SEASONAL AND INSHORE-OFFSHORE VARIATIONS IN THE STANDING STOCKS OF MICRONEKTON AND MACROZOOPLANKTON OFF OREGON

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ABSTRACT

Dry weights of pelagic animals captured along an inshore-offshore station line with Isaacs-Kidd mid-water trawls and 1-m diameter plankton nets during a 5-yr period provided evidence for seasonal changes in the standing stocks of carnivores. Micronekton catches (fishes, shrimps, and squids) were largest inshore (28 and 46 km offshore) in the winter (November-April), and offshore (84 and 120 km) during the summer (May-October), the season of coastal upwelling. No seasonal difference was detected in the biomass of herbivores, or in its primary components, the copepods and euphausiids. Increased biomass of medusae during the summer resulted in significant seasonal differences in the planktonic carnivores at the inshore stations.

The average biomass (grams per square meter) of small nektonic and planktonic carnivores, averaged over the year, peaked at the 84-km station. The biomass of fishes was greater than shrimps and the biomass of shrimps was greater than that of squids at all stations, except 46 km where shrimps predominated. Herbivore biomass was maximal at 46 km, over the inner continental slope, largely because of the high catches of euphausiids at this station. The occurrence of largest average catches at intermediate distances from shore, and inshore-offshore shifts in peak biomass with seasons, may result from seasonal changes in upwelling and downwelling and exclusion of vertical migrants from shoal waters on the shelf.

Herbivore:carnivore biomass ratios differed significantly between inshore and offshore stations. Standing stocks of herbivores were several times larger than those of carnivores in nearshore waters, but the ratio was about 1.0 in offshore waters. Coefficients of variation $(s/\bar{x})$ of herbivore and planktonic carnivore stocks for the entire sampling period were highest inshore, indicating high variability, and decreased markedly in offshore waters. These trends suggest that, compared to offshore or oceanic communities, the pelagic inshore-upwelling ecosystem may be less predictable and have a lower ecological efficiency.

This research was designed to answer two ecological questions about intermediate consumers in the pelagic food chain off Oregon:

(1) Are seasonal variations obvious in the standing stocks of small nekton and macrozooplankton off Oregon, perhaps in response to upwelling along the coast during the summer?

(2) Are there trends in the standing stocks of these animals from oceanic waters into neritic waters and, if so, do they reflect basic ecological differences in these pelagic communities?

Pelagic animals such as fishes, squids, shrimps, and euphausiids are ubiquitous in the open oceans and are important intermediates in the food chain between small plankton and large pelagic carnivores. Yet little is known about their seasonal variations, inshore-offshore distributions, or general ecology. The life span and generation time of many of these intermediate consumers are 1 yr or greater, limiting short-term changes in population sizes. Moreover, many of these animals reside below the depth of seasonal temperature change much of the time. They may undertake diel vertical migrations, and some species may migrate through the thermocline at night. In any event, seasonal changes in physical environment are expected to be less pronounced than those experienced by inhabitants of surface waters. Thus, seasonal variations in population size of these animals are expected to be less than those of small planktonic organisms.

Movements of water may also affect seasonal changes in the abundance of animals at one locality, or spatial distributions within a general region. In areas where water masses and associated pelagic fauna overlap and mix, species structure may be complicated, primarily a result

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of advective processes rather than biological interactions (McGowan 1971). In the headwater region of the California Current off Oregon, however, the water type is predominantly Subarctic and common species of some taxonomic groups of pelagic animals are the same within and among years (Pearcy 1972).

In addition to in situ population changes and changes affected by advection, small nektonic animals may be able to swim or to migrate horizontally. Though migrations of large nektonic animals such as tuna, salmon, hake, etc., are known to result in large seasonal changes in the abundance of these animals off Oregon, little evidence exists for horizontal movements of micronekton, even on a reduced scale. This is another reason to expect temporal stability of their populations.

Basic differences in the structure and energy pathways of neritic and oceanic ecosystems in the northeastern Pacific have been inferred by differences in the seasonal production cycle, seasonal variations in chlorophyll *a* concentrations, and the size of individual phytoplankton and microzooplankton (McAllister et al. 1960; Anderson 1965; Parsons and LeBrasseur 1970; LeBrasseur and Kennedy 1972). Inshore-offshore differences in the standing stocks of pelagic herbivores and carnivores, which have not been studied, are therefore to be expected.

METHODS

Micronekton and macrozooplankton were collected at night with 1.8-m Isaacs-Kidd mid-water trawls (IKMT) and with 1-m diameter plankton nets (MN) along stations west of Newport, Oreg. (lat. 44°39.1'N). The stations were located 28, 46, 84, 120, and >120 km, respectively, offshore (Figure 1). Collections, made about every month, totalled 243 IKMT tows between August 1962 and July 1967, and 179 MN collections between June 1963 and July 1967.

The IKMT had a 5-mm (bar measure) nylon liner throughout. Oblique tows were made to a depth of approximately 200 m, except at inshore stations where about one-half the depth of the water column was sampled (40 m and 130 m at the 28- and 46-km stations, respectively). Tow speed was 6 knots. The trawl was lowered at 50 m wire/min until a 4:1 scope was attained. The trawl was then retrieved at 30 m wire/min to the surface. Volume of water filtered and depth of

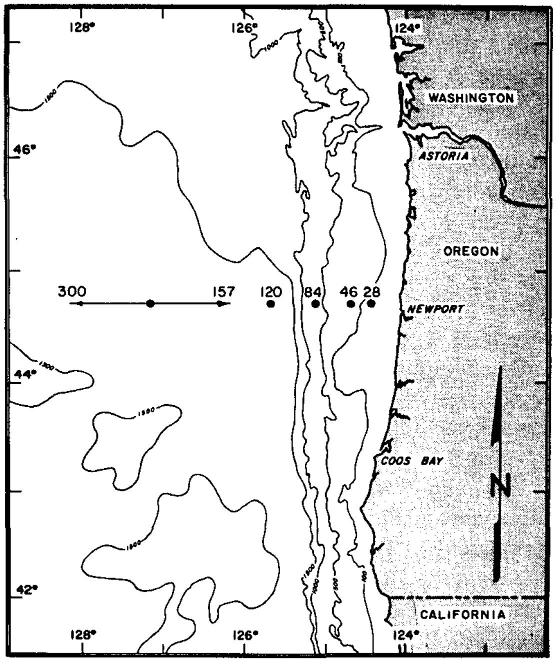

FIGURE 1.—Location of the sampling stations off Newport, Oreg. Stations are designed in kilometers from the coast. Depth contours are in fathoms (100 fathoms = 183 m, 500 fathoms = 914 m, 1,000 fathoms = 1,829 m, 1,500 fathoms = 2,743 m).

trawling was estimated from TSK[2] depth-distance recorders and flowmeters.

The meter nets, which were made of 0.571-mm Nitex, were towed immediately before or after each IKMT tow. From June to November 1963 oblique tows were made to approximately the same depths as the IKMT tows, but because of difficulties resulting from preferential sampling of near-surface waters, oblique tows were abandoned in favor of vertical tows in December 1963. Vertical tows were from 200 m to the surface, or from 60 or 150 m to the surface at the two inshore stations. After a vertical wire angle was obtained, they were retrieved at 50 m wire/min. Flowmeters mounted in the mouth of MN's provided estimates of volumes filtered. In a few instances flowmeters malfunctioned. Volumes were then estimated from the distance towed and 85% IKMT filtration efficiency (Pearcy and Laurs 1966) or from the average volume of other MN tows to the same depth.

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

Samples were preserved with Formalin at sea and sorted into taxonomic groups ashore. Wet (drained) weights were obtained for micronekton (fishes, shrimps, and squids). Micronekton from 32 different IKMT collections were dried to a constant weight in a drying oven at 65°C. The mean dry weight: wet weight ratios were then used to convert wet weights of other collections to dry weights. The means and standard deviations of the dry:wet weight ratios were 0.23 ± 0.06 for fishes, 0.15 ± 0.02 for shrimps, and 0.11 ± 0.04 for squids.

Dry weights were obtained for all major taxa sorted from MN samples: euphausiids, copepods, chaetognaths, medusae, amphipods, salps-doliolids, and shrimps. These taxa generally comprised over 95% of the total collection weights. The remainder usually consisted of annelids, pteropods, and heteropods. Ctenophores usually disintegrated in the samples, but when fragments were identifiable they were weighed with the medusae. In this paper, dry weights are used as a measure of standing stock, which is considered to be synonymous with biomass.

Sampling Variability

Several series of IKMT's at a single station during a single night were taken to assess sampling variability. The variability of total micronektonic dry weight per 1,000 m³ (Table 1) indicates that the variance for these series was appreciably less than the mean. These data on total biomass of micronekton, which are not in disagreement with the high variability encountered for individual species of micronekton captured in repeated tows at one station (e.g., Pearcy 1964; Ebeling et al. 1970), suggest that most of the temporal fluctuations of biomass illustrated in Figure 2 are independent of short-term sampling variability.

Variances of macrozooplankton biomass from repeated MN tows, on the other hand, were much larger than those for the IKMT (Table 1). In two out of the five series, variance surpassed the mean. Hence, a larger portion of the temporal variability of zooplankton can be ascribed to sampling variability.

TABLE 1.—Sampling variability of total biomass of micronekton and macroplankton (grams dry weight per 1,000 m³) collected during repeated tows during separate nights.

Gear	Date	Distance offshore (km)	No. tows	Average ($\bar{x}$)	Variance (s^2)
Mid-water trawl	Dec. 1964	84	5	2.7	0.6
	Nov. 1966	120	3	4.7	0.9
	Feb. 1967	120	5	1.8	0.2
	Feb. 1967	120	3	1.5	0.02
	June 1967	306	6	1.9	0.01
	June 1967	120	6	2.2	0.4
Meter net	June 1964	93	6	5.0	3.1
	June 1966	93	5	20.3	99.0
	Nov. 1966	111	7	9.6	2.4
	Feb. 1967	46	3	4.6	1.1
	Mar. 1967	787	6	10.0	101.8

RESULTS

Micronekton

Variations of the dry weights of micronekton (fishes, shrimps, and squids) captured per 1,000 m³ are shown in Figure 2 for four stations, 1962-67. Several trends are apparent. Seasonal peaks in the biomass occur inshore at the 28- and 46-km stations during the winter months, with very low values during intervening months. A reversed trend, though less pronounced, is found offshore at the 84- and 120-km stations where maximum catches generally were made during the summer or fall months. Average biomass values appear to be lowest inshore, highest at 84 km, and lower again at 120 km where total variability is the lowest.

The spatial peak of micronekton biomass at 84 km is more obvious in Figure 3, where dry weight is plotted per square meter instead of per cubic meter (to compensate for different depths of sampling at inshore stations). The standing stocks of fishes were greater than shrimps, and shrimp stocks were greater than squids at all stations except at 46 km where shrimps predominated. The neritic, benthopelagic shrimp, *Pandalus jordani*, occasionally made up the bulk of the biomass of collections at both 28 and 46 km (Pearcy 1970). However, mesopelagic animals comprised most of the nighttime IKMT catches: mainly the fishes *Stenobrachius leucopsarus, Diaphus theta, Tarletonbeania crenularis*, and *Tactostoma macropus* (Pearcy 1964, 1972; Pearcy and Laurs 1966; Pearcy and Mesecar 1971); the shrimp *Sergestes similis* (Pearcy and Forss 1966, 1969); and the squids *Gonatus* spp. and *Abraliopsis felis* (Pearcy 1965, 1972).

Seasonal variations in the total biomass (grams/10 m²) of micronekton are illustrated in Figure 4 for two general seasons: May-October, which includes the upwelling season; and November-April, when surface currents are usu-

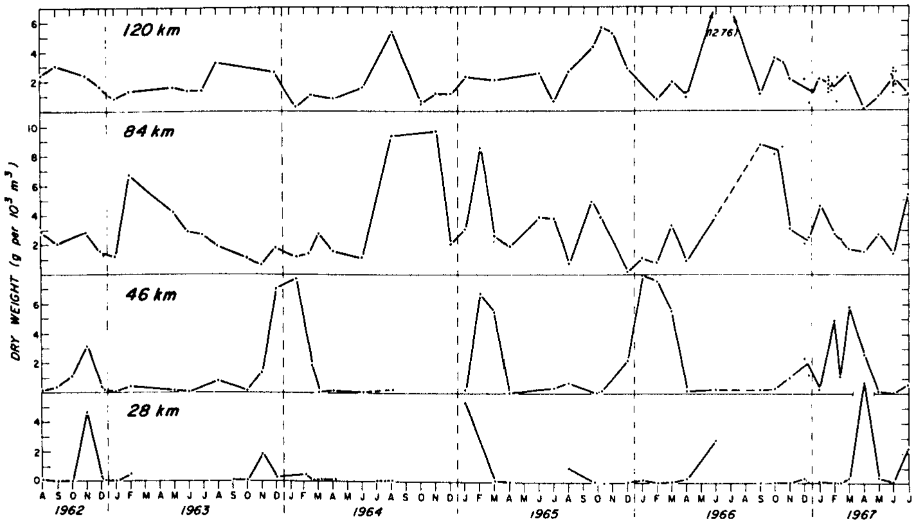

FIGURE 2.—Biomass of micronekton captured in Isaacks-Kidd mid-water trawl collections at four stations, 1962-1967. Each point represents one collection. Average depth of tows was 40 m for 28-km station, 130 m for 46-km station, and 200 m for 84- and 120-km stations.

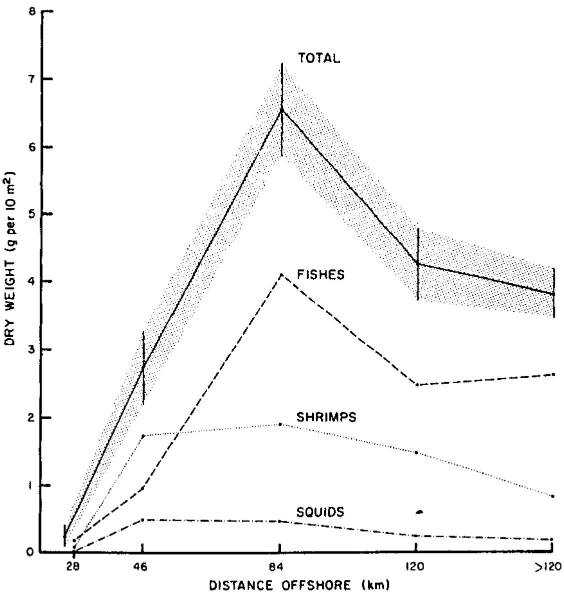

FIGURE 3.—Inshore-offshore variations in the average total micronekton biomass (grams per 10 m² ± 1 SE) and in its component fishes, shrimps, and squids.

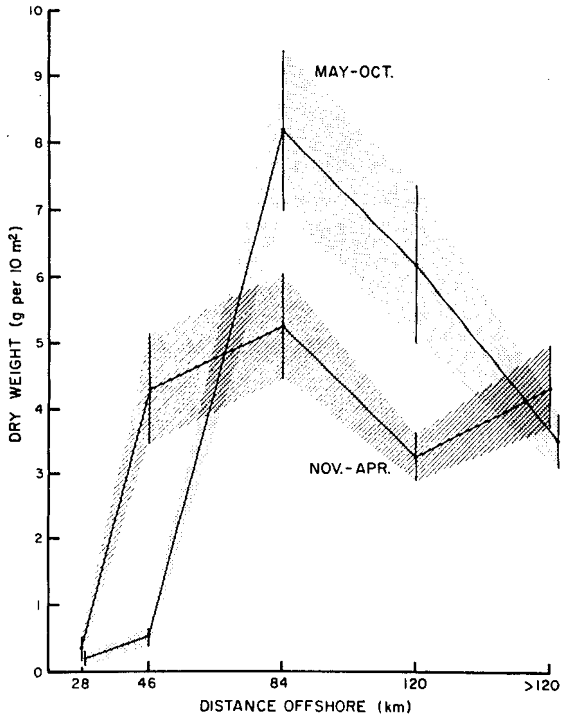

FIGURE 4.—Inshore-offshore variations in the biomass of micronekton during two seasons, May-October and November-April. Shaded areas included means ± 1 SE.

ally reversed, downwelling occurs, and the Davidson Current is often present along the coast (Wyatt et al. 1972; Bakun 1973). The means and medians of the biomass of total micronekton per 10 m², and of its constituents—fishes, shrimps, and squids—are given in Table 2 for these two seasons, along with the probabilities that the two seasonal values are the same. Seasonal differences of total biomass are significant ($P<0.05$) at 46

TABLE 2.—The mean and median biomass (grams dry weight per 10 m²) for micronekton and macroplankton during summer (S = May-October) and winter (W = November-April) at five stations (28, 46, 84, 120 and >120 km) off the Oregon Coast. Probabilities resulting from Mann-Whitney U and t tests of seasonal differences are given.

Item	Stn. 28 km		Stn. 46 km		Stn. 84 km		Stn. 120 km		Stn. >120 km	
	S	W	S	W	S	W	S	W	S	W
Total micronekton										
Mean	0.19	0.32	0.51	4.30	8.20	5.24	6.20	3.26	3.50	4.30
Median	0.004	0.03	0.38	2.75	7.84	4.04	5.04	2.76	3.28	3.18
Probabilities										
U	NS		S<W** P<0.01		S>W P=0.08		S>W* P=0.04		NS	
t	NS		S<W** P<0.01		S>W* P<0.05		S>W** P<0.01		NS	
Probabilities										
U test										
Fishes	†		S<W** P<0.01		S>W** P=0.01		S>W* P=0.02		NS	
Shrimps	†		S<W* P=0.03		NS		NS		NS	
Squids	†		NS		S>W** P<0.01		NS		NS	
Total macroplankton										
Mean	24.9	19.3	31.3	38.7	37.0	15.6	27.4	26.6	11.8	15.7
Median	12.6	12.1	9.4	8.1	12.2	6.5	8.0	8.6	4.9	5.0
Probabilities										
U	NS		NS		S>W* P<0.04		NS		NS	
t	NS		NS		S>W** P<0.01		NS		NS	
Probabilities										
U test										
Copepods	NS		NS		NS		NS		NS	
Euphausiids	NS		NS		NS		NS		NS	
Salps	†		†		†		†		NS	
Medusae	S>W** P<0.01		S>W** P<0.01		S>W P=0.06		NS		NS	
Chaetognaths	NS		NS		NS		NS		NS	
Amphipods	NS		NS		NS		NS		NS	
Shrimps	†		†		S>W* P<0.05		NS		NS	

NS - not significant.
† - too many zeros for valid tests.

and 120 km using the non-parametric Mann-Whitney U test (Tate and Clelland 1957) and at 46, 84, and 120 km using the parametric t test. Mann-Whitney U tests for the three taxa of micronekton indicated significant seasonal differences for standing stocks of fishes at 46, 84, and 120 km, for shrimps at 46 km and for squids at 84 km.

Macrozooplankton

Values for the biomass of macrozooplankton collected at four stations during 1963-67 are shown in Figure 5 and Table 3. Inshore-offshore and seasonal trends are less apparent than for micronekton. The total MN biomass per 10 m² is lowest at the 28-km stations, greater at the 120-km stations, and highest at the 46-, 84-, and 120-km stations (Table 3).

Of the taxonomic groups composing the MN samples, copepods were most important on an average dry weight basis at all stations except at 46 km where euphausiids were very abundant (Table 3). The standing stock of medusae ranked second after copepods at all stations except at 46 km where it ranked third after copepods. Even though the maximum biomass of all groups occurred at 46, 84, or 120 km on a square meter basis, the maximum weights of copepods and

TABLE 3.—Biomass of zooplankton per 10 m² collected with 1-m diameter nets at the stations off Newport, Oreg.

Item		Stn. 28 km	Stn. 46 km	Stn. 84 km	Stn. 120 km	Stn. >120 km
Total biomass						
Mean		21	36	26	27	14
Median		8.0	15	16	15	10
SD		34	58	27	33	10
No. collections		36	40	41	37	25
Ave. sampling depth		60	152	200	200	200
Copepods	Mean	11.9	12.2	7.9	11.7	4.3
	Median	2.4	2.0	2.1	2.5	1.5
Euphausiids	Mean	2.6	20.0	6.2	2.4	2.5
	Median	0.6	3.7	2.2	1.5	1.1
Salps	Mean	0.04	0.03	3.2	4.1	1.4
	Median	0	0	0.002	0.002	0
Medusae	Mean	5.8	2.3	6.8	6.4	3.8
	Median	1.2	1.1	3.2	2.5	2.0
Chaetognaths	Mean	0.5	0.9	1.6	1.7	0.9
	Median	0.07	0.6	1.0	1.1	0.7
Amphipods	Mean	0.07	0.1	0.2	0.3	0.3
	Median	0.02	0.06	0.2	0.2	0.2
Shrimps	Mean	0.02	0.6	0.5	0.6	0.8
	Median	0	0	0.2	0.2	0.1

medusae on a cubic meter basis were found at 28 km, nearest the coast.

Differences in the biomass of macrozooplankton between the two seasons were only significant at one station, 84 km offshore (Table 2), although distinct peaks occurred during the summers of 2 yr at 120 km (Figure 5). Surprisingly, most of the taxonomic groups of zooplankton, including copepods and euphausiids, evidenced no seasonal changes at any stations. The only significant

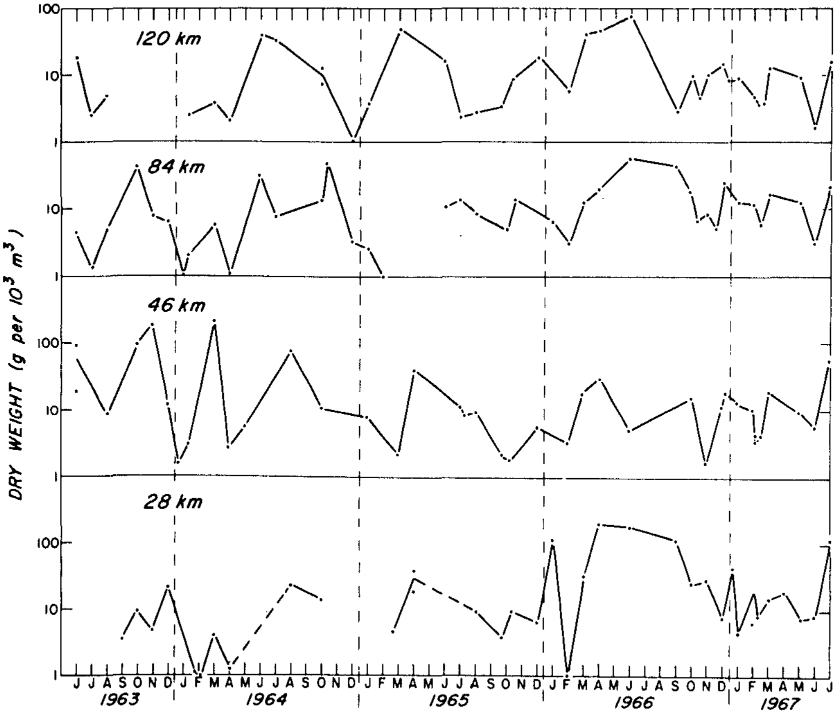

FIGURE 5.—Biomass of macrozooplankton captured in 1-m diameter plankton nets at four stations, 1963-1967. Each point represents one collection.

differences were for medusae, whose standing stocks in the summer exceeded those in the winter at 28 and 46 km (Mann-Whitney U, $P<0.01$) and perhaps at 84 km ($P = 0.06$), and for shrimps at 84 km, where again biomass was larger during summer than winter (Table 2).

Trophic Groups

To estimate seasonal and inshore-offshore variations in the standing stocks of the lower trophic levels of oceanic consumers, the dry weights of the various taxa were combined. Herbivores were assumed to include copepods, euphausiids, and salps-doliolids. Planktonic carnivores included chaetognaths, medusae, amphipods, and shrimps. Nektonic carnivores included fishes, squids, and shrimps. Although it is recognized that some euphausiids and copepods may be carnivorous, the main species captured off Oregon, *Euphausia pacifica, Thysanoessa spinifera*, and *Calanus* spp., are considered to be largely herbivorous.

Inshore-offshore variations in standing stocks are illustrated in Figure 6. On the average, the biomass of herbivores was greater than planktonic

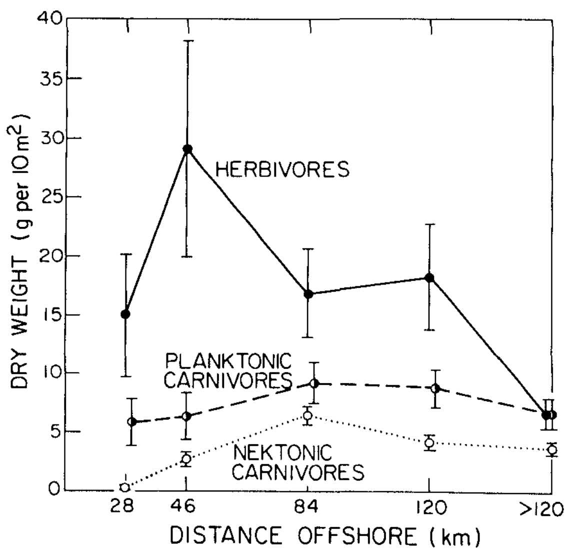

FIGURE 6.—Inshore-offshore variations in the average biomass (± 1 SE) of herbivores, planktonic carnivores, and nektonic carnivores at five stations.

carnivores, and the biomass of these organisms was greater than that of micronektonic carnivores at all stations. The high catches of herbivores at 46 km were due to abundant concentrations of euphausiids. Both groups of carnivores, on the other hand, had lowest biomass at the inshore stations and attained maxima farther offshore.

Seasonal variations in the standing stocks of herbivores and planktonic carnivores are illustrated in Figure 7. Mann-Whitney U tests of differences between the two seasons were not significant (all $P>0.1$) for any station, providing no evidence for seasonal changes in the biomass of herbivores. The biomass of planktonic carnivores increased with distance offshore during the winter and tended to decrease during summer. The biomass at 28 km was higher in summer than winter ($P<0.01$), largely due to high catches of medusae during the summer. At 84 km,

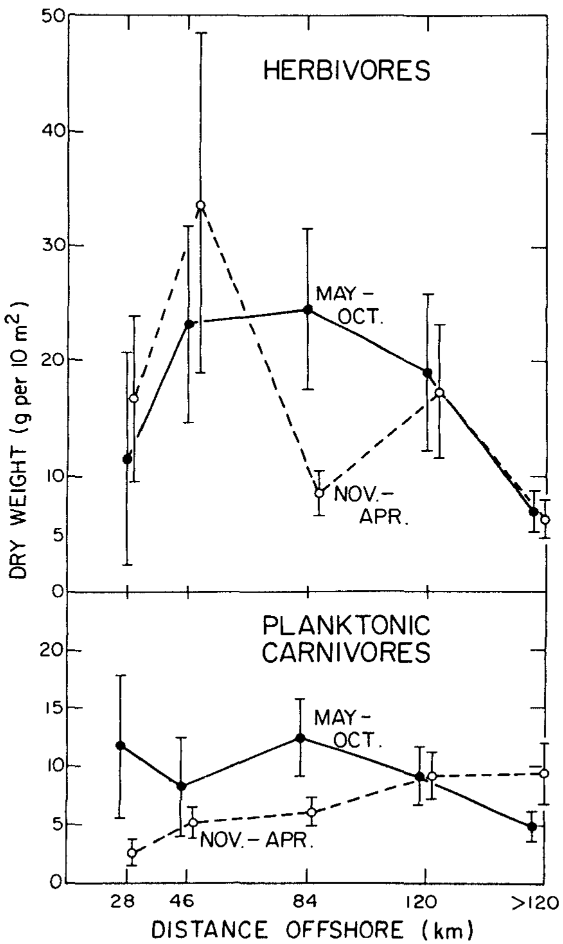

FIGURE 7.—Seasonal variations in the average biomass (± 1 SE) of herbivores (upper) and planktonic carnivores (lower).

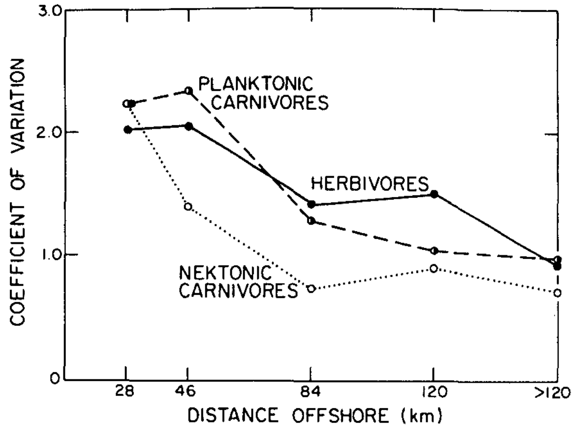

FIGURE 8.—Variability in the catches of herbivore, planktonic carnivores, and nektonic carnivores vs. distance offshore. Variability is expressed as coefficients of variation based on dry weights per 1,000 m^3.

planktonic carnivores also appeared to be more abundant during the summer (P = 0.08), again because of higher catches of medusae. No seasonal differences were apparent at other stations ($P>0.1$).

The ratio of herbivore:carnivore biomass, as expected from the data shown in Figure 6, averages about 2.0 at 28 km and 4.0 at 46 km, but only about 1.0 at the oceanic stations 84, 120, and >120 km. These ratios were ranked among stations for individual cruises. The sum of the ranks for stations were significantly different ($P<0.01$, Friedman two-way ANOVA by ranks, Tate and Clelland 1957). Thus herbivores predominated over carnivores in inshore waters, whereas the standing stocks of herbivores and carnivores were about equal in oceanic waters 84 km offshore and beyond. No seasonal differences in herbivore:carnivore ratios were found ($P>0.05$, Mann-Whitney U tests).

As a measure of variability of the standing stocks of trophic groups over the sampling period, coefficients of variation ($s/\bar{x}$) of the catches are plotted for each station in Figure 8. A marked decline in the variability of both herbivores and carnivores takes place from inshore into offshore waters.

DISCUSSION

Regional Comparisons of Zooplankton Standing Stocks

Values for the standing stocks of zooplankton in the upper 140 to 300 m are summarized by Cushing (1971) for upwelling regions of the world. The average biomass of zooplankton collected within 120 km of the Oregon coast (Table 4) is within the range of values given by Cushing, after conversion to displacement volume per 1,000 m^3 and to grams carbon per square meter.

Zooplankton standing stocks off Oregon can also be compared with those reported by the California Cooperative Oceanic Fisheries Investigations (CALCOFI) which used 0.25-0.55-mm mesh in nets towed obliquely from 140 m to the surface. Zooplankton displacement volumes near the Oregon coast accord with values of Reid et al. (1958) and Reid (1962) greater than 400 cm^3/1,000 m^3 for July and August 1955 from Point Conception, Calif., to northern Washington, and with Thrailkill's (1956) values of 100-900 cm^3/1,000 m^3 for 1949 and 1950 off Oregon and northern California. Smith's (1971) median displacement volumes for pooled areas within 100 miles of shore between Point Conception and San Francisco Bay, Calif., are 200-400 cm^3/1,000 m^3 during April-July 1951-60, with decreased volumes south of Point Conception. Median displacement volumes for Oregon (either on an annual or a summer basis, Tables 2 and 4) are appreciably lower than Smith's values for northern California. This difference may be ascribed to differences between vertical and oblique tows, mesh size, or annual differences in standing stocks. Or, a real trend may exist for the nearshore zooplankton standing stocks to increase in the California Current system between Oregon and northern California, a trend that may be attributed to the more intense upwelling—and hence higher productivity—that occurs off northern California (Bakun 1973).

Zooplankton volumes within 120 km of Oregon are several times those given by McAllister

TABLE 4.—Dry weight of Oregon zooplankton converted to displacement volumes and grams carbon.

Item	Stn. 28 km	Stn. 46 km	Stn. 84 km	Stn. 120 km	Stn. >120 km
Mean cm^3/1,000 m^3*	552	450	228	274	85
Median cm^3/1,000 m^3	160	157	140	121	83
Mean gC/m^2†	1.1	1.8	1.3	1.3	0.7
Mean gC/m^2‡	2.3	3.9	2.8	2.9	1.5

*Conversion based on data of Ahlstrom and Thrailkill (1963, Table 7): wet weight plus interstitial water (≅displacement volume) × 0.06 = dry weight.

†C was estimated to be 50% of the dry weight (see Omori 1969, Table 5).

‡Calculated using Cushing's (1971) conversion of 0.065 × displacement volume = gC. This conversion assumes that displacement volumes do not include interstitial water, but according to the data of Ahlstrom and Thrailkill (1963, Table 7) an average of 42% of the wet weight of mixed zooplankton is interstitial water.

(1961) and LeBrasseur (1965) for oceanic areas of the Gulf of Alaska (0-150 m vertical tows with a 0.45-cm diameter net, 0.35-mesh), even after their catches are adjusted for the relatively low catching power of their net (McAllister 1969; LeBrasseur and Kennedy 1972). Average volumes at weather station "P" (lat. 50°N, long. 145°W) were more similar to those at the station >120 km off the Oregon coast. Increased productivity associated with coastal upwelling along Oregon, therefore, enhances the average zooplankton standing stocks out to about 120 km from shore several times above the stocks farther offshore or upstream in the North Pacific Drift (see also Reid 1962). The width of this zone of high zooplankton standing stocks appears to be considerably less than the 200-500 km reported by Cushing (1971) for the region off northern California.

Seasonality of Standing Stocks

Seasonality in the biomass of zooplankton, with maxima in the summer and minima in the winter, has been reported in the California Current system off central California (Lasker 1970; Smith 1971) and in waters off the Oregon-Washington coast (Peterson 1972). Yet there was limited evidence for differences in macrozooplankton standing stocks between the two seasons in Oregon waters. Thus seasonality of standing stocks appeared to be more pronounced for micronekton than macrozooplankton, or for carnivores than herbivores. This may be because the high variability of macrozooplankton catches (Figure 8) makes important seasonal changes difficult to detect. Also the months selected for the two seasons may not match the periodicity of natural cycles. Another possible explanation is that the seasonality in catches of common animals such as *Euphausia pacifica* and *Calanus* spp. may be less than that in small herbivores with shorter life spans and generation times. Small copepods such as *Pseudocalanus, Oithona*, and *Acartia*, which were not sampled adequately with my nets, are known to be abundant in Oregon-Washington waters in the summer, especially in upwelled waters along the coast (Frolander 1962; Cross 1964; Peterson 1972; Peterson and Miller 1975).

Inshore-Offshore Variations

Largest standing stocks of macrozooplankton and micronekton (grams per square meter but not grams/1,000 m^3, Tables 3 and 4, Figure 6) were found intermediate distances off the Oregon coast, namely over the continental slope at stations 46 and 84 km offshore. A trend for maxima at intermediate distances offshore has been reported for other regions. Standing stocks of zooplankton were highest at the edge of the shelf or over the inner slope off New York (Grice and Hart 1962), intermediate distances from shore off California (Smith 1971), and near mid-shelf in the Florida Current off Cape Hatteras, N.C. (St. John 1958). Macrozooplankton and micronekton collected with a 0.9-m IKMT off Vancouver Island, Canada and Washington were maximal over the outer edge of the shelf (Day 1971). The reduced feeding activity of pink, chum, and sockeye salmon as they approach the coast is purportedly explained by the low macroplankton concentrations in neritic waters and higher concentrations in offshore waters of the northwestern Pacific off Kamchatka (Andrievskaya 1957; Mednikov 1958). All of these studies indicate that small intermediate consumers may achieve maximum importance in the pelagic food chain in deep waters beyond the inner shelf (see also Williams et al. 1968).

The reason why catches of micronekton and macrozooplankton were higher offshore than nearshore may be related to their vertical migrations. Most of the species of micronekton and euphausiids caught in upper waters at night undertake diel vertical migrations (Pearcy and Laurs 1966; Pearcy and Forss 1966; Brinton 1967; Pearcy and Mesecar 1971); hence they may be most abundant in waters deep enough to permit vertical movements but where productivity is enhanced near land (Pearcy 1964). If they drift over the shelf, they may be eaten by large benthic or pelagic predators (Isaacs and Schwartzlose 1965; Pereyra et al. 1969).

The inshore-offshore changes in standing stocks of micronekton for the two seasons (Figure 4) suggest that these distributions are interrelated. Movement of animals may be correlated with seasonal oceanographic changes. During the summer, when the biomass increases greatly from 46 km to a peak at 84 km, large inshore-offshore gradients also occur in physical properties because of upwelling, and there is an offshore component of nearshore surface waters (Pillsbury 1972). During the winter, when biomass from 46 to >120 km is relatively uniform, inshore-offshore gradients are weak, surface currents are onshore, and downwelling occurs (Hebard 1966; Laurs 1967). The significant increase in biomass at 46 km in the winter may be caused by inshore advection of surface water and animals and the concentrating effect of shallow water near the edge of the shelf on vertical migrants. The peak at 84 km in the summer, though far from the coast, may be related to upwelling. Sometimes Laurs (1967) found maximum biomass of carnivores at 65-84 km and maxima of lower trophic levels closer inshore off Brookings, Oreg., during the summer, suggesting a succession of trophic level maxima such as reported by Sette (1955), King (1958), and Vinogradov and Voronina (1962) in areas of oceanic upwelling in equatorial waters.

Herbivore:Carnivore Ratios

Others have also found that the herbivore: carnivore biomass ratios decrease from shallow, eutrophic waters to oceanic waters. Grice and Hart (1962) reported that well over one-half of the zooplankton by volume in shelf waters off New York herbivorous, while in the Sargasso Sea only about one-half belonged to this trophic level. The percentage of herbivores in the zooplankton catches decreased from inshore waters that were affected by upwelling into offshore waters of the California Current off Baja California (Longhurst 1967). Greze (1970) reported that the biomass and production of herbivores and carnivores was a larger percentage of that of primary producers in the Equatorial Atlantic or Ionian Sea than the shallow waters of the Black Sea or Sevastopol Bay. These trends suggest that (a) a smaller fraction of the herbivorous biomass is captured in oceanic than neritic waters because of escapement through coarse mesh or avoidance, (b) production per unit biomass of herbivores is higher relative to that of carnivores in offshore waters, or (c) that ecological efficiences (food consumed by tropic level $n + 1$ to food consumed by trophic level n) are higher in oceanic than neritic waters.

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