertebrate group associated with the giant kelp. Data are averaged over the entire 19-mo study; proportions of total numbers or biomass (all species) are presented in parentheses.

| Zone | Gammarids | Copepods | Mysids | Shrimps | Total |
|---|---|---|---|---|---|
| Canopy | | | | | |
| Numbers | 882 ± 267 (33.9) | 1.128 ± 370 (43.4) | 91 ± 58 (3.5) | 136 ± 48 (5.2) | 2,599 ± 580 |
| Biomass | 589 ± 236 (33.8) | 56 ± 18 (3.2) | 336 ± 255 (19.3) | 583 ± 300 (33.4) | 1,743 ± 765 |
| Middle | | | | | |
| Numbers | 4.123 ± 890 (59.8) | 1.977 ± 541 (28.7) | 152 ± 39 (2.2) | 65 ± 28 (0.9) | 6,900 ± 1,382 |
| Biomass | 1,634 ± 359 (68.4) | 99 ± 27 (4.1) | 218 ± 68 (9.1) | 174 ± 71 (7.3) | 2,387 ± 493 |
| Bottom | | | | | |
| Numbers | 3,118 ± 715 (50.8) | 2,453 ± 441 (39.9) | 108 ± 51 (1.7) | 51 ± 16 (0.8) | 6,153 ± 937 |
| Biomass | 1,388 ± 337 (67.4) | 123 ± 22 (6.0) | 143 ± 83 (6.9) | 116 ± 37 (5.6) | 2,061 ± 454 |

species present, copepods among the smallest (Table 4).

The number of species collected from all zones totaled 114, but ranged from 51 to 75 for any given month (Fig 1). When ranked by the mean monthly abundance, 7 species were dominant (>100/kg), 23 were common (10-100/kg), 24 were uncommon (1-10/kg), and 60 were rare (<1/kg). Crustaceans and gastropods had the greatest species representation with 63 and 36 species present, respectively. The 10 most abundant species within the canopy and bottom and 9 of the top 10 species in the middle were crustaceans; of the 14 crustacean species represented, 6 were gammarid amphipods and 4 were harpacticoid copepods (Table 5).

## Vertical Patterns of Distribution, Abundance, and Sizes

Invertebrate numbers and biomass ($\overline{\text{no.}}$/kg kelp, $\overline{\text{mg}}$/kg kelp) were greatest in the middle (6,900, 2,387) and bottom (6,143, 2,061) zones, lowest in the canopy (2,599, 1,743; Table 3). Similarly, the number of species was always lowest in the canopy, intermediate in the middle, and highest in the bottom (Student's $t$-test, $P < 0.05$; Fig. 1).

Gammarid amphipods were the most important taxon associated with *Macrocystis*, dominating the invertebrate assemblage within each zone in terms of numbers (34-60%) and biomass (34-68%; Table 3). Twenty species were collected with fewer species present in the canopy (11) than in the middle (16) or bottom (18).

Collectively, *Microjassa litotes*, *Gitanopsis vilordes*, and *Aoroides columbiae* comprised 83% by number of all gammarids in the canopy, 92% of those in the middle, and 70% of the gammarids in the bottom. The most abundant gammarid in the canopy was *G. vilordes* (53.0%); *M. litotes* was most abundant in the middle (49.0%) and bottom (33.8%; Table 6, Fig. 2). Among the other gammarids present, *Ampithoe plea* and *Hyale frequens* were much more common in the canopy than in the lower zones, whereas *Batea transversa* and *Pontogeneia rostrata* were abundant in the bottom zone and uncommon in the canopy (Table 6).

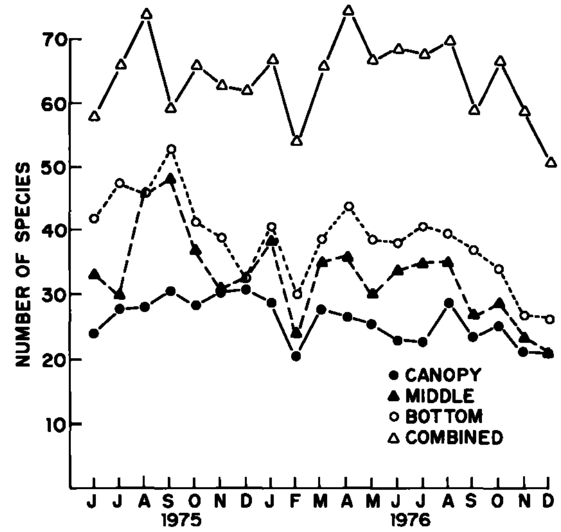


FIGURE 1.—The number of invertebrate species present in each of the vertical zones. Many species are present in more than one zone. Grand means (± width of 95% C.I./2): 26.7 ± 1.6 (C), 33.0 ± 3.3 (M), 38.9 ± 3.2 (B).

Numerically, copepods formed a major portion of the invertebrate assemblage (29-43%), but contributed very little to the total biomass (3-6%; Tables 3, 4). Although numerous in all zones, copepods were more abundant in the middle and bottom (Table 3, Fig. 2). Most (88% by number) in the middle zone consisted of *Porcellidium viridae*, *Porcellidium* sp. A, and *Tisbe* sp. In the canopy and bottom zones, *P. viridae*, *Tisbe* sp., and *Scutellidium lamellipes* accounted for 89 and 92%, respectively.

Mysids and shrimps were minor numerical components of the assemblage (2-3 and 1-5%, respectively), but formed major proportions of the invertebrate biomass (7-19, 6-33%; Tables 3, 4). Each of the three

TABLE 5.—The ten most abundant invertebrate species in each zone. Abundances are mean monthly values for the 19-mo study (C = copepod, G = gammarid amphipod, M = mysid, O = ostracod, S = shrimp, E = echinoid [urchin]).

| Canopy | $\overline{\text{No.}}$/kg kelp | Middle | $\overline{\text{No.}}$/kg kelp | Bottom | $\overline{\text{No.}}$/kg kelp |
|---|---|---|---|---|---|
| *Porcellidium viridae* (C) | 557 | *Microjassa litotes* (G) | 2,018 | *Porcellidium viridae* (C) | 1,768 |
| *Gitanopsis vilordes* (G) | 466 | *Gitanopsis vilordes* (G) | 1,551 | *Microjassa litotes* (G) | 1,054 |
| *Tisbe* spp. (C) | 303 | *Porcellidium viridae* (C) | 1,106 | *Gitanopsis vilordes* (G) | 778 |
| *Macrocyprina pacifica* (O) | 165 | *Aoroides columbiae* (G) | 600 | *Pontogeneia rostrata* (G) | 397 |
| *Aoroides columbiae* (G) | 164 | *Tisbe* spp. (C) | 358 | *Tisbe* spp. (C) | 374 |
| *Scutellidium lamellipes* (C) | 144 | *Porcellidium* sp. A (C) | 270 | *Aoroides columbiae* (G) | 350 |
| *Hippolyte clarki* (S) | 137 | *Strongylocentrotus* sp. (E) | 260 | *Batea transversa* (G) | 342 |
| *Microjassa litotes* (G) | 103 | *Siriella pacifica* (M) | 148 | *Scutellidium lamellipes* (C) | 163 |
| *Ampithoe plea* (G) | 91 | *Scutellidium lamellipes* (C) | 137 | *Porcellidium* sp. A (C) | 113 |
| *Acanthomysis sculpta* (M) | 74 | *Macrocyprina pacifica* (O) | 88 | *Siriella pacifica* (M) | 99 |

TABLE 6.—The ten most abundant gammarid amphipods in each zone. Abundances are mean monthly values for the 19-mo study.

| Canopy | $\overline{\text{No.}}$/kg kelp | Middle | $\overline{\text{No.}}$/kg kelp | Bottom | $\overline{\text{No.}}$/kg kelp |
|---|---|---|---|---|---|
| *Gitanopsis vilordes* | 466 | *Microjassa litotes* | 2,018 | *Microjassa litotes* | 1,054 |
| *Aoroides columbiae* | 164 | *Gitanopsis vilordes* | 1,183 | *Gitanopsis vilordes* | 778 |
| *Microjassa litotes* | 103 | *Aoroides columbiae* | 600 | *Pontogeneia rostrata* | 435 |
| *Ampithoe plea* | 91 | *Batea transversa* | 82 | *Aoroides columbiae* | 350 |
| *Hyale frequens* | 24 | *Pontogeneia rostrata* | 40 | *Batea transversa* | 342 |
| *Batea transversa* | 2 | *Ampithoe plea* | 37 | *Ampithoe plea* | 147 |
| *Pontogeneia rostrata* | 1 | *Pleustes platypa* | 5 | *Pleustes platypa* | 12 |
| *Pleustes platypa* | 1 | *Erichthonius braziliensis* | 1 | *Erichthonius braziliensis* | 8 |
| *Erichthonius braziliensis* | 1 | *Pleusirus secorrus* | 1 | *Amphilochus* sp. | 2 |

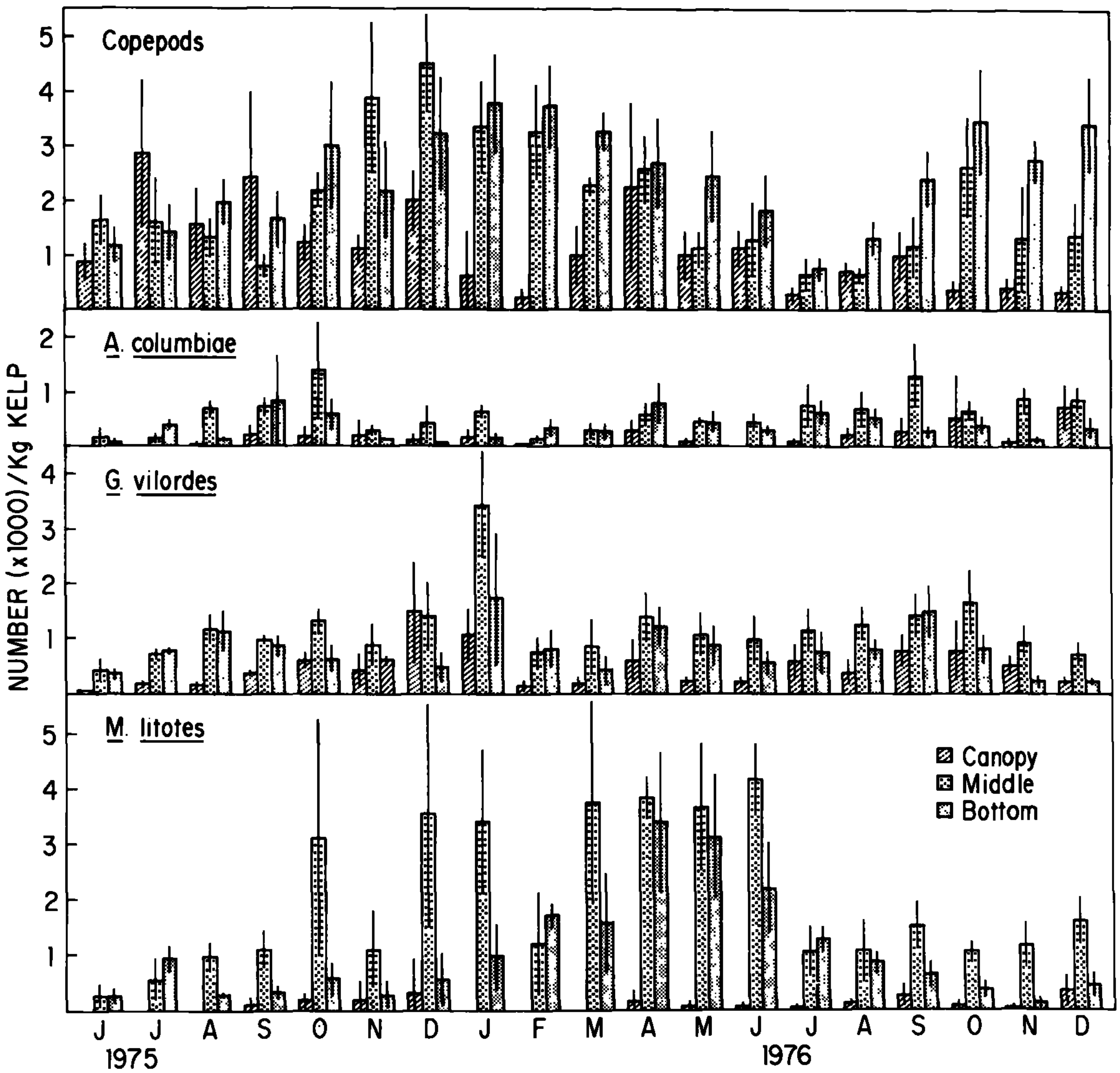


FIGURE 2.—Monthly abundances (mean and 95% C.I.) of copepods (all species) and the gammarid amphipods (*Aoroides columbiae*, *Gitanopsis vilordes*, *Microjassa litotes*) in each vertical zone. Each value represents the mean of three (July-September 1975) or five (October 1975-December 1976) replicate samples.

mysid species present differed in their patterns of vertical distribution. *Acanthomysis sculpta* essentially was confined to the canopy ($\overline{no.}$/kg ± width of 95% C.I./2 = 73.6 ± 56.4 [C], 4.0 ± 2.2 [M], 7.7 ± 5.2 [B]), and accounted for 80.5% (by number) of all mysids in the zone, whereas *S. pacifica* was less abundant in the canopy (17.8 ± 6.3 [C], 147.6 ± 39.1 [M], 99.2 ± 46.9 [B]), but was dominant in the middle (97.2%) and bottom (92.2%). An unidentified erythropinid rarely was encountered and, when present, found only in the lower zones (0 [C], 0.2 ± 0.2 [M], 0.7 ± 0.5 [B]). Nearly all (99.9%) of the shrimps associated with the kelp fronds were *Hippolyte clarki*, and this species was most abundant in the canopy (Table 3, Fig. 3).

Throughout most of the study, gammarid sizes were largest in the canopy, intermediate in the bottom, and smallest in the middle (K-S test; C-M, C-B, M-B: $P < 0.01$; Table 4, Fig. 4). Mysids and shrimps also were largest in the canopy, but were smallest in the bottom (K-S test; C-M, C-B, M-B: $P < 0.001$; Table 4, Fig. 4). Among the mysids, *S. pacifica* was more slender (mm, $\overline{mg}$ = 6.5, 2.9 [C], 4.7, 1.2 [M], 4.5, 1.2 [B]) than *A. sculpta* (6.2, 3.7 [C], 4.2, 1.7 [M], 3.1, 1.1 [B]). Combined size distributions of the four major taxa for the 19-mo study (weighted according to mean monthly abundance) revealed proportionately greater numbers of large individuals present in the canopy than in either the middle or the bottom (K-S test; C-M, C-B: $P < 0.001$; M-B: ns; Fig. 5)

## Seasonal Patterns of Species, Abundances, and Sizes

No seasonal patterns were apparent for total number of invertebrates in the canopy; however, total biomass increased dramatically (from 1,696 to 6,315 g/kg kelp) during winter 1975-76 (Fig. 6). In the lower zones, both numbers and biomass were highest during winter 1975-76 and the following spring (Fig. 6).

Seasonal patterns of abundance for the major species were evident only for the shrimp *H. clarki*, which displayed maximum abundance during both winters of the study (Fig. 3). The canopy mysid, *A. sculpta*, was abundant (113.2-395.5/kg kelp) during winter 1975 and early spring 1976, but was uncommon (6.5/kg kelp) during the following winter (Fig. 3). Single monthly samples collected in winter 1974-75 also indicated high numbers (79.2-169.8/kg kelp) of the canopy mysid. Seasonal patterns were not evident for the three most common gammarids (Fig. 2). As a group, copepods were most abundant during winter and early spring in the lower zones, but no seasonal pattern was apparent (Fig. 2).

Seasonal variations in the sizes of gammarids, mysids, and shrimps were frequently observed (Fig. 4). Gammarid sizes were largest during winter and spring in the canopy (2.76-3.85 mm), but no seasonal patterns were present in the lower zones. Carapace lengths of *S. pacifica* were largest during winter in the canopy (1.68-1.89 mm) and middle (1.24-1.45 mm) with 1976 measurements greater than 1975. Smallest sizes were present during summer in both the canopy (1.28-1.39 mm) and middle (0.92-1.22 mm). No seasonal patterns were present in the bottom. The shrimp *H. clarki* was largest in the canopy during winter-spring of both years (1.55-2.08 mm) and during spring 1975 and winter 1976 in the middle (1.56-1.64 mm) and bottom (1.36-1.43 mm). Smallest shrimps were present during fall in all three zones (1.30-1.42 mm [C]; 1.01-1.17 mm [M]; 1.02-1.03 mm [B]). No pattern was observed for *A. sculpta*.

# DISCUSSION

## Kelp Density

Elevated temperatures and/or low nutrients may have caused the Habitat Reef kelp forest to decline in late 1976. Kelp forests in southern California deteriorate when the water temperature exceeds 20°C for substantial periods (North 1971), and high temperatures often are associated with low nutrients (Jackson 1977). Significantly, temperatures at Habitat Reef did not reach 20°C in 1975, but exceeded 20°C from mid-June to November 1976. During the second half of 1976, other areas of southern California also experienced warm water and corresponding declines in *Macrocystis* standing crop (Southern California Edison Co. 1978[3]).

## Preference of *Macrocystis* as a Habitat

Few of the 114 species associated with *Macrocystis* fronds at Habitat Reef were restricted to the frond habitat. Most were present, and many were more abundant in *Macrocystis* holdfasts, understory algae, or other habitats within or adjacent to Habitat Reef (Hobson and Chess 1976; Hammer and Zimmerman 1979). A few, however, such as the gammarid *M. litotes*, the shrimp *H. clarki*, and both species of mysids, were more abundant in the *Macrocystis* fronds than in other habitats.

[3]Southern California Edison Company. 1978. Annual operating report, San Onofre Nuclear Generating Station, Vol. IV. Biological, sedimentological, and oceanographic data analyses. Southern California Edison Co., Rosemead, CA 91770, 300 p.

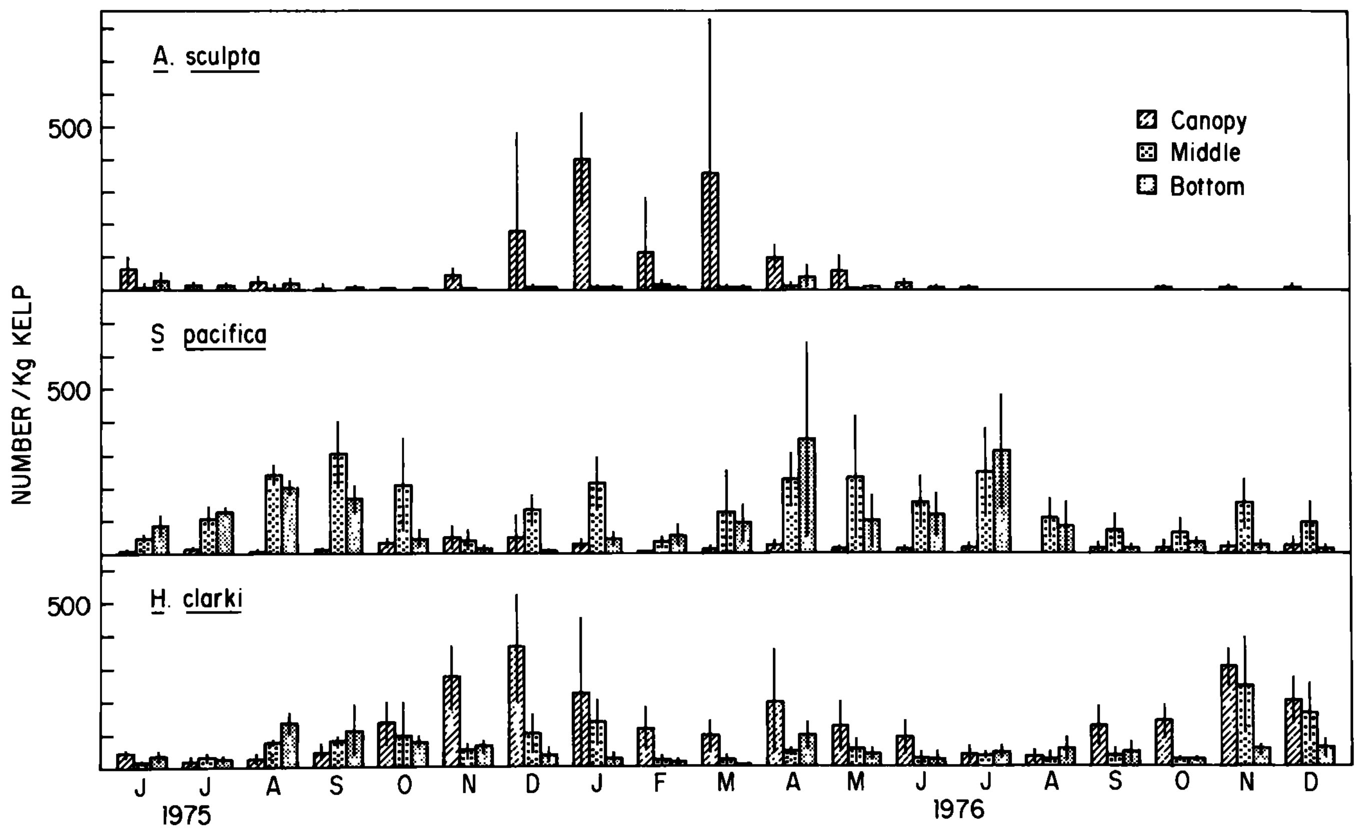


FIGURE 3.—Monthly abundances (mean and 95% C.I.) of the mysids (*Acanthomysis sculpta*, *Siriella pacifica*) and the shrimp (*Hippolyte clarki*) in each vertical zone. Each value represents the mean of three (July-September 1975) or five (October 1975-December 1976) replicate samples.

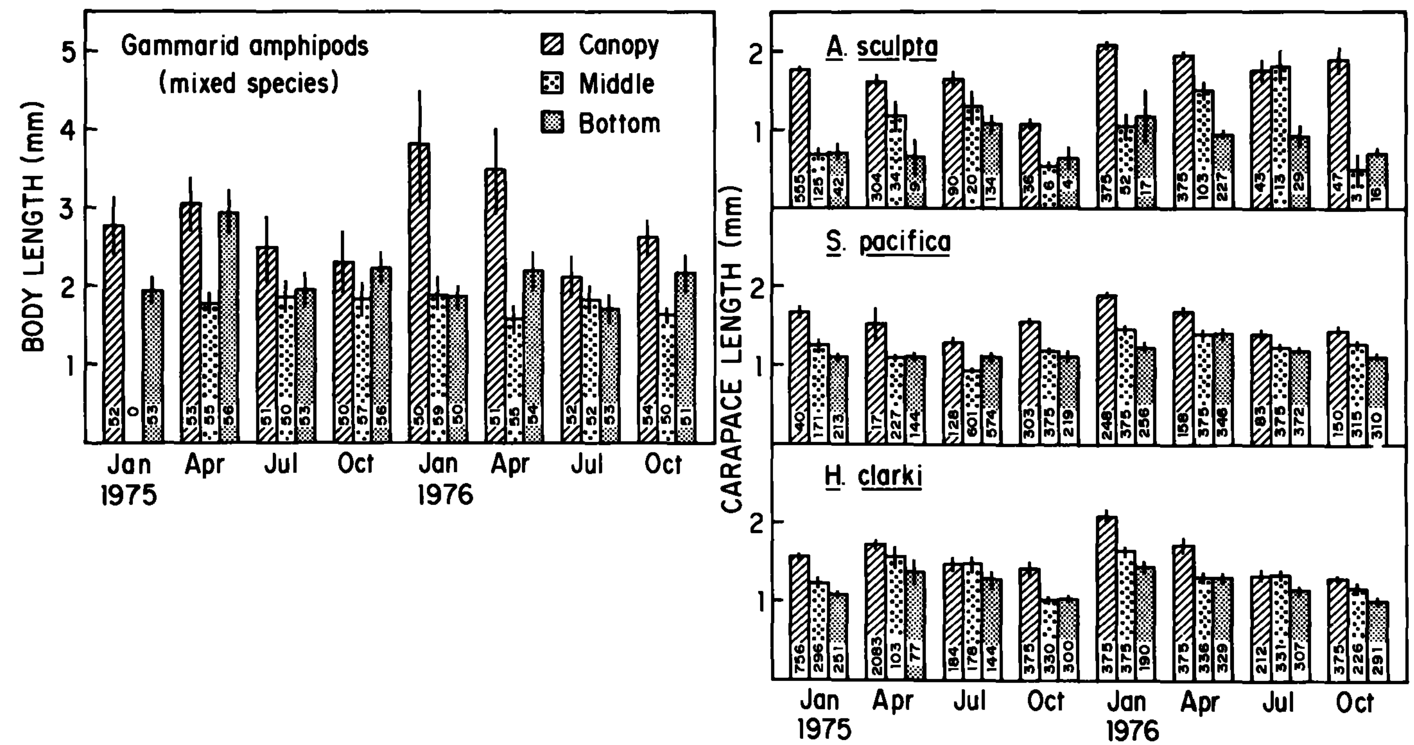


FIGURE 4.—Mean sizes (mean and 95% C.I.) of gammarid amphipods (all species), mysids (*Acanthomysis sculpta*, *Siriella pacifica*), and shrimps (*Hippolyte clarki*) within each vertical zone. Values from January and April 1975 for gammarids, mysids, and shrimps are from a single sample. Subsequent values for mysids and shrimps represent pooled subsamples from either three (July 1975) or five (October 1975-October 1976) replicate samples; subsequent gammarid values are from one randomly selected replicate. In all cases, the total number of individuals measured is noted within the columns.

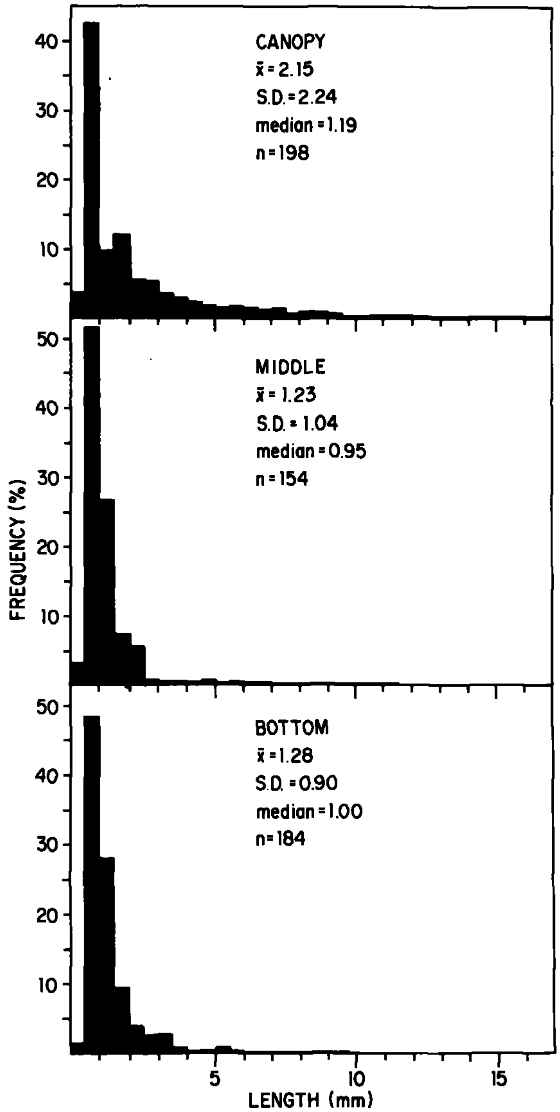


FIGURE 5.—Combined size-frequency distributions of copepods, gammarid amphipods, mysids, and shrimps measured quarterly from July 1975 through October 1976 for each of the three vertical zones. Copepods were measured during 1 mo only because of their small size and variability. After normalization (%), the distributions of each taxon were weighted according to mean monthly abundance to create the combined distributions. The numbers of each taxon measured before weighting are (C, M, B): copepods (54, 54, 55), gammarids (308, 323, 317), mysids (2,037, 2,625, 2,500), and shrimps (1,896, 1,776, 1,561). Statistics determined after weighting are displayed in the figure.

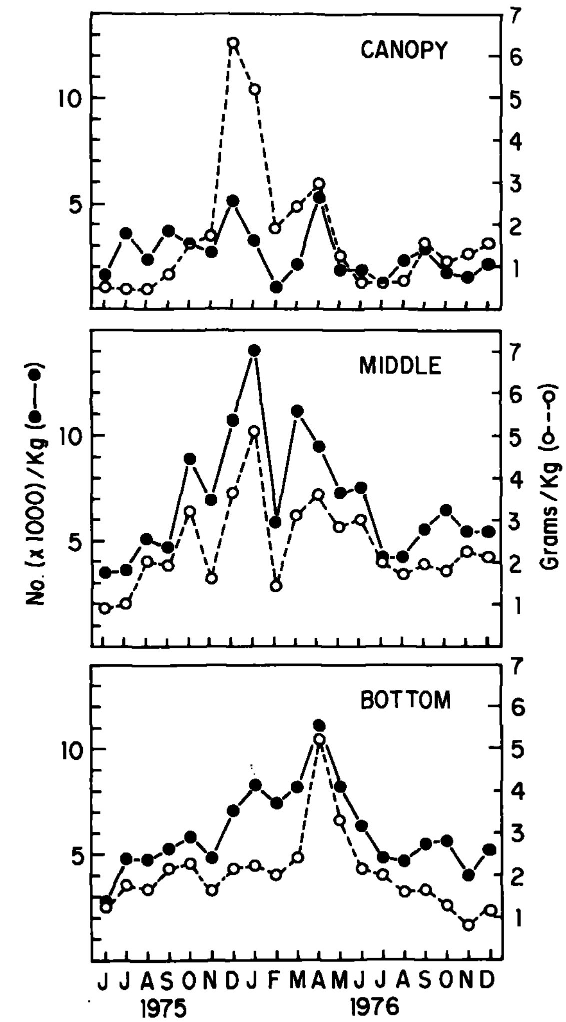


FIGURE 6.—Monthly variation in numbers and biomass of all invertebrate taxa (combined) within each vertical zone. Each monthly value for the canopy, middle, and bottom represents a mean of three (June-September 1975) or five (October 1975-December 1976) replicate samples.

Mysids are remarkably specific in habitat preferences. Clarke (1971) found 12-14 species of mysids cooccurring in the kelp forests off San Diego and Baja California, but only *A. sculpta* and *S. pacifica* were associated with the kelp fronds. Similar patterns were observed at Habitat Reef, as both *A. sculpta* and *S. pacifica* were present in large numbers within the kelp fronds, but were rarely observed in *Macrocystis* holdfasts or other algal habitats within or near Habitat Reef (Hammer and Zimmerman 1979). Hobson and Chess (1976) found a few individuals of *A. sculpta* in the water column at night, but most remained closely associated with the kelp which was utilized as food. In contrast, *S. pacifica* migrated from kelp fronds into the surrounding open water at night to capture small plankton (Hobson and Chess 1976).

## Vertical Patterns of Species, Abundances, and Sizes

Several of the commonly occurring species within the Habitat Reef kelp forest were far more abundant in the canopy than in the lower zones. *Ampithoe plea*, *Hyale frequens*, *Acanthomysis sculpta*, and *Hippolyte clarki* all displayed this type of distribution, and other investigators have noted the canopy preferences of these species. Limbaugh (1955) described a large canopy-dwelling amphipod (*Ampithoe* sp.) that formed a tube by rolling and "stitching" the edge of a *Macrocystis* blade. Several investigators working in kelp forests off San Diego and at Habitat Reef have noted the canopy occurrence of *Acanthomysis sculpta* (Limbaugh 1955; Clutter 1967; Clarke 1971; Hobson and Chess 1976) and *H. clarki* (Hobson and Chess 1976). Lowry (unpubl., cited in Lowry et al. 1974) observed large numbers of *H. californiensis*, a close relative of *H. clarki*, in the canopy of kelp forests off central California.

The canopy contained larger gammarids, mysids, and shrimps as well as proportionately greater numbers of large individuals of these groups than in either of the lower zones. Size-selective predation by fishes frequently has been documented to be a major factor in structuring aquatic communities (Brooks and Dodson 1965; Archibald 1975; Vince et al. 1976; Macan 1977; Nelson 1979) and may account for the size distributions of invertebrates observed at Habitat Reef. The interdigitating fronds of the canopy greatly increase the structural complexity in this zone and may offer more spatial refuge for motile invertebrates than provided by the middle and bottom zones. As increased structural complexity has been demonstrated to decrease effectiveness of prey capture by fishes, particularly larger prey (Vince et al. 1976; Brock 1979; Coen et al. 1981; Heck and Thoman 1981; Savino and Stein 1982), the canopy complexity may discourage extensive foraging by fishes.

Relatively few fishes forage within the kelp canopies off southern California. The most abundant fish is the kelp perch, *Brachyistius frenatus*, a small diurnal species that forages preferentially in the canopy and preys extensively on small gammarids and copepods (Hobson 1971; Bray and Ebeling 1975; Hobson and Chess 1976). Other fishes are observed in the kelp canopy, but the large-mouthed species are much less abundant than the kelp perch and forage more often in other areas of the kelp forest, and the small-mouthed species capture small planktonic prey or utilize small invertebrates attached directly to the kelp surfaces (Bray and Ebeling 1975; Hobson and Chess 1976; Bernstein and Jung 1979). Consequently, predation pressure on larger individuals of motile prey in the canopy may be reduced relative to the lower zones, resulting in a proportionately greater abundance of larger individuals. For example, the mysid *S. pacifica* was much more abundant in the lower zones than in the canopy, yet the largest individuals consistently were present in the canopy.

Alternate hypotheses may explain the size stratification of some species. Intraspecific behavioral interactions may confine certain size classes to specific zones, as demonstrated experimentally for an amphipod (Van Dolah 1978). Larger individuals may be more abundant in the canopy simply in response to the presence of preferred food types and/or sizes, although this hypothesis has not been examined.

The size distribution of invertebrates in the lower zones resembled the size distribution of insects in temperate terrestrial forests (Schoener 1971), in that both areas supported large numbers of small, and few large, individuals. The size distribution in the canopy, however, was somewhat similar to the insect size distribution of tropical terrestrial forests where there are proportionately greater numbers of large insects (Schoener and Janzen 1968; Schoener 1971). The presence of larger insects in the tropical forests effectively expands the food size dimension relative to the temperate forests (assuming equal abundance). The expansion has been hypothesized to account for some of the increased diversity of bird species in the tropics, as much of this increase is due to the addition of insectivorous birds adapted to capture large insects (Schoener 1971).

In contrast to the tropical forests, the higher proportion of large prey items in the Habitat Reef kelp canopy apparently did not attract additional species of fish predators. Nevertheless, it may be useful to examine the size distributions of important prey items in other kelp forests to determine whether a relationship exists between prey size distributions and fish species diversity.

## Seasonal Patterns of Species, Abundances, and Sizes

The kelp-associated invertebrates as a group did not exhibit seasonal cycles. Numbers and biomass generally were highest during winter 1975, with the marked increase in biomass due primarily to increased abundances of the relatively large canopy mysid *A. sculpta* and shrimp *H. clarki*. Gammarid amphipods, particularly *M. litotes*, were largely responsible for the increased abundances in the lower zones during this period.

Fluctuations in the population size of several species may have been associated with changes in kelp biomass, particularly the general decline of kelp biomass beginning in fall 1976. The canopy mysid probably attains its greatest population size during winter; however, the canopy was markedly reduced in area by winter 1976-77 and the mysid was rare. Copepods and gammarids displayed decreased canopy abundances during late 1976, and in the lower zones, abundances of the gammarid *M. litotes* began to decline as kelp biomass was reduced. As the canopy mysid and *M. litotes* were major components of the general invertebrate peak observed during winter 1975-76, their reduced abundances in late 1976 undoubtedly were a major reason for the absence of a general invertebrate peak in late 1976.

Reduction in kelp biomass, however, did not affect *H. clarki*. Even though the shrimp was most numerous in the canopy, its abundance in the reduced canopy of late 1976 was similar to levels recorded in the larger canopy of late 1975.

Although the amount of kelp biomass ultimately must determine the abundance and occurrence of kelp-associated invertebrates, the importance of proximal factors remains to be determined. Proximal factors may be particularly important in many areas of southern California, where the kelp forests are characterized by relatively long-term cycles of loss and renewal (Rosenthal et al. 1974). In such conditions of relative biomass constancy, abundances of some species may not be correlated with seasonal changes (i.e., temperature, day length, nutrients, etc.). Additional research is necessary to determine the importance of proximal factors such as kelp quality (healthy vs. decomposing), inter- and intraspecific competition for space and food, and predation by fishes and/or motile invertebrates, in determining the abundance and occurrence of kelp-associated invertebrates.

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