PATCHINESS AND NUTRITIONAL CONDITION OF ZOOPLANKTON IN THE CALIFORNIA CURRENT

STEWART W. WILLASON, JOHN FAVUZZI, AND JAMES L. COX[1]

ABSTRACT

Zooplankton and water samples were collected from 81 stations off the California coast in April 1981 during CalCOFI cruise 8104 aboard the RV *David Starr Jordan*. Abundance, weight (wet and dry), digestive enzyme activity (laminarinase), and biochemical composition of three zooplankton species were determined. The indices measured provided estimates of zooplankton nutritional history on time scales of 1 day to 3 weeks.

Upwelling was taking place along the California coast, from Point Conception to San Francisco during the study period. The resulting low surface temperatures were most evident south of San Francisco and just north of Point Conception. Just south of these areas patches of high phytoplankton standing crop (up to 14.7 mg chlorophyll a/m^3) were found. The two herbivorous species, *Euphausia pacifica* and *Calanus pacificus*, showed highest laminarinase activity in areas with the highest density of phytoplankton: enzyne activity was particularly high in the waters off Point Conception. Zooplankters in the southern and offshore regions of the sampling grid showed very low digestive enzyme activity. The larger size (weight) and higher lipid content of *C. pacificus* near Point Conception and south of San Francisco in comparison to animals in other parts of the California Current suggest that animals in these areas experience prolonged periods of better nutrition. *Nematoscelis difficilis*, which is not a herbivore, did not show these patterns. This study illustrates the importance of upwelling regions, such as Point Conception, and shows the large spatial variability of trophic interactions within the California Current System.

The nearshore, pelagic marine environment is extremely variable and heterogeneous. Spatial heterogeneity of physical conditions elicit behavioral or physiological responses from marine organisms which contribute to biological patchiness (Haurey et al. 1978; Steele 1978). Patchiness of pelagic marine organisms occurs on all temporal and spatial scales (Haury et al. 1978); one of the most important of these is the mesoscale (a few kilometers to 100's of kilometers, and a few weeks to months). Mesoscale processes, such as coastal upwelling, play a major role in structuring the physical and biological environment at all scales (Haury 1982). Although upwelling regions are very productive (e.g., Ryther 1969), trophic interactions within these important areas are poorly understood.

Along the California coast episodic upwelling takes place during the spring and summer months (Reid et al. 1958; Bernstein et al. 1977; Owen 1980; Lasker et al. 1981; Parrish et al. 1981). Upwelling results in mesoscale phytoplankton patchiness along the coast and in the southward flowing California Current (Owen 1974; Cox et al. 1982; Smith and Baker 1982; Pelaez and Guan 1982). It is thought that phytoplankton patchiness in this area influences the survival and physiological condition of larval fish populations (Lasker 1975; Lasker and Smith 1977; Lasker and Zweifel 1978; O'Connell 1980). In addition, nutrition of herbivorous zooplankton (estimated by digestive enzyme activity) is influenced by phytoplankton patchiness (Cox et al. 1982; Cox et al. 1983; Willason and Cox in press).

This study investigates the impact that mesoscale and larger scale phytoplankton patchiness have on zooplankton populations within the California Current along the central and southern California coast. Results of measurements of temperature, phytoplankton biomass, zooplankton abundance, and zooplankton nutrition are presented. Nutritional status was evaluated using intrinsic properties which reflect previous feeding conditions. Short-term feeding history was estimated from measurements of the activity of the digestive enzyme, laminarinase. Although digestive enzyme levels of zooplankton do not always provide a good measure of instantaneous digestive or feeding rates (Hassett and Landry 1983; Head et al. 1984; Willason and Cox in press), the level of activity in field captured animals does give an indication of relative feeding history on the order of 1 to 5 d (Cox 1981; Cox and Willason 1981; Cox et al. 1983; Willason 1983). Longer term nutritional condition was assessed from biochemical composition and animal size (wet and dry weight) measurements.

[1]Marine Science Institute, University of California, Santa Barbara, CA 93106.

Manuscript accepted April 1985.
FISHERY BULLETIN: VOL. 84, NO. 1, 1986.

Lipid content, size, and water content of a zooplankton species reflect feeding history on the order of 1 to 3 wk (Omori 1970; Lee et al. 1970, 1971; Bamstedt 1975; Childress 1977; Boyd et al. 1978; Vidal 1980; Hakanson 1984). Spatial patterns derived from these data are used to estimate relative differences in feeding and nutritional condition of zooplankton from different areas within the California Current. An understanding of the interrelationships of these variables in different areas may provide insights into mechanisms which generate and maintain physical and biological mesoscale features.

METHODS

Species Studied

Two euphausiid species, *Euphausia pacifica* Hansen and *Nematoscelis difficilis* Hansen, and the copepod, *Calanus pacificus* Brodsky, were chosen for the present study because 1) all are common in the California Current region (Fleminger 1964; Brinton 1967b), 2) all have been used in previous digestive enzyme studies (Cox 1981; Cox and Willason 1981; Hassett and Landry 1982, 1983; Cox et al. 1983; Willason 1983; Willason and Cox in press), and 3) a large base of information exists on the sizes, feeding rates, and energetics of these zooplankters (Brinton 1967a; Mullin and Brooks 1976; Vidal 1980; Ross 1982; Cox et al. 1983; Torres and Childress 1983; Willason 1983; Hakanson 1984; Willason and Cox in press). *Euphausia pacifica*, the most abundant euphausiid in the California Current (Brinton 1967b; Brinton and Wyllie 1976; Youngbluth 1976), and *C. pacificus*, the most abundant copepod along the California coast (Fleminger 1964; Star and Mullin 1981), are considered primarily herbivorous (Mullin and Brooks 1976; Ross 1982; Willason and Cox in press). By contrast, *N. difficilis* does not appear to be a herbivore (Nemoto 1967; Mauchline and Fisher 1969; Willason and Cox in press).

Sample Collection

The sampling program was conducted off the California coast from 7 to 27 April 1981 in conjunction with the California Cooperative Fisheries Investigation (CalCOFI) survey. Zooplankton and water samples were collected from 81 stations during CalCOFI cruise 8104 aboard RV *David Starr Jordon*. Figure 1 shows the stations sampled and the sampling sequence during the cruise. The grid covered an area of about 270,000 km^2; nearshore stations were sometimes within 1 km of the coast and offshore stations were located up to 300 km from the coast.

Although the mean flow of the California Current is south through the sampling grid at this time of the year (Lynn et al. 1982), smaller regions within the grid are often subjected to different hydrographic influences. For example, the waters of the offshore regions intergrade with the waters of the Central Pacific Gyre (Bernstein et al. 1977); the nearshore region south of Point Conception (the Southern California Bight) is characterized by a semipermanent, counterclockwise eddy and is hydrographically distinct from the other areas of the grid (Owen 1980); and the nearshore area adjacent to and north of Point Conception is characterized by periods of intense coastal upwelling during the spring and summer months (Parrish et al. 1981). To compare the biological and nutritional properties of zooplankton in the different hydrographic regions, the sampling grid was divided into four sections: southern nearshore (I), northern nearshore (II), southern offshore (III), and northern offshore (IV) (Fig. 1).

Surface chlorophyll a concentration (depth of 2 m) was used as an indicator of phytoplankton standing crop. Previous studies have shown that there are positive correlations between surface chlorophyll a, integrated chlorophyll a, and primary production in the waters of the California Current (Lorenzen 1970; Hayward and Venrick 1982). Measurements of surface chlorophyll a, therefore, give a relative approximation of phytoplankton biomass within the sampling grid.

Two replicate water samples (0.25 to 2.0 L) for chlorophyll a analysis were taken at each of the 81 stations from a depth of about 2 m using the ship's seawater pumping system. Each sample was filtered through a 4.5 cm Whatmann GF/C filter; two drops of a seawater-saturated $MgCO_3$ solution were added during filtrations. The filters were folded in half and stored frozen in aluminum foil at $-20°C$. An additional 15 water samples were taken for chlorophyll a analysis along the cruise track adjacent to and immediately south of the Point Conception region while the ship was under way. Measurements of surface water temperature ($\pm 0.1°C$) were also taken at each station using a glass mercury thermometer.

Paired bongo nets (designated net 1 and net 2) with mouth openings of 0.396m^2 and mesh openings of 505 μm were used for the collection of zooplankton samples. A General Oceanics[2] flowmeter was mount-

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

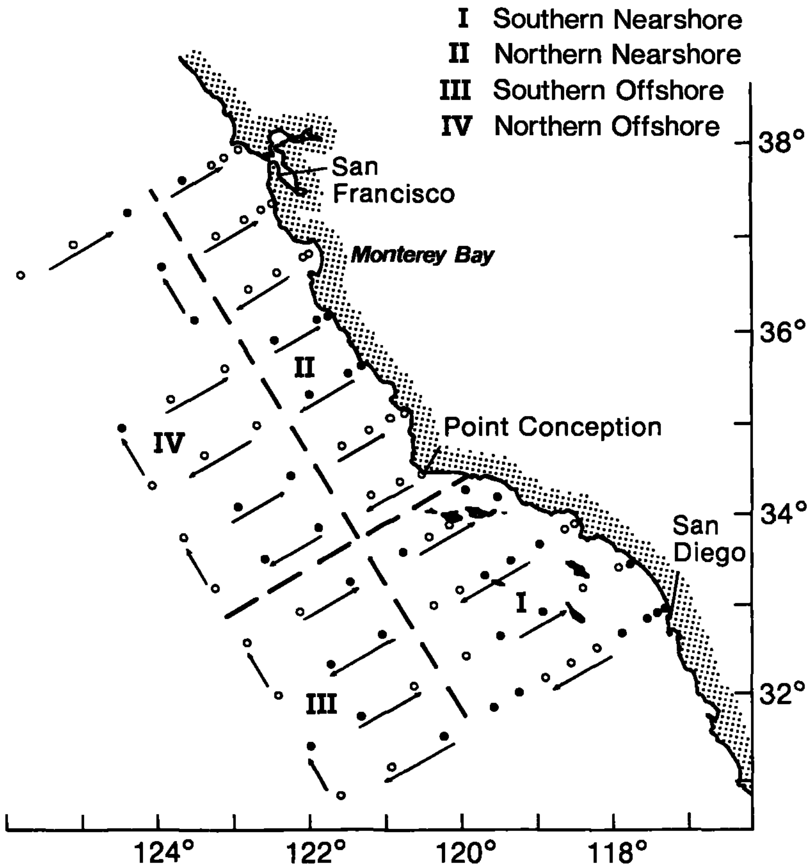

FIGURE 1.—Sampling grid. Open circles are day stations and closed circles are night stations. Arrows show the sampling sequence. The first station, adjacent to San Diego, was occupied on 7 April 1981. The last station, just north of San Francisco, was occupied on 27 April 1981.

ed inside the mouth of each net to measure the volume of water filtered. An oblique net tow was made to a depth of about 210 m at each station (bottom depth permitting); each net filtered about 400 m^3 of water. Ship speed during the net tows was 1.5 to 2.0 kn. Thirty-six stations were occupied at night (after sunset and before sunrise) and 45 were occupied during the day.

The euphausiids, *Euphausia pacifica* and *Nematoscelis difficilis*, and the copepod, *Calanus pacificus*, were separated from the catch of net 1 immediately after collection. Adult euphausiids were sorted for males and females and copepods sorted for females and stage V copepodites. Specimens of *E. pacifica* and *N. difficilis* were considered adults if they were larger than 11 mm and 15 mm, respectively (Brinton and Townsend 1981). Fifty undamaged animals of each species and sex (or stage) were saved from each net tow if adequate numbers were captured. For *C. pacificus*, which were very abundant, 50 females and stage V's were saved from 72 and 75 of the 81 stations, respectively. Two replicate groups of 50 females of *C. pacificus* were taken from 7 stations and two replicate groups of 50 stage V copepodites from 9 stations. After sorting, animals from each net tow were wrapped in parafilm in groups (5 to 50 animals of each sex or stage) and frozen at −20°C for biochemical analyses in the laboratory. Catches from net 1 that could not be sorted on the ship (10 of the 81 stations sampled) were frozen whole at −20°C and sorted in the laboratory after the cruise. The entire catch of net 2 was preserved in Formalin immediately after collection.

The abundances (numbers per 1,000 m^3) of adult euphausiids at each station were estimated by counting all adults captured in net 1 and dividing by the volume of water filtered. Copepod abundances (numbers per 1 m^3) were estimated by counting all females and stage V copepodites in triplicate aliquots taken from the preserved catches of net 2.

Sample Analyses

All frozen samples were analyzed in the laboratory within 6 wk of the time of collection. Plant pigments were extracted from the filters in 90% acetone in darkness at 4°C for 48 h. Chlorophyll a concentration was determined by the method of Strickland and Parsons (1972) using a model 10-005 Turner Designs fluorometer. The two chlorophyll a measurements from each station were averaged.

Groups of frozen animals (separate species and sexes) were thawed in the laboratory, blotted lightly to remove excess water, and weighed (±0.01 mg). Animals were then freeze-dried for 24 h at −50°C and reweighed. Groups were then immediately ground in cold (4°C) succinic acid buffer (pH 5.0) using a Polytron grinder (for euphausiids) or a hand glass tissue grinder (for copepods). Homogenates were analyzed for total proteins by the Lowry method using Sigma protein standard (Merchant et al. 1964). Laminarinase activity (LA) of the homogenates was determined by the methods described by Cox (1981) and Willason (1983). LA was expressed as a function of the animal's wet weight: μg glucose produced per gram wet weight per minute of incubation. Copepod homogenates were also analyzed for total lipids using stearic acid as the standard (Bligh and Dyer 1959; Marsh and Weinstein 1966).

Data Analysis

Willason and Cox (in press) found that *E. pacifica* exhibits a diel rhythm in enzyme activity associated with feeding activity at night. Thus, to compare LA of *E. pacifica* collected at different times of the day from different localities, enzyme levels had to be standardized with respect to the time of capture. Calibration factors, which convert the LA of *E. pacifica* collected at different times to a standardized maximum value (between 0200 and 0800 h), were derived from the results of the 24-h time-series collections in Willason and Cox (in press). These factors are based on the average relative increases and decreases of enzyme activity over a 24-h period (Table 1). LA of *N. difficilis* and *C. pacificus* do not show diel changes (Cox et al. 1983; Willason and Cox in press) and, therefore, were not standardized.

The data set for each station consists of surface temperature, surface chlorophyll a, zooplankton abundance, LA, individual wet and dry weights, protein content, and lipid content (copepods only). To permit parametric statistical comparisons between the various biological and physical properties and between regions, chlorophyll a, zooplankton abundance, and zooplankton LA were normalized by log transformation. The log transformed values were used for all parametric statistical tests. Zooplankton wet weight, dry weight, protein content, and lipid content were found to be normally distributed by probit analysis and were not log transformed. Nontransformed values from all data sets were used to construct contour maps. The contour maps are intended to show general trends and patchiness within the sampling grid.

TABLE 1.—Correction factors for standardizing laminarinase activity (LA) of *Euphausia pacifica*. These factors account for diel changes in LA and are based on the time of capture. They were derived from the 24-h time-series collections of Willason and Cox[1]. LA was standardized to the 0200-0800 time period. LA of euphausiids captured during other time periods was multiplied by the corresponding factor.

	Correction factor	
Time period	Females	Males
2000-0200	1.042	1.132
0200-0800	1.000	1.000
0800-1400	1.253	1.281
1400-2000	1.486	1.453

[1]Willason, S. W., and J. L. Cox. In press. Diel feeding, laminarinase activity and phytoplankton consumption by euphausiids. Biol. Oceanogr.

RESULTS

Surface Water Temperature and Surface Chlorophyll a

Surface water temperatures along the California coast during April 1981 ranged from 9.6° to 16.0°C. The coldest water was located in the northern nearshore region and the warmest was found in the southern offshore region (Table 2, Fig. 2). Two small areas showed very low surface water temperatures: close to the shore along the central coast of California and just off San Francisco Bay (Fig. 2). A cold water plume extended from Point Conception south into the Southern California Bight.

Chlorophyll a concentrations showed greater than 100-fold variation between stations and were inversely correlated with surface water temperatures (r = 0.83, $P < 0.001$). Lowest values, 0.09 to 0.16 mg chlorophyll a/m^3, were found in the southern offshore region. Highest concentrations occurred in the northern nearshore region (Table 2, Fig. 3). Within

TABLE 2.—Mean surface water temperature and mean surface chlorophyll a. Chlorophyll a expressed as mg/m^3. The numbers in parentheses are one standard deviation.

	Southern Nearshore (I)	Southern Offshore (III)	Northern Nearshore (II)	Northern Offshore (IV)
Temperature (°C)	14.85 (0.72)	15.03 (0.49)	11.56 (0.82)*	13.68 (0.78)
Chlorophyll a	0.659 (0.88)	0.141 (0.04)	5.110 (4.42)	0.485 (0.29)
Log Chlorophyll a	−0.378 (0.38)	−0.883 (0.12)	0.555 (0.39)*	−0.404 (0.31)
No. of stations	27	12	25	17

* indicates value(s) significantly different from those of other regions ($P < 0.05$, t-test).

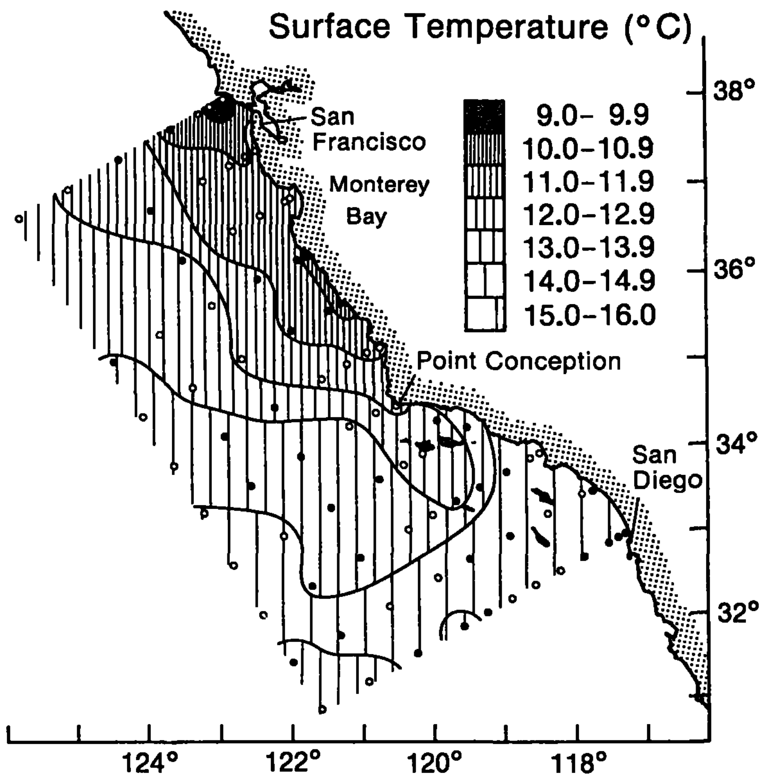

FIGURE 2.—Surface water temperatures (°C) along the California coast.

this region two areas of very high chlorophyll a (up to 14.7 mg/m^3) were found: near Point Conception and just south of San Francisco Bay. These areas were located just south of the areas of coldest surface waters.

Euphausiid Distribution and Abundance

Euphausia pacifica adults were captured at 43 of the 81 stations sampled and *Nematoscelis difficilis* adults were captured at 38 stations. As there was no significant difference between numbers of males and females captured of either species ($P > 0.3$, Wilcoxon test), the abundances shown in Figures 4 and 5 represent the sum of both sexes. Both the number of specimens of *N. difficilis* captured at each station ($P < 0.01$, t-test) and the proportion of stations where individuals were caught ($P < 0.01$, χ^2 test) were greater at night. For *E. pacifica*, there were no significant day-night differences in the numbers of animals captured ($P > 0.2$, t-test), however, like *N. difficilis*, the proportion of stations where individuals were captured was greater at night ($P < 0.05$, χ^2 test). The day-night differences may represent net avoidance by euphausiids or undersampling during the day because of vertical migration. Thus, the data presented in Figures 4 and 5 represent general trends and are intended to show relative differences between areas. Because euphausiids were captured at only about one half of the stations, statistical comparisons were made only between the north and south (i.e., nearshore and

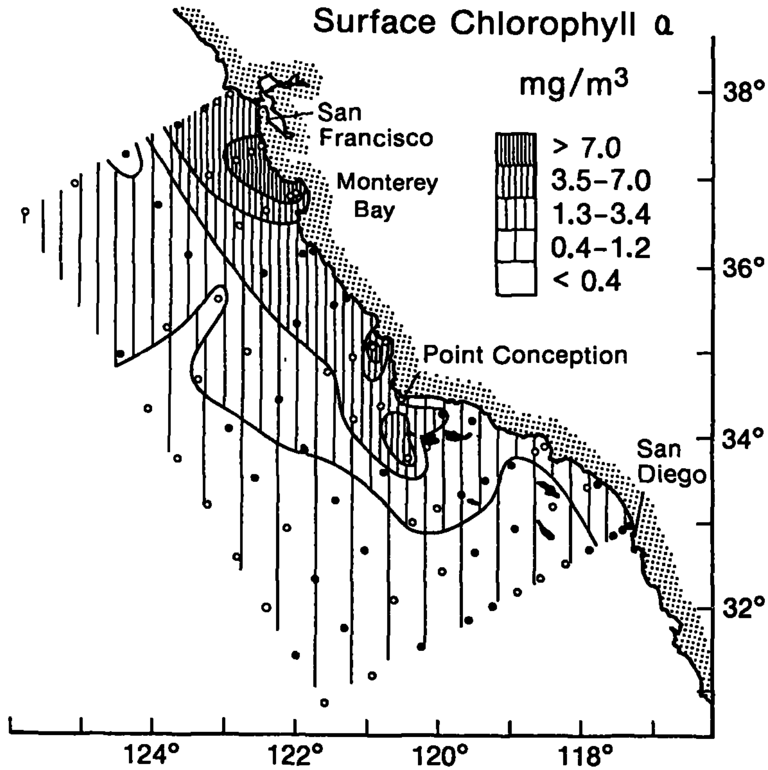

FIGURE 3.—Surface chlorophyll a. Expressed as mg chlorophyll a per m^3.

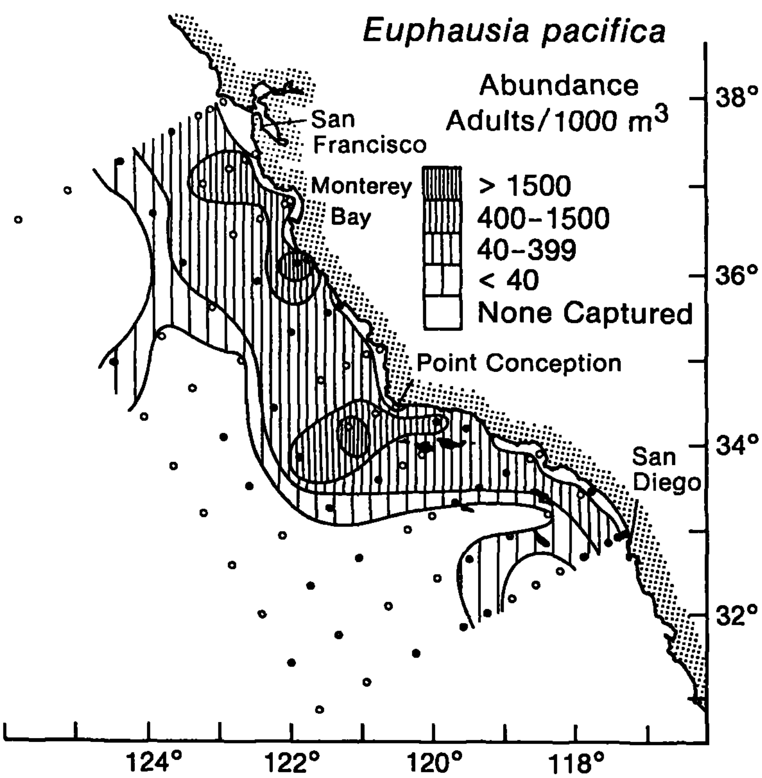

FIGURE 4.—*Euphausia pacifica* abundance. Expressed as number of adults per 1,000 m^3.

offshore regions for the north and south were combined).

Specimens of *E. pacifica* were captured in significantly greater numbers north of Point Conception (Table 3) and were rare or absent at most offshore stations (regions III and IV). This species was especially abundant off Point Conception and just south of Monterey Bay along the central coast (Fig. 4). These two areas were located close to the areas of highest chlorophyll a concentration. The abundance of *E. pacifica* was significantly correlated with chlorophyll a over the entire grid (Table 4).

The distribution of *N. difficilis* (Fig. 5) was quite different from that of *E. pacifica*. This species was captured at only 30% of the stations where *E. pacifica* was found and was distributed farther off-

TABLE 3.—Mean abundance and laminarinase activity (LA) of *Euphausia pacifica* and *Nematoscelis difficilis* in the north and south regions. Numbers in parentheses are one standard deviation. Log values were used for statistical comparisons.

	South Regions (I & III)		North (Regions (II & IV)	
	Males	Females	Males	Females
Euphausia pacifica				
Abundance (No./1,000 m³)	96.07 (100.4)	96.41 (102.5)	200.6 (234.4)	270.2 (337.3)
Log abundance	1.604 (0.623)*	1.647 (0.666)*	2.035 (0.551)	2.119 (0.579)
LA	122.5 (47.8)	165.1 (59.9)	109.7 (68.9)	153.2 (111.9)
Log LA	2.058 (0.167)	2.186 (0.183)	1.965 (0.263)	2.099 (0.269)
No. of stations	16	15	27	27
Nematoscelis difficilis				
Abundance (No./1,000 m³)	13.71 (12.78)	18.06 (16.07)	55.11 (70.31)	75.17 (83.84)
Log abundance	1.001 (0.327)*	1.061 (0.461)*	1.530 (0.441)	1.657 (0.453)
LA	167.3 (87.5)	208.6 (102.9)	104.4 (41.9)	130.4 (55.1)
Log LA	2.172 (0.237)*	2.270 (0.207)*	1.992 (0.174)	2.041 (0.191)
No. of stations	16	18	20	19

* indicates value(s) significantly different between north and south ($P < 0.05$, t-test).

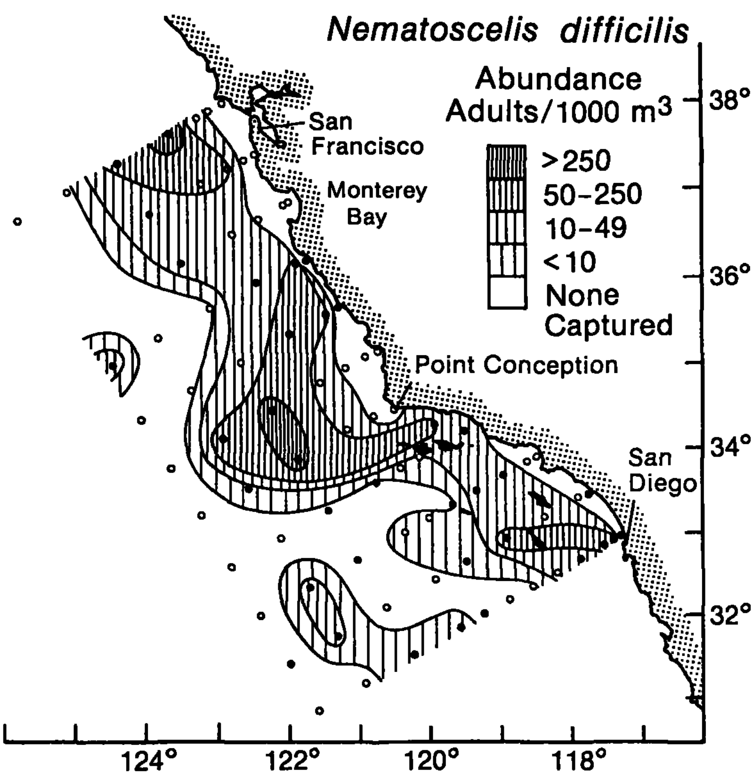

FIGURE 5.—*Nematoscelis difficilis* abundance. Expressed as number of adults per 1,000 m³.

shore. As with *E. pacifica*, both sexes of *N. difficilis* were found in significantly greater numbers in the north (Table 3). The abundance of *N. difficilis* was not correlated with surface chlorophyll a (Table 4).

Euphausiid Laminarinase Activity

Similar to the results of Willason (1983) and Willason and Cox (in press), males of both euphausiid species showed significantly less LA than females ($P < 0.01$, both cases, Wilcoxon test). Males in this study had about 70% (*Euphausia pacifica*) or 80% (*Nematoscelis difficilis*) of the LA of females (Table 3). To simplify the presentation of the data on the contour maps, LA values of males and females at each station were averaged.

The values of LA for *Euphausia pacifica* within the sampling grid ranged from 50 to 430. Euphausiids with the lowest LA values were found in offshore areas and in the nearshore area along the central coast. *Euphausia pacifica* with the highest levels of LA were found just south of San Francisco Bay and adjacent to the south of Point Conception (Fig. 6). These areas overlapped with and extended just south of the regions of highest surface chlorophyll a. There was a positive correlation between LA of *E. pacifica* and chlorophyll a over the entire grid (Table 4).

TABLE 4.—Correlations between chlorophyll a, zooplankton abundance, and laminarinase activity (LA) for *Euphausia pacifica*, *Nematocelis difficilis*, and *Calanus pacificus*. For euphausiids, abundance and LA values used in the analyses are the averages of males and females. Numbers in parentheses refer to the number of samples used in regression analyses.

	Correlation coefficients			
Correlation	*E. pacifica* (43)	*N. difficilis* (38)	*C. pacificus* ♀ (81)	*C. pacificus* V (81)
Chlorophyll a vs. abundance	0.61	[1]0.27	0.24	0.31
Chlorophyll a vs. LA	0.57	[1]0.03	0.53	0.62
LA vs. abundance	0.40	[1]0.14	0.38	0.48

[1]Correlation coefficients which were not significant at the 95% level.

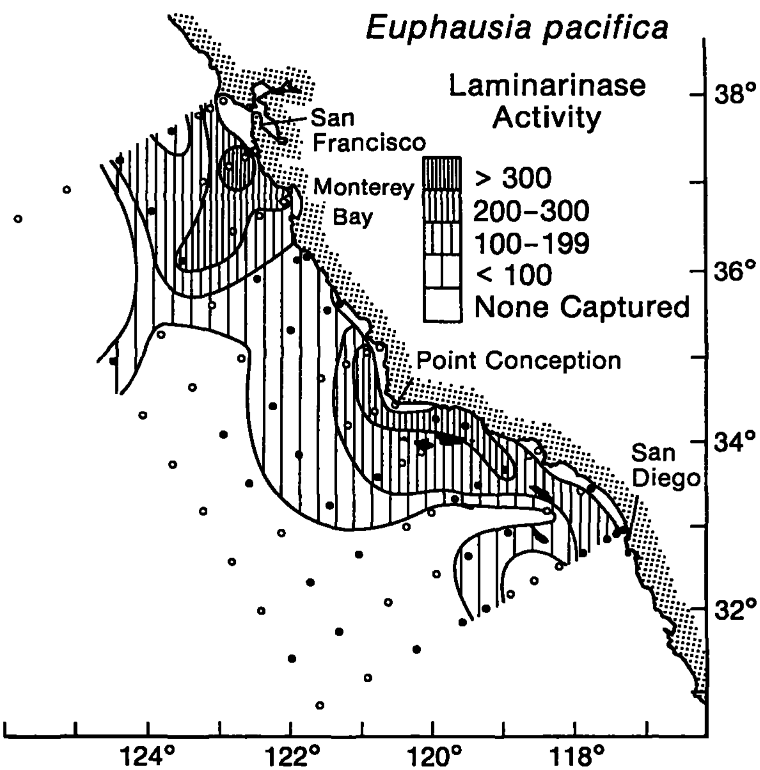

FIGURE 6.—*Euphausia pacifica* laminarinase activity (LA). Expressed as μg glucose per gram wet weight per minute.

The values of LA for *Nematoscelis difficilis* were in the same range as those of *Euphausia pacifica* (50 to 400), but showed a different distributional pattern (Fig. 7). Regions of highest activity were located in three small areas: adjacent to San Diego, in the Santa Barbara Channel (just south of Point Conception), and in an area about 150 km off Monterey Bay. Both males and females of *N. difficilis* had significantly higher levels of LA in the southern portion of the grid (Table 3). LA of *N. difficilis* was not correlated with chlorophyll a (Table 4). *Nematoscelis difficilis* with high LA were often found in areas with very low phytoplankton biomass and vice versa.

Euphausiid Size and Chemical Composition

Mean wet and dry weights, water content, and protein content (expressed as percent dry weight and percent wet weight) of *Euphausia pacifica* and *Nematoscelis difficilis* are presented in Table 5. Female *E. pacifica* and both sexes of *N. difficilis* had significantly higher wet and dry weights in the north. The water content of both euphausiid species ranged from 76.5 to 81.7% and was very similar between species, sexes, and regions (Table 5). Protein content was also very similar between species, sexes, and regions. The protein values reported here (51 to 56% of dry weight) are within the range of previously reported values (Childress and Nygaard 1974).

Copepod Distribution and Abundance

Female and stage V copepodites of *Calanus pacificus* were captured at all 81 stations sampled. There were no significant differences between day and night catches for either *C. pacificus* ($P < 0.01$, *t*-test). For comparisons between regions, mean abundances were calculated using both the log transformed and nontransformed values (Table 6). The log transformed values were used for statistical comparisons. The overall abundances of females and stage V copepodites were similar to one another in all regions ($P > 0.1$, *t*-test, all cases). Both *C. pacificus* stages were significantly more abundant in the two nearshore regions (I and II) than in the two offshore regions (III and IV) (Table 6). Figures 8 and 9 show that the distributions of females and stage V *C. pacificus* were patchy within regions. Copepods were particularly abundant in the area close to and just south of Point Conception. An extremely dense aggrega-

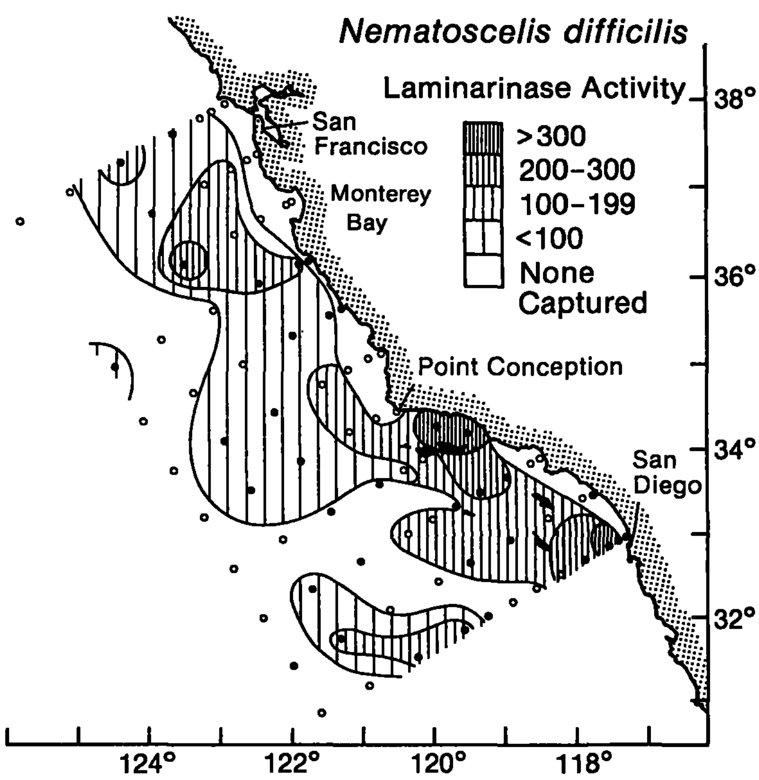

FIGURE 7.—*Nematoscelis difficilis* laminarinase activity (LA). Expressed as μg glucose per gram wet weight per minute.

TABLE 5.—Mean individual wet weight, dry weight, % water, and protein content of *Euphausia pacifica* and *Nematoscelis difficilis* from the north and south. Numbers in parentheses are one standard deviation.

	South (Regions I & III)		North (Regions II & IV)	
	Males	Females	Males	Females
Euphausia pacifica				
Wet weight (mg)	31.01 (11.55)	32.57 (10.81)*	37.73 (11.24)	42.38 (12.11)*
Dry weight (mg)	6.48 (2.38)	6.75 (2.53)*	7.91 (2.57)	8.98 (2.41)*
% water	79.10	79.28	79.04	78.81
Protein (% dry wt)	54.57	56.16	52.62	52.26
Protein (% wet wt)	11.40	11.62	11.05	11.02
No. of stations	16	15	27	27
Nematoscelis difficilis				
Wet weight (mg)	27.63 (7.07)*	34.73 (11.28)*	35.23 (7.26)*	43.59 (8.72)*
Dry weight (mg)	5.96 (2.21)	7.22 (2.49)*	7.43 (2.22)	9.19 (2.78)*
% water	78.43	79.22	78.82	78.94
Protein (% dry wt)	56.59	51.23	52.92	54.96
Protein (% wet wt)	12.22	10.65	11.17	11.58
No. of stations	16	18	20	19

* indicates value(s) significantly different between north and south ($P < 0.05$, t-test).

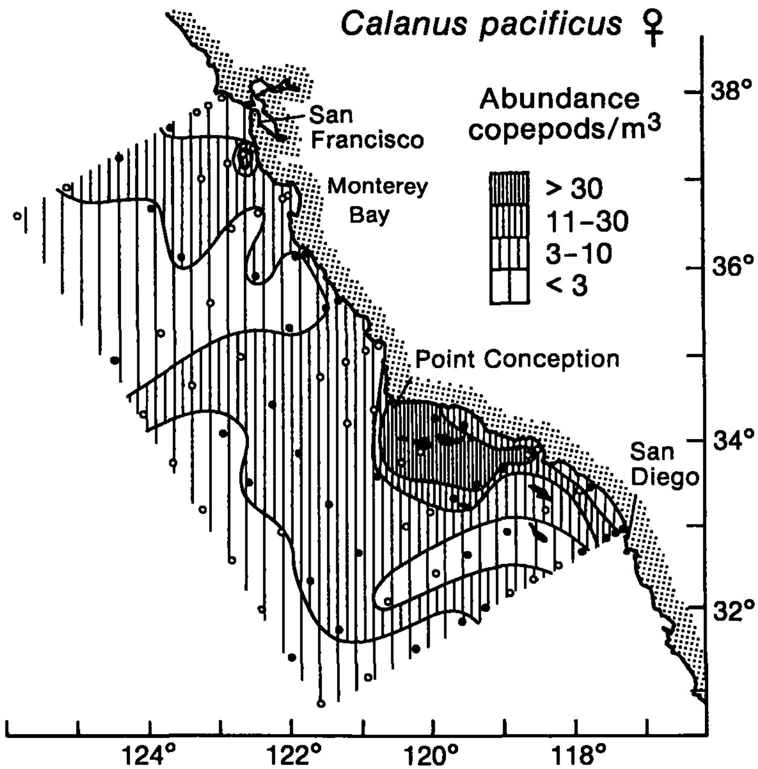

FIGURE 8.—*Calanus pacificus* females, abundance. Expressed as number of copepods per m^3.

tion of stage V *C. pacificus* (474 copepods/m^3) was found at the station adjacent to Point Conception. The areas where *C. pacificus* showed the highest abundances were located near regions of high chlorophyll a concentration. However, the abundances of both *C. pacificus* stages were poorly correlated (although significant at the 95% level) with chlorophyll a over the entire grid (Table 4).

Copepod Laminarinase Activity

LA of female and stage V copepodites was much higher than the levels of both euphausiid species when expressed on a per weight basis. Like the euphausiid results, there was large variability in the LA of *C. pacificus* among stations. For example, LA of stage V copepodites ranged from <150 at offshore

TABLE 6.—*Calanus pacificus*. Mean abundance and laminarinase activity (LA) of stage V copepodites and females from each region. Numbers in parentheses are one standard deviation. Log values were used for statistical comparisons.

	Southern Nearshore (I)	Southern Offshore (III)	Northern Nearshore (II)	Northern Offshore (IV)
Stage V copepodites				
Abundance (No./m^3)	22.89 (32.11)	1.70 (0.86)	26.07 (93.90)	1.82 (1.44)
Log abundance	0.924 (0.681)*	0.175 (0.233)	0.571 (0.733)*	0.139 (0.299)
LA	825.4 (455)	538.6 (254)	1,527.5 (792.1)	933.2 (659.4)
Log LA	2.845 (0.272)	2.688 (0.201)	3.129 (0.231)*	2.891 (0.258)
Females				
Abundance (No./m^3)	14.21 (14.72)	2.54 (2.21)	6.67 (10.79)	3.05 (2.03)
Log abundance	0.807 (0.692)*	0.253 (0.411)	0.621 (0.400)*	0.343 (0.351)
LA	927.6 (466.2)	635.2 (413.5)	1,272.9 (610.3)	1,041.5 (547.5)
Log LA	2.913 (0.281)	2.734 (0.222)	3.072 (0.204)*	2.856 (0.261)
No. of stations	27	12	25	17

* indicates value(s) significantly greater than those of other regions ($P < 0.05$, t-test).

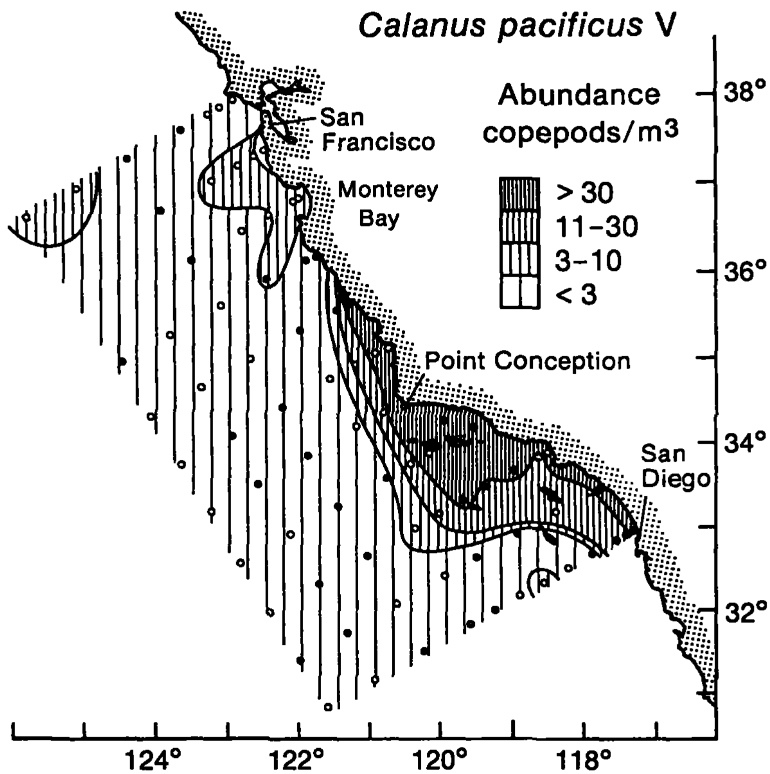

FIGURE 9.—*Calanus pacificus* Stage V copepodites, abundance. Expressed as number of copepods per m^3.

stations to 3,855 at the station adjacent to Point Conception. LA of replicate groups of 50 copepods from the same station were very similar indicating that the variability was due to differences between stations ($P < 0.05$, ANOVA).

Calanus pacificus LA also showed large differences among the four hydrographic regions. Both females and stage V copepodites from the northern nearshore region (II) had significantly higher levels of LA than copepods from the other regions (Table 6). Copepods in the southern offshore region had the lowest levels. The contour maps of *C. pacificus* LA show patches of copepods with high LA located adjacent to and just south of Point Conception and off Monterey Bay (Figs. 10, 11). These areas were located near the regions of highest *E. pacifica* LA (Fig. 6) and close to the regions of highest chlorophyll a (Fig. 3). There were significant positive cor-

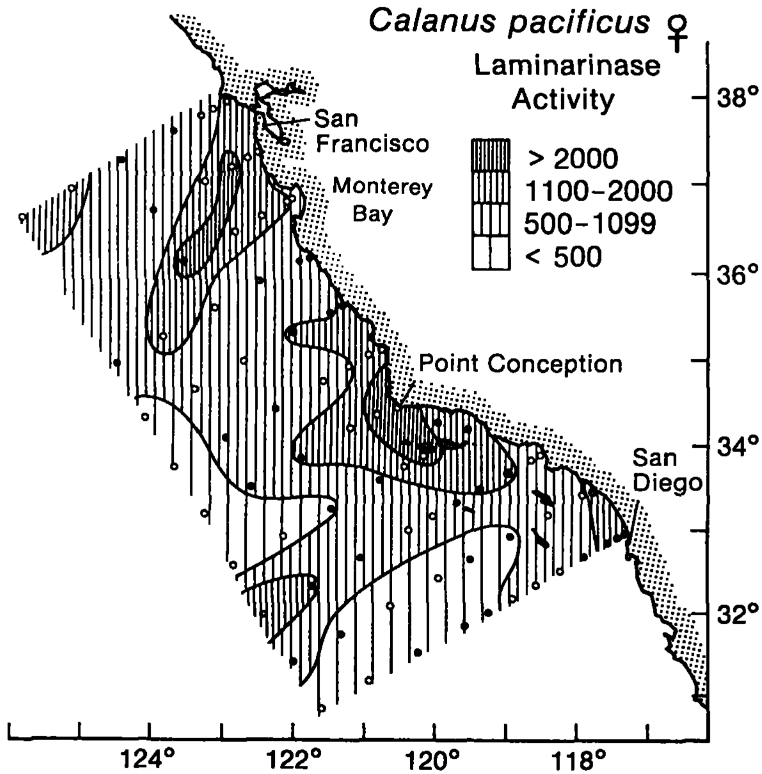

FIGURE 10.—*Calanus pacificus* females, laminarinase activity (LA). Expressed as μg glucose per gram wet weight per minute.

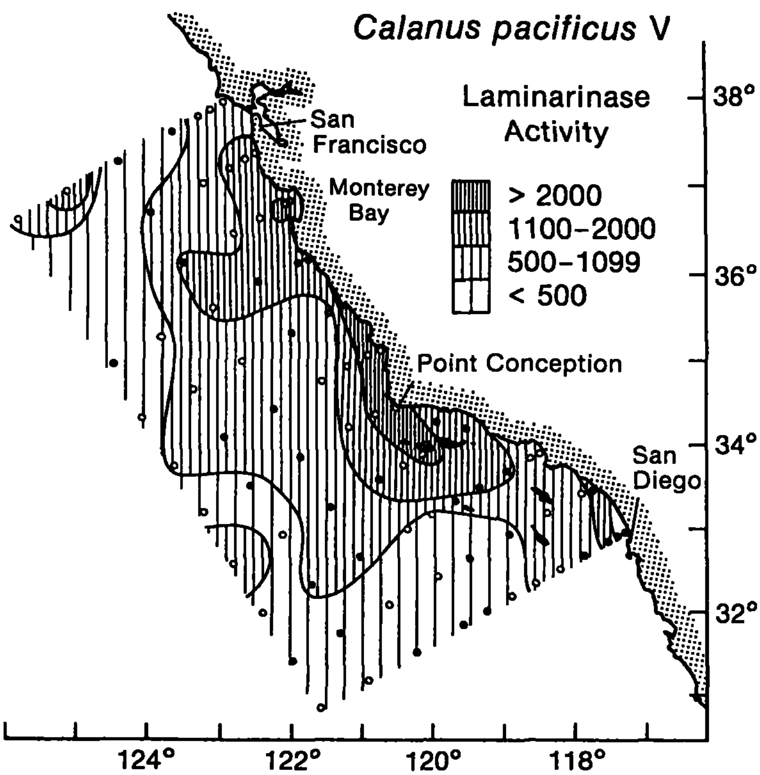

FIGURE 11.—*Calanus pacificus* Stage V copepodites, laminarinase activity (LA) Expressed as μg glucose per gram wet weight per minute.

relations between the LA of both *C. pacificus* stages and the concentration of chlorophyll a (Table 4).

Copepod Wet and Dry Weights

The largest female and stage V *C. pacificus* in terms of weight were located in the northern nearshore region and the smallest copepods were found in the southern regions (Table 7). The average water content of both *C. pacificus* stages from the four regions was inversely related to the average dry weights. Specimens of *C. pacificus* with the lowest water content were found in the northern nearshore region and those with highest water content were located in the southern offshore region (Table 7).

Figures 12 and 13 show the distribution of wet weights of *C. pacificus* females and stage V copepodites, respectively. Since wet and dry weights were highly correlated (r = 0.81 and 0.83, $P < 0.001$) only wet weights are shown. Both figures show a band of large copepods in the nearshore region along the central coast. The figures also show the variation in size of each stage between areas. Copepods (both stages) in the "heavy band" along the central coast were almost twice the weight of copepods at some of the offshore and southern stations.

Copepod Protein and Lipid Content

Total protein content (μg per copepod) of both *C. pacificus* stages was highest in the northern nearshore region and lowest in the two southern regions (Table 7). This appears to reflect differences in copepod size between regions as there were highly significant correlations between the protein content and the wet weight for both female (r = 0.82, $P < 0.001$) and stage V *C. pacificus* (r = 0.69, $P < 0.001$). Protein content was not mapped since the patterns were very similar to those of wet weight.

Protein content of *C. pacificus*, expressed as percent of wet weight, was quite similar between regions: 8.9 to 10.5% for stage V copepodites and 9.3 and 10.8% for females (Table 7). However, both stages from the southern offshore region did show slightly higher protein content when expressed as percent dry weight. This probably reflects the high water content of copepods from the southern offshore region.

The distributions of lipid content of female and stage V *C. pacificus* were very patchy and showed greater than fourfold variation between areas (Figs. 14, 15). Copepods with highest lipid values were found in the area surrounding Point Conception and off San Francisco Bay. Although copepod size (wet weight) probably influenced the total lipid content of *C. pacificus* to some extent, the variability of lipid content cannot be attributed solely to weight. Lipid content, unlike protein content, was poorly correlated with wet weight (r = 0.26 for females and r = 0.38 for stage V copepodites).

TABLE 7.—*Calanus pacificus*. Mean wet weight, dry weight, percent water, protein content, and lipid content for stage V copepodites and females from each region. Numbers in parentheses are one standard deviation.

	Southern Nearshore (I)	Southern Offshore (III)	Northern Nearshore (II)	Northern Offshore (IV)
Stage V copepodites				
Wet weight (μg)	471 (81)	447 (83)	555 (92)*	465 (95)
Dry weight (μg)	98 (21)	88 (23)	125 (26)*	98 (25)
% water	79.20	80.31	77.54	78.89
Protein (μg/copepod)	41.88 (12.24)	44.82 (9.31)	52.15 (11.26)	48.58 (8.02)
Protein (% dry wt)	44.12	49.25	42.75	48.10
Protein (% wet wt)	8.89	10.03	9.40	10.45
Lipid (μg/copepod)	19.74 (7.82)	13.94 (4.96)	29.33 (7.72)*	15.74 (5.71)
Lipid (% dry wt)	20.78	15.32	24.04	15.58
Lipid (% wet wt)	4.19	3.12	5.28	3.38
Females				
Wet weight (μg)	1,023 (170)	1,083 (160)	1,278 (180)*	1,125 (190)
Dry weight (μg)	191 (47)	185 (38)	263 (40)*	225 (29)
% water	81.34	82.83	79.40	80.20
Protein (μg/copepod)	94.92 (22.71)	100.84 (24.84)	137.81 (26.40)*	115.62 (23.33)
Protein (% dry wt)	49.70	54.51	52.74	51.38
Protein (% wet wt)	9.28	9.31	10.78	10.28
Lipid (μg/copepod)	26.71 (13.31)	21.96 (9.00)	35.27 (11.47)	30.19 (10.21)
Lipid (% dry wt)	13.81	11.69	13.41	13.47
Lipid (% wet wt)	2.61	2.03	2.76	2.68
No. of stations	27	12	25	17

* indicates value(s) significantly greater than those of other regions ($P < 0.05$, t-test).

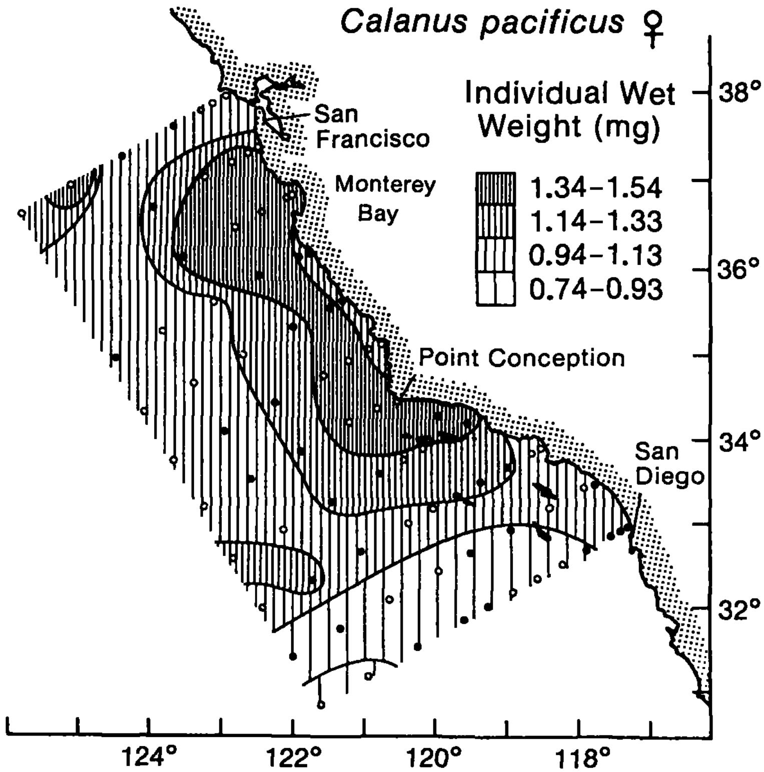

FIGURE 12.—*Calanus pacificus* females. Average individual wet weight in mg.

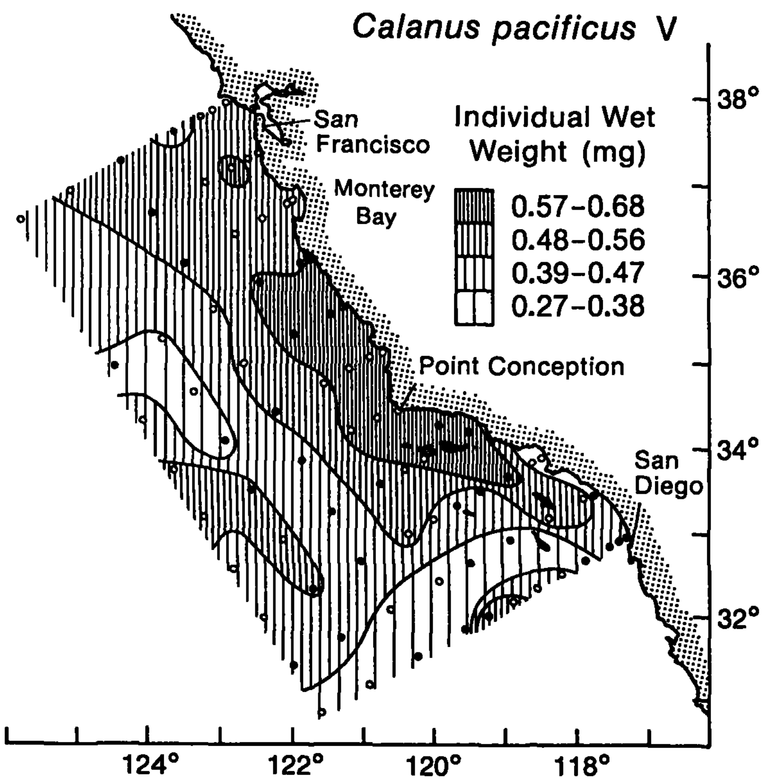

FIGURE 13.—*Calanus pacificus* Stages V copepodites. Average individual wet weight in mg.

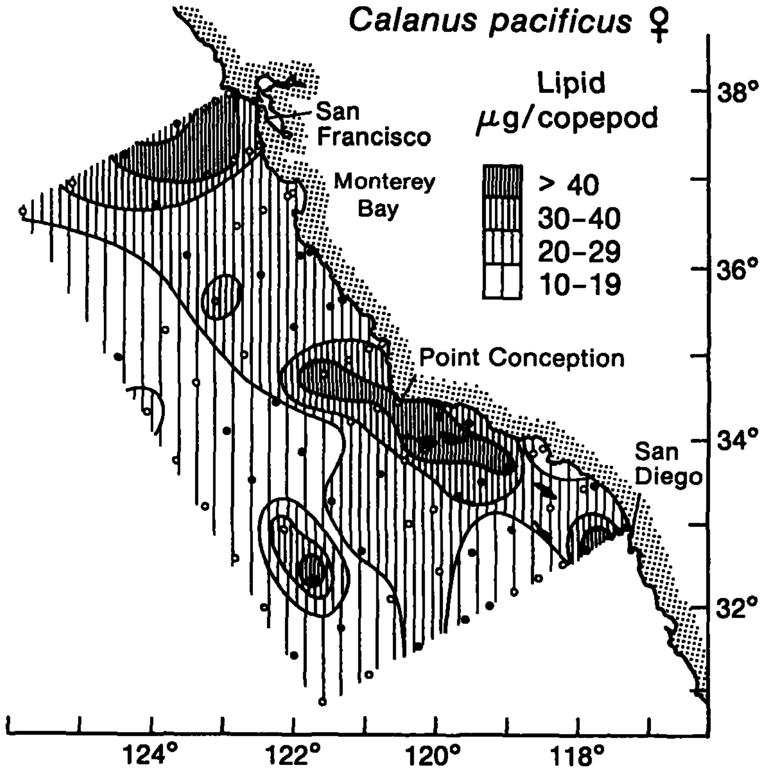

FIGURE 14.—*Calanus pacificus* females. Average lipid content per copepod in µg.

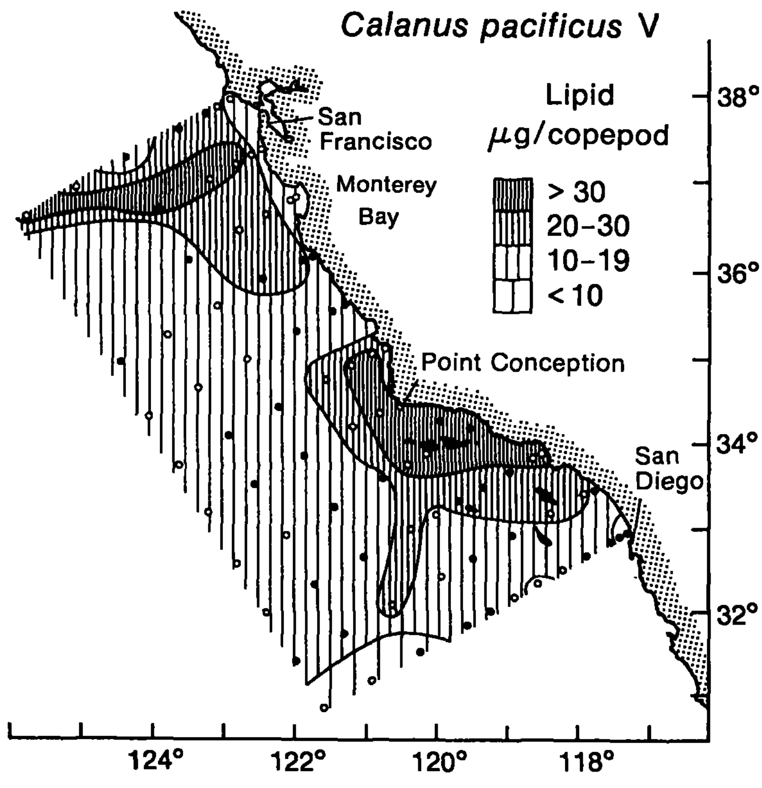

FIGURE 15.—*Calanus pacificus* Stage V copepodites. Average lipid content per copepod in µg.

Lipid content of female *C. pacificus*, expressed as percent dry weight or percent wet weight, was lowest in the southern offshore region, but was quite similar between the other three regions (Table 7). Lipid content (percent dry or wet weight) of stage V copepodites from the northern nearshore region was higher than the other regions. This stage showed the lowest lipid content in the southern offshore region (Table 7).

DISCUSSION

Upwelling was taking place along the California coast during April 1981. The resulting coastal low surface water temperatures were most evident in the northern part of the sampling grid, especially just north of Point Conception. An upwelling index calculated for this region during mid-April was higher than the 20-yr mean (Howe et al. 1981). The cold-water plume extending into the Southern California Bight (Fig. 2) is a common phenomenon that occurs when cold, upwelled water from the Point Conception region becomes entrained into the southward flowing California Current (Reid et al. 1958; Bernstein et al. 1977; Lasker et al. 1981). The distribution of phytoplankton biomass (estimated by surface chlorophyll a) was the most obvious biological feature associated with coastal upwelling. Phytoplankton patchiness in turn influenced zooplankton biomass and nutritional parameters. The following discusses 1) the relationships between various biological properties influenced by upwelling and 2) the persistence and consequences of biological mesoscale patchiness within the California Current System.

The distributions and abundances of both euphausiid species were similar to previous reports (Brinton 1962, 1967b, 1976, 1981; Brinton and Wyllie 1976; Youngbluth 1976). *Euphausia pacifica* is generally more abundant than *Nematoscelis difficilis*, and the center of its distribution is located closer to the coast. The abundance of *E. pacifica* within the sampling grid was positively correlated with phytoplankton biomass, as has been noted by Youngbluth (1976). Other herbivorous euphausiids (e.g., *Thysanoessa raschii* and *T. inermis*) also show this same relationship (Sameoto 1976).

The distribution and abundance of *Calanus pacificus* stages were also similar to previous reports (Fleminger 1964; Longhurst 1967). Both females and stage V copepodites were most abundant close to the coast near upwelling regions. In contrast to *E. pacifica*, abundances of the two *C. pacificus* stages showed rather poor (but significant at 95% level) correlations with phytoplankton biomass (r values of 0.24 and 0.31). This result was surprising since both species are considered herbivores. The weak correlations between *C. pacificus* abundance and phytoplankton standing crop probably resulted from small-scale heterogeneity and poor mobility of the *C. pacificus* population. Populations of *C. pacificus* along the California coast show a great deal of small-scale patchiness on the order of 10's to 100's of meters (Mullin and Brooks 1976; Star and Mullin 1981; Cox et al. 1982). Grazing by copepods within these patches can greatly reduce the local phytoplankton standing crop. When samples are taken on scales of 1 km or less, a poor or inverse correlation between phytoplankton and zooplankton biomass results (Mackas and Boyd 1979; Star and Mullin 1981). Zooplankton samples in this study were collected from net tows that covered distances of about 1 km or less. Thus, the poor correlations in the present study confirm results of previous studies and can be explained on the basis of the sampling procedure.

Laminarinase activity (LA) of *C. pacificus* and *E. pacifica* was positively related to phytoplankton standing crop. However, a strong relationship between these variables did not exist for either species (correlation coefficients between 0.53 and 0.62). These results were expected because, although most studies agree that zooplankton digestive enzyme activity and feeding rates are closely linked, enzyme levels do not always represent instantaneous ingestion rates nor are they always related to the food environment at the time of collection (Head and Conover 1983; Hassett and Landry 1983; Head et al. 1984; Willason and Cox in press).

We propose three, non-exclusive explanations for the observed weak correlations between LA and phytoplankton biomass. First, time lags of 1 to 7 d in the response of zooplankton digestive enzymes to changing food concentrations (Mayzaud and Poulet 1978; Cox and Willason 1981; Willason 1983) can influence the association between enzyme levels and the food environment. Because the standing stock of phytoplankton is often very patchy and can change rapidly, especially in upwelling regions, zooplankters are probably continually acclimating to new conditions and an equilibrium may seldom be reached between enzyme activity, feeding rates, and food concentration.

Second, phytoplankton concentration may occasionally be high in terms of chlorophyll a, but poor in quality resulting in low consumption rates and low digestive enzyme activity. Herbivorous zooplankton feeding rates have been shown to be greatly depressed by the presence of unpalatable or toxic phytoplankton (Fielder 1982).

Third, recent evidence indicates that zooplankton digestive enzymes do not show a substrate-specific response. Head and Conover (1983) found that LA in *C. hyperboreus* was induced in animals which were fed an algae that did not contain laminarin. Willason (1983) found that levels of laminarinase in *E. pacifica* increased when animals consumed small, nonreactive charcoal particles. This increase in activity, however, was less than that of animals given phytoplankton as a food source. Hence, some types of nonphytoplankton food, such as detrital particles or fecal pellets, may also elicit a positive digestive enzyme response. However, since *E. pacifica* and *C. pacificus* are primarily herbivorous and are found close to the coast where phytoplankton is abundant, LA of these zooplankters is probably, for the most part, controlled by phytoplankton consumption.

Because of large-scale patchiness within the sampling grid, relationships between the various biological properties are much clearer when stations were grouped and regions or mesoscale features compared. Mesoscale patches (100 to 200 km) of *C. pacificus* and *E. pacifica* with high LA values were clearly associated with areas of highest phytoplankton standing crop: south of San Francisco Bay and particularly in the area adjacent to and just south of Point Conception. Although laminarinase levels may not always accurately represent the feeding conditions at a single station (because of the reasons stated above), large-scale comparisons indicate that digestive enzyme levels of herbivorous zooplankton are stongly influenced by overall food concentration within an area. This suggests that animals near the coastal upwelling regions were feeding at higher rates than animals from other areas of the sampling grid.

In contrast to *E. pacifica*, neither the abundance nor the LA of *N. difficilis* were correlated with phytoplankton standing crop. These differences between the two euphausiid species are due most likely to different feeding modes or different food preferences. *Nematoscelis difficilis*, unlike *E. pacifica* and *C. pacificus*, is probably not a herbivore. Nemoto (1967) concluded that its mouthparts were very different from those of most herbivorous euphausiids, and Willason and Cox (in press) found that phytoplankton was only a small part of the diet of *N. difficilis*. What is puzzling, however, are the high levels of LA we sometimes found in *N. difficilis*, a range of values similar to those of *E. pacifica*. Laminarinase levels in *N. difficilis* are apparently controlled by consumption of a food source other than phytoplankton. Since we did not examine the gut contents of *N. difficilis* nor quantify potential food other than phytoplankton, the type of food eaten by *N. difficilis* could not be determined.

Based on the weight and biochemical composition of *C. pacificus*, the areas of high feeding activity along the California coast appear to have been persistent for periods of at least 1 to 2 wk. *Calanus pacificus* from the northern nearshore region and from the area near Point Conception were heavier, had a lower water content, and a higher lipid content than copepods from other areas. This indicates that these copepods have had prolonged exposure to better feeding conditions. The use of zooplankton biochemical composition and weight as indices of relative "physiological" or "nutritional" state has been documented in laboratory experiments. Vidal (1980) showed a direct relationship between food concentration and weight of adult and stage V *C. pacificus*. Since *C. pacificus* completes a life cycle in about 30 d (Vidal 1980; Huntley and Brooks 1982) and has a fixed number of molts to maturity, 1 or 2 wk at higher food concentrations can have a large impact on adult size. The lipid content of a zooplankton species represents an energy reserve and is an excellent indicator of nutritional state. Lipid content increases in well-fed animals and decreases in starved animals (Lee et al. 1970, 1971; Mayzaud 1976; Hakanson 1984). During periods of starvation, crustaceans in the laboratory also show an increase in water content (Hiller-Adams and Childress 1983).

Two field studies have shown that changes in food quality and quantity can cause physiological or nutritional changes in zooplankton populations (Omori 1970; Boyd et al. 1978). In both of these cases, zooplankters were displaced from their optimal habitat to areas of lower food concentration by currents or eddies. The displaced zooplankters showed a lower lipid content and a higher water content presumably due to suboptimal nutrition. This may be what happened to individuals of *C. pacificus* in the offshore areas of the California Current. These copepods weighed less and were in poorer physiological condition (high water content and low lipid content) than *C. pacificus* located close to the upwelling regions. Although the origins of these copepods are not known, physical processes within the California Current System such as eddy extensions (Bernstein et al. 1977; Pelaez and Guan 1982; Haury 1984) or offshore surface transport mechanisms (Parrish et al. 1981) could displace zooplankters such as *C. pacificus* to the food-poor offshore waters.

Because euphausiids were captured at only about one-half of the stations, comparisons of weight and water content between specific regions were difficult. Although the average weight of adults of both euphausiid species were greater in the northern area (nearshore and offshore combined), water content of both species was similar in all areas. The weight and biochemical composition of adult euphausiids may be less susceptible to short-term changes in food concentration than copepods because of their larger size and longer life cycle (>1 yr, Ross 1982).

Thus far, it is apparent that processes which occur in relatively small areas along the California coast, in particular the area near Point Conception, have a considerable influence on the nutritional state of two common herbivorous zooplankters, *E. pacifica*, and *C. pacificus*. What are the long-term implications of this mesoscale patchiness?

The regions of high phytoplankton standing crop found in April 1981 appear to be relatively predictable from year to year. Although upwelling events in these areas are episodic and seasonal, previous studies have shown similar patterns. CalCOFI surveys (Owen 1974) and recent satellite imagery (Smith and Baker 1982; Pelaez and Guan 1982) indicate that in past years Point Conception and the area off Monterey Bay have consistently been regions of high phytoplankton production during the spring and summer months. This enhanced production has undoubtedly influenced zooplankton populations in preceding years in much the same way that was found during the present study. Previous investigations concerning zooplankton distributions and grazing activity along the California coast support this conclusion (Fleminger 1964; Brinton 1976, 1981; Cox et al. 1982, 1983).

Although reproduction was not estimated, it is likely that well-fed zooplankters in the California Current produce more eggs than poorly fed animals. This has clearly been demonstrated in the laboratory for copepods (Marshall and Orr 1955; Checkley 1980) and has been suggested for euphausiids (Brinton 1976). Larger individuals of a species also produce more eggs (Brinton 1976; Nemoto et al. 1972; Ross et al. 1982). Thus, the larger, better fed copepods and euphausiids near Point Conception and off Monterey Bay probably have a higher reproductive output than animals from other areas. There is some evidence which suggests that enhanced reproduction of zooplankton takes place near Point Conception. Arthur (1977) noted that the highest densities of copepod nauplii in the Southern California Bight were located in a cold-water upwelling plume extending south from Point Conception. In addition, eggs and larvae of *E. pacifica* are more abundant in the Southern California region following periods of upwelling (Brinton 1976).

In summary, our results show that upwelling and phytoplankton variability have a significant impact on the herbivorous zooplankton in the California Current. Not only did we find patchiness of zooplankton abundances, but more importantly, zooplankton nutritional states were also highly variable (i.e., mesoscale and larger scale patchiness of trophic interactions). Zooplankton in upwelling regions appear to experience better feeding conditions for periods of up to several weeks. Prolonged periods of better feeding conditions in specific areas should influence secondary production as well. This implies that the relatively small, productive regions along the California coast, south of San Francisco Bay and particularly the area near Point Conception, have a disproportionally large impact on the biology of marine organisms within the California Current System.

ACKNOWLEDGMENTS

We thank M. Page, T. Bailey, L. Haury, D. Morse, and R. Trench for critical review of the manuscript. We also thank P. Smith and the research staff at the Southwest Fisheries Center in La Jolla for support during CalCOFI cruise 8104 and for providing access to preserved samples. This work was supported by NSF grants OEC 79-9317 and OEC 81-09934 and by the Marine Science Institute at the University of California, Santa Barbara.

LITERATURE CITED

AUTHUR, D. K.
1977. Distribution, size, and abundance of microcopepods in the California Current system and their possible influence on the survival of marine teleost larvae. Fish. Bull., U.S. 75:601-611.

BAMSTEDT, U.
1975. Ecological aspects of individual variations in weight and protein and lipid content of *Euchaeta norvegica* (copepoda). Sarsia 59:31-46.

BERNSTEIN, R. L., L. BREAKER, AND R. WHRITNER.
1977. California Current eddy formation: ship, air, and satellite results. Science 195:353-359.

BLIGH, E. G., AND W. J. DYER.
1959. A rapid method of total lipid extraction. Can. J. Biochem. Physiol. 37:911-917.

BOYD, S. H., P. H. WIEBE, AND J. L. COX.
1978. Limits of *Nematoscelis megalops* in the northwestern Atlantic in relation to Gulf Stream cold core rings. II. Physiological and biochemical effects of expatriation. J. Mar. Res. 36:143-159.

BRINTON, E.
1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., Univ. Calif. 8:51-270.

1967a. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12:451-483.
1967b. Distributional atlas of Euphausiacea (Crustacea) in the California Current region, Part I. Calif. Coop. Oceanic Fish. Invest. Atlas, Vol. 5, 275 p.
1976. Population biology of *Euphausia pacifica* off southern California. Fish. Bull., U.S. 74:733-762.
1981. Euphausiid distributions in the California Current during the warm winter-spring of 1977-78, in the context of a 1949-1966 time series. Calif. Coop. Oceanic Fish. Invest. Rep. 22:135-154.

BRINTON, E., AND A. W. TOWNSEND.
1981. A comparison of euphausiid abundances from bongo and 1-m nets. Calif. Coop. Oceanic Fish. Invest. Rep. 22:111-125.

BRINTON, E., AND J. G. WYLLIE.
1976. Distributional atlas of euphausiid growth stages off southern California, 1953-1956. Calif. Coop. Oceanic Fish. Invest. Atlas Vol. 24, 289 p.

CHECKLEY, D. M., JR.
1980. The egg production of a marine planktonic copepod in relation to its food supply: Laboratory studies. Limnol. Oceanogr. 25:430-446.

CHILDRESS, J. J.
1977. Physiological approaches to the biology of midwater organisms. *In* N. R. Andersen and B. J. Zahuranec (editors), Oceanic sound scattering prediction, Vol. 5, p. 301-324. Plenum Press, N.Y.

CHILDRESS, J. J., AND M. NYGAARD.
1974. Chemical composition and buoyancy of midwater crustaceans as a function of depth of occurrence off Southern California. Mar. Biol. (Berl.) 27:225-238.

COX, J. L.
1981. Laminarinase induction in marine zooplankton and its variability in zooplankton samples. J. Plankton Res. 3:345-356.

COX, J. L., L. R. HAURY, AND J. J. SIMPSON.
1982. Spatial patterns of grazing-related parameters in California coastal surface waters, July 1979. J. Mar. Res. 40:1127-1153.

COX, J. L., AND S. W. WILLASON.
1981. Laminarinase induction in *Calanus pacificus*. Mar. Biol. Lett. 2:307-311.

COX, J. L., S. W. WILLASON, AND L. HARDING.
1983. Consequences of distributional heterogeneity of *Calanus pacificus* grazing. Bull. Mar. Sci. 33:213-226.

FIEDLER, P. C.
1982. Zooplankton avoidance and reduced grazing responses to *Gymnodinium splendens* (Dinophyceae). Limnol. Oceanogr. 27:961-965.

FLEMINGER, A.
1964. Distributional atlas of calanoid copepods in the California Current region, Part I. Calif. Coop. Oceanic Fish. Invest. Atlas, Vol. 2, 313 p.

HAKANSON, J. L.
1984. The long and short term feeding condition in field-caught *Calanus pacificus*, as determined by the lipid content. Limnol. Oceanogr. 29:794-804.

HASSETT, R. P., AND M. R. LANDRY.
1982. Digestive carbohydrase activities in individual marine copepods. Mar. Biol. Lett. 3:211-221.
1983. Effects of food-level acclimation on digestive enzyme activities and feeding behavior of *Calanus pacificus*. Mar. Biol. (Berl.) 75:47-55.

HAURY, L. R.
1982. Mesoscale processes: The biological and physical connections. [Abstr.] EOS 63-68. Trans. Am. Geophys. Union.
1984. An offshore eddy in the California Current System Part IV: Plankton distributions. Prog. Oceanogr. 13:95-111.

HAURY, L. R., J. A. MCGOWAN, AND P. H. WIEBE.
1978. Pattern and processes in the time-space scales of plankton distributions. *In* J. H. Steele (editor), Spatial patterns in plankton communities, p. 277-327. Plenum Press, N.Y.

HAYWARD, T. L., AND E. L. VENRICK.
1982. Relation between surface chlorophyll, integrated chlorophyll and integrated primary production. Mar. Biol. (Berl.) 69:247-252.

HEAD, E. J. H., AND R. J. CONOVER.
1983. Induction of digestive enzymes in *Calanus hyperboreus*. Mar. Biol. Lett. 4:219-231.

HEAD, E. J. H., R. WANG, AND R. J. CONOVER.
1984. Comparison of diurnal feeding rhythms in *Temora longicornis* and *Centropages hamatus* with digestive enzyme activity. J. Plankton Res. 6:543-551.

HILLER-ADAMS, P., AND J. J. CHILDRESS.
1983. Effects of prolonged starvation on O_2 consumption, NH_4^+ excretion, and chemical composition of the bathypelagic mysid *Gnathophausia ingens*. Mar. Biol. (Berl.) 77: 119-127.

HOWE, J. T., D. B. GIBSON, T. O. EVANS, L. BREAKER, R. C. WRIGLEY, AND W. W. BROENKOW.
1981. Biological and physical oceanographic observations pertaining to the trawl fishery in a region of persistent coastal upwelling. NASA Tech. Mem. 81332.

HUNTLEY, M., AND E. R. BROOKS.
1982. Effects of age and food availability on diel vertical migration of *Calanus pacificus*. Mar. Biol. (Berl.) 71:23-31.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.

LASKER, R., AND P. E. SMITH.
1977. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy, *Engraulis mordax*. Calif. Coop. Oceanic Fish. Invest. Rep. 19:128-137.

LASKER, R., AND J. R. ZWEIFEL.
1978. Growth and survival of first-feeding northern anchovy larvae (*Engraulis mordax*) in patches containing different proportions of large and small prey. *In* J. H. Steele (editor), Spatial pattern in plankton communities, p. 329-354. Plenum Press, N.Y.

LASKER, R., J. PELÁEZ, AND R. M. LAURS.
1981. The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy (*Engraulis mordax*). Rem. Sens. Environ. 11:439-453.

LEE, R. F., J. C. NEVENZEL, G. A. PAFFENHOFER, AND A. A. BENSON.
1970. The metabolism of wax esters and other lipids by the marine copepod, *Calanus helgolandicus*. J. Lipid Res. 11: 237-240.

LEE, R. F., J. HIROTA, AND A. M. BARRETT.
1971. Distribution and importance of wax esters in marine copepods and other zooplankton. Deep-Sea Res. 18:1147-1165.

LONGHURST, A. R.
1967. Diversity and trophic structure of zooplankton communities in the California Current. Deep-Sea Res. 14:393-408.

LORENZEN, C. J.
1970. Surface chlorophyll as an index of the depth, chlorophyll content, and primary productivity of the euphotic layer. Limnol. Oceanogr. 15:479-480.

LYNN, R. J., K. A. BLISS, AND L. E. EBER.
1982. Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-t, dynamic height, oxygen, and oxygen saturation in the California Current, 1950-1978. Calif. Coop. Oceanic Fish. Invest. Atlas, Vol. 30, 513 p.
MACKAS, D. L., AND C. BOYD.
1979. Spectral analysis of zooplankton spatial heterogeneity. Science 204:62-64.
MARSH, J. B., AND D. B. WEINSTEIN.
1966. Simple charring method for determination of lipids. J. Lipid Res. 7:574-576.
MARSHALL, S. M., AND A. P. ORR.
1955. The biology of a marine copepod, *Calanus finmarchicus*. Oliver and Boyd., Edinb., 188 p.
MAUCHLINE, J., AND L. R. FISHER.
1969. The biology of euphausiids. Adv. Mar. Biol. 7:1-454.
MAYZAUD, P.
1976. Respiration and nitrogen excretion of zooplankton. IV. The influence of starvation on the metabolism and the biochemical composition of some species. Mar. Biol. (Berl.) 37:47-58.
MAYZAUD, P., AND S. A. POULET.
1978. The importance of the time factor in the response of zooplankton to varying concentrations of naturally occurring particulate matter. Limnol. Oceanogr. 23:1144-1154.
MERCHANT, D. J., R. H. KAHN, AND W. H. MURPHY, JR.
1964. Handbook of cell and organ culture. Burgess Publ., Minneap., 269 p.
MULLIN, M. M., AND E. R. BROOKS.
1976. Some consequences of distributional heterogeneity of phytoplankton and zooplankton. Limnol. Oceanogr. 21:784-796.
NEMOTO, T.
1967. Feeding pattern of euphausiids and differentiations in their body characteristics. Inf. Bull Planktol. Jpn, Commem. No. Y. Matusue, p. 157-171.
NEMOTO, T., K. KAMADA, AND K. HARA.
1972. Fecundity of a euphausiid crustacean, *Nematoscelis difficilis*, in the North Pacific Ocean. Mar. Biol. (Berl.) 14:41-47.
O'CONNELL, C. P.
1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. Fish. Bull., U.S. 78:475-489.
OMORI, M.
1970. Variations of length, weight, respiration rate, and chemical composition of *Calanus cristatus* in relation to its food and feeding. *In* J. H. Steele (editor), Marine food chains, p. 113-126. Oliver and Boyd, Edinb.
OWEN, R. W., JR.
1974. Distribution of primary production, plant pigments, and secchi depth in California Current 1969. Calif. Coop. Oceanic Fish. Invest. Atlas 20:98-117.
1980. Eddies of the California Current system: physical and ecological characteristics. *In* D. M. Power (editor), The California Islands: Proceedings of the Multidisciplinary Symposium, p. 237-263. Santa Barbara Mus. Nat. Hist.
PARRISH, R. H., C. S. NELSON, AND A. BAKUN.
1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175-203.
PELÀEZ, J., AND F. GUAN.
1982. California Current chlorophyll measurements from satellite data. Calif. Coop. Oceanic Fish. Invest. Rep. 23: 211-225.
REID, J. L., G. I. RODEN, AND J. G. WYLLIE.
1958. Studies on the California Current system. Calif. Coop. Oceanic Fish. Invest. Rep. 6:27-57.
ROSS, R. M.
1982. Energetics of *Euphausia pacifica* I. Effects of body carbon and nitrogen and temperature on measured and predicted production. Mar. Biol. (Berl.) 68:1-13.
ROSS, R. M., K. L. DALY, AND T. S. ENGLISH.
1982. Reproductive cycle and fecundity of *Euphausia pacifica* in Puget Sound, Washington. Limnol. Oceanogr. 27:304-314.
RYTHER, J. H.
1969. Photosynthesis and fish production in the sea. Science 166:72-76.
SAMEOTO, D. D.
1976. Distribution of sound scattering layers caused by euphausiids and their relationships to chlorophyll a concentrations in the Gulf of St. Lawrence Estuary. J. Fish. Board Can. 33:681-687.
SMITH, R. C., AND K. S. BAKER.
1982. Oceanic chlorophyll concentrations as determined by satellite (Nimbus-7 coastal zone color scanner). Mar. Biol. (Berl.) 66:269-279.
STAR, J. L., AND M. M. MULLIN.
1981. Zooplankton assemblages in three areas of the North Pacific as revealed by continuous horizontal transects. Deep-Sea Res. 28A:1303-1322.
STEELE, J. H.
1978. Some comments on plankton patches. *In* J. H. Steele (editor), Spatial patterns in plankton communities, p. 1-20. Plenum Press, N.Y.
STRICKLAND, J. D. H., AND T. R. PARSONS.
1972. A practical handbook of seawater analysis. Fish. Res. Board Can., Bull. 167, 310 p.
TORRES, J. J., AND J. J. CHILDRESS.
1983. The relationship of oxygen consumption to swimming speed in *Euphausia pacifica* I. Effects of temperature and pressure. Mar. Biol. (Berl.) 74:79-86.
VIDAL, J.
1980. Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. Mar. Biol. (Berl.) 56:111-134.
WILLASON, S. W.
1983. Spatiotemporal patterns of grazing and laminarinase activity of zooplankton off the California coast. Ph.D. Thesis, Univ. of California, Santa Barbara, 176 p.
WILLASON, S. W., AND J. L. COX.
In press. Diel feeding, laminarinase activity, and phytoplankton consumption by euphausiids. Biol. Oceanogr.
YOUNGBLUTH, M. J.
1976. Vertical distribution and diel migration of euphausiids in the central region of the California Current. Fish. Bull., U.S. 74:925-936.