VARIABILITY OF NEAR-SURFACE ZOOPLANKTON OFF SOUTHERN CALIFORNIA, AS SHOWN BY TOWED-PUMP SAMPLING

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ABSTRACT

Variations in the density of near-surface populations of small copepods, large copepods, euphausiids, and chaetognaths are described for an area of 6,000 square miles off the coast of southern California from three cruises in the autumn of 1961 and two cruises in the autumn of 1962. Samples were collected with a towed pump at a depth of 5 m. Approximately 162 samples, each representing a 1-mile transect, were collected on each cruise.

Median densities for the cruises showed some significant differences for each species group. The frequency distribution of densities within the area on individual cruises varied from positive skewness at low general levels to relative symmetry at high general levels for the three crustacean groups, but was skewed at all levels for chaetognaths. Within sampling blocks of 20 square miles, the range of density varied with the median as $\log R = 0.35 + 0.8 \log M$. Range is greater than the median when the latter is less than 50, but less than the median when it is higher than 50.

Euphausiids and large copepods showed greater diurnal change than small copepods and chaetognaths. Dry weight concentration of samples, averaged over all cruises, was 17.3 mg/m^3 for the day period (0600-1800) and 25.1 mg/m^3 for the night period. Most of the nighttime increase is attributable to the euphausiid group.

The three crustacean groups, and dry weight, showed significant inverse trends with temperature, but not with distance from land. The trends with temperature reflect events in 1961 but not in 1962.

These variations suggest that food potential of plankton for pelagic fishes may be appreciably greater than indicated by general averages for the area, depending on the degree of selectivity and orientation to small-scale features of distribution by the fishes.

Little is known about the effects of plankton variability on the distribution, movements, or rate of feeding of pelagic fishes which feed on plankton. It has been demonstrated experimentally (Ivlev, 1961) for some fishes that rate of feeding varies not only with average density but also with the degree of aggregation of food organisms in an area. Plankton density is known to vary diurnally (Cushing, 1951; King and Hida, 1954) as well as seasonally and annually, and there is evidence of aggregation in the variation for both small and broad spatial scales (Barnes and Marshall, 1951; Cassie, 1959, 1962, 1963). The plankton pump surveys reported here were undertaken to obtain information on variability and trends in variability for four plankton species groups commonly present in near-surface waters along the southern California coast. Though surveys were limited to the autumn seasons of 2 consecutive years, the data should be a useful guide in evaluating the food potential of near-surface plankton distributions in the region.

COLLECTION OF SAMPLES

Samples were collected with the towed pump and shipboard filtering system described by O'Connell and Leong (1963). The 1.9-cm (¾-inch) orifice of the pump pointed forward to achieve a coring orientation, and the rate of pumping (98 liters/min) exceeded the passive coring rate to produce in effect a 5.8-cm (2-inch) diameter coring cross-section. Operation of the system was essentially a matter of leaving the pump in tow and running throughout a cruise pattern with the incoming water stream diverted to the scuppers except while traversing sampling blocks, at which time the flow was directed through the filtering apparatus. The stainless steel filtering screen (105μ mesh) retained

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virtually all organisms as small as 200μ in length (O'Connell and Leong, 1963) or 100μ in diameter (Leong, 1967). The upper size limit was less easily defined, but organisms as long as 14 mm were delivered at the filtering apparatus, though the large individuals were often mutilated.

Five cruises were carried out, three in September to November 1961 and two in the same period of 1962. For each cruise a pattern of 18 sampling blocks was selected from a possible 281 that covered an area of almost 6,000 square miles (Figure 1). To insure reasonably good coverage of the entire area, the population of blocks was divided into three approximately equal subareas and a set of six blocks was selected at random from each. The blocks were occupied by the shortest practical track from northwest to southeast. Each cruise pattern required about 2.5 days of vessel time.

Each sampling block was 51.8 km^2 (20 square miles) in area, the only exceptions being some of the blocks adjacent to the coast or to islands. Nine 1.6-km (1-mile) samples were collected at each block in a continuous series along two connecting sides (Figure 1, insert) and were preserved in Formalin for laboratory processing.

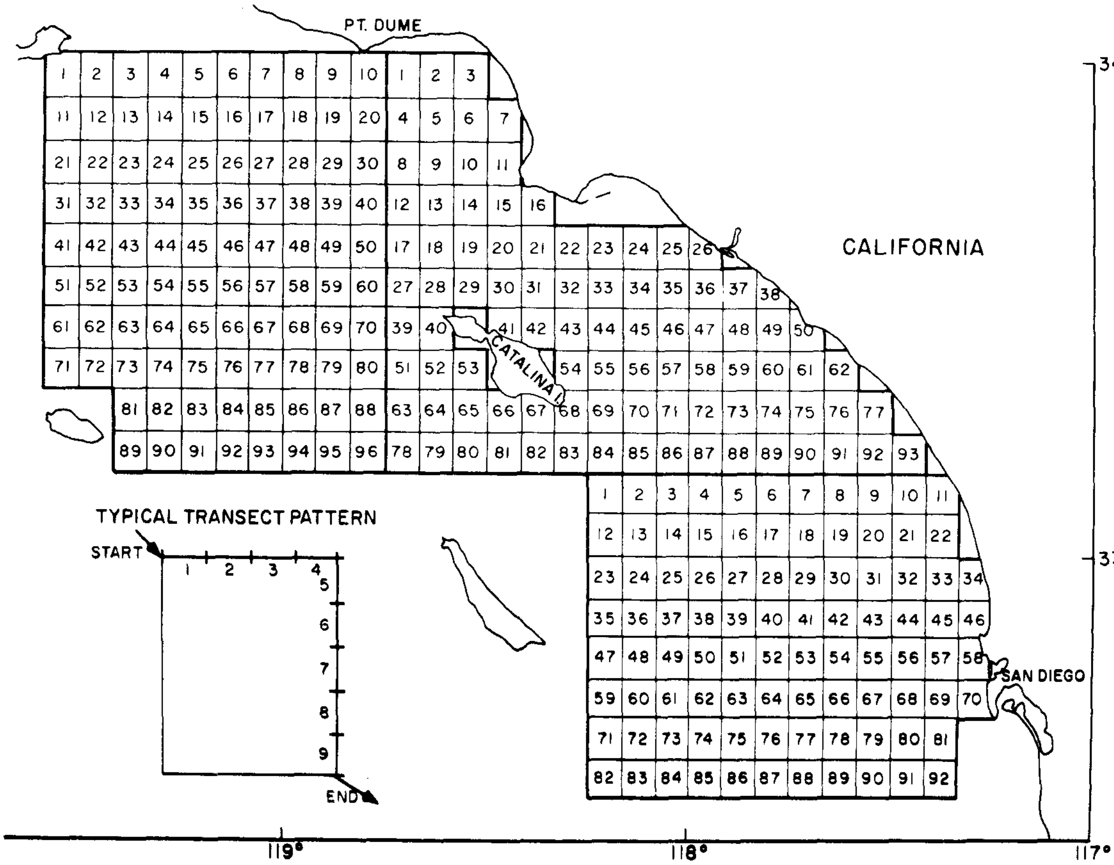

FIGURE 1.—The sampling area and entire population of sampling blocks. Six blocks were randomly selected from each of the three subareas for each cruise and occupied by the shortest route from north to south. Sampling blocks are 4 × 5 miles and the insert shows the manner of transect sampling. Four of the nine samples from each block were selected randomly for organism enumeration.

Consecutive 1.6-km samples were separated by shifting the incoming stream to a new filter every 6.5 min. Water volume, recorded for each sample from a meter in the incoming line, averaged 636.7 liters (standard deviation 47.8). Water temperature of the incoming stream was recorded at approximately the midpoint of each series of block samples. Continuous thermograph records indicated that surface water temperature did not change appreciably during the sampling of individual blocks.

SAMPLE PROCESSING

Four of the nine samples from each block were randomly selected for the estimation of numbers of organisms. Of the remaining five, one was chosen at random to be reserved for special purposes such as length and dry weight measurements of species groups, and the other four were pooled to obtain a dry weight value for the block. Estimates were standardized as quantities per m^3 on the basis of the actual volumes of water filtered in the samples.

Estimates for two size categories of copepods, 0.2 to 0.9 mm in length and all over 1.0 mm long, and for euphausiids and chaetognaths, were made by volumetric subsampling with replacement, i.e., each subsample was returned to the sample before the next subsample was drawn. The volumetric subsampling technique yields estimates of satisfactory precision only if organisms are randomly distributed in the sample container prior to the removal of each subsample. Simple stirring accomplished this for all species groups except the small copepods, probably because they were entangled in phytoplankton present in the samples. Random distribution was assumed to exist where the value s^2/x did not exceed $\chi^2/N\text{-}1$ for a series of subsamples (Holmes and Widrig, 1956). A random distribution was achieved for the small copepods by subjecting the sample to a few 1-sec bursts of rapid stirring in a Waring Blender.[2] However, because this treatment fragmented some larger organisms a two-step procedure was employed: all organisms except the small copepods were estimated by subsampling following gentle stirring; the sample was then agitated in the Waring Blender, after which the small copepods were estimated by subsampling.

[2] The use of trade names is merely to facilitate descriptions; no endorsement is implied.

Estimates for the small copepods were always based on subsample counts totaling 200 to 300 from the sample. With the assumption of random distribution, the number in the sample should in all cases be within 15% of the estimate for $p = 0.05$ (Holmes and Widrig, 1956). More than half of the sample estimates for the other three species groups were based on counts of 30 or more, for which the number in the sample should have been within 40% of the estimate. For the remainder, where numbers counted were low, examination was not extended beyond subsamples totaling one-third the volume of the sample container, 2,000 ml.

In addition to the four species groups counted, the samples contained larvaceans and small invertebrate eggs (0.15-0.35 mm diameter), sometimes in moderately high numbers. Larvacean tails and heads were separated, however, and invertebrate eggs were not readily distinguishable from the latter. Cladocerans and polychaetes were generally absent or low in number, though each occurred in high numbers in a few samples. Fish eggs occurred rarely and in low numbers.

SIZE OF ORGANISMS

Length measurements for 10 day samples (0600-1800) and 10 night samples are summarized in Table 1 and Figure 2. Measurements were total length except for euphausiids, which were measured from the carapace behind the eye to the junction of the abdomen and telson. Data from day and night samples were pooled for small copepods and chaetognaths but not for large copepods and euphausiids, which showed appreciable size frequency differences for the two periods.

The length-frequency distribution for the small copepod group, composed largely of naupliar and copepodite stages, is nearly symmetrical, with the mean and the median close to the midpoint of the predetermined size range (0.20-0.99 mm long). Almost one-third of the organisms

TABLE 1.—Length data for species groups.

	Mean length	Median length	Minimum length	Maximum length
	mm	*mm*	*mm*	*mm*
Small copepods	0.58	0.56	0.20	0.99
Large copepods:				
Day	1.94	1.90	1.00	5.30
Night	1.75	1.61	1.00	4.20
Euphausiids:				
Day	2.3	2.1	0.6	9.7
Night	5.7	5.9	1.1	10.6
Chaetognaths	6.4	5.5	2.0	14.5

were between 0.5 and 0.6 mm in length. It is possible that the decline in numbers below the median length was partly the result of increasing escapement with diminishing size, but the escaping fraction, known to be negligible for sizes above 0.4 mm, is assumed to be relatively small for sizes down to 0.2 mm (O'Connell and Leong, 1963). On this assumption the length-frequency distribution is considered representative for this size range of copepods.

The large-copepod group shows a modal shift to smaller sizes at night, although the size range and degree of skewness are not markedly different for the two periods. Organisms less than 1.5 mm in length were largely copepodites, while

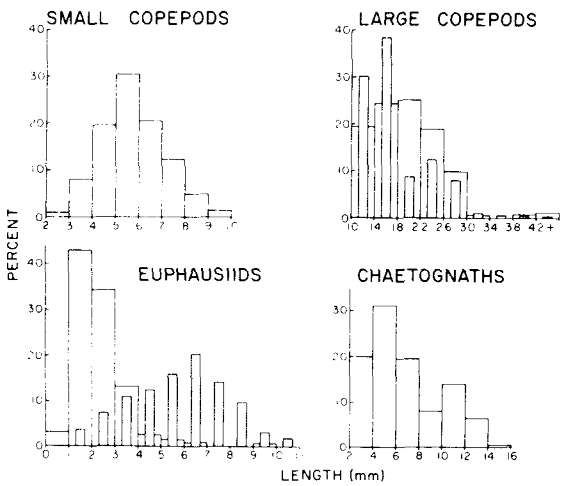

FIGURE 2.—Length-frequency histograms of organisms in four species groups, as determined from selected samples. For large copepods and euphausiids the wide bars show day frequencies and the narrow bars night frequencies.

those between 1.5 and 3.0 mm were adult *Calanus helgolandicus* and *Paracalanus* sp., with *Centropages* sp. also present in the night samples. Those larger than 3.0 mm were largely *Rhincalanus* sp. in both day and night samples.

The euphausiid group, which appeared to be composed largely of *Euphausia pacifica*, though *Nyctiphanes simplex* and *Nematoscelis difficilis* were also in evidence, showed a marked shift to larger sizes at night, obviously the result of vertical migration. It is apparent from the sizes involved that the day samples were composed mostly of larval stages and the night samples of larval stages and juveniles, with few if any adults. The largest individuals in the samples were considerably smaller than the maximum total length for the species, 25 mm (Boden, Johnson, and Brinton, 1955).

The pump samples did show some evidence of fragmentation of larger euphausiids, and for this reason the size frequency distribution for the night period might be slightly biased in favor of the smaller sizes, and estimates of numbers sampled might be a little low.

Fragmentation probably involved far more juveniles than adults. Samples from opening-closing nets 1 m in mouth diameter taken in spring and summer off southern California (Brinton, 1962) showed adults to be scarce or absent in the upper 10 m during the night as well as the day. Juveniles were predominant at this stratum. Even at depths where adults were most abundant at night—40 m in one case and 140 to 280 m in another—they were only one-fifth and one-tenth as numerous as juveniles. Nighttime oblique hauls with nets 1 m in mouth diameter off central Baja California indicated essentially the same kind of vertical distribution for euphausiid species in that area (Ahlstrom and Thrailkill, 1963). On the basis of such evidence it seems probable that the size-frequency distributions shown by the pump samples are reasonably representative of the day and night populations near the surface, though certainly not of the population in the entire water column.

The chaetognath group was composed largely, if not entirely, of *Sagitta euneritica*, and the size range is probably representative for the near-surface population sampled. The size range for the species is 1.0 to 15.5 mm in length (Alverino, 1961), and the samples contained individuals from 2.0 to 14.5 mm long.

VARIATION BETWEEN CRUISES

Table 2 shows characteristics of the frequency distributions of all 1.6-km samples by cruise and period of the day for the four species groups. Median densities are lower than mean densities in every instance but one, the nighttime period for small copepods on cruise 5, indicating that distributions for virtually all arrays show some degree of positive skewness. Differences between cruises are described in terms of the medians to avoid undue effects of extreme values that can arise in moment measures on nonnormal populations.

Nighttime median densities are higher than daytime medians on all cruises for small copepods and euphausiids, and on all but the fifth cruise for large copepods. However, variation was such that day and night medians differed significantly ($p<0.05$, Tate and Clelland, 1957) in only one instance for small copepods, three instances for large copepods, and two instances for euphausiids. Though none of these groups can be considered to show consistently higher densities at night for the area as a whole, real differences occurred more often for the large copepods and euphausiids than for the small copepods. Day and night median densities for chaetognaths do not differ significantly for any of the cruises.

Daytime median densities do not differ significantly between cruises for chaetognaths or euphausiids, but those for small copepods and large copepods differ significantly ($p<0.05$) for about half the comparisons. Nighttime medians (Figure 3) show a pattern similar to the daytime sets for the two copepod groups but show, in addition, a number of significant differences between cruises for the euphausiids and one difference for chaetognaths. Median densities of the small copepods were significantly higher for

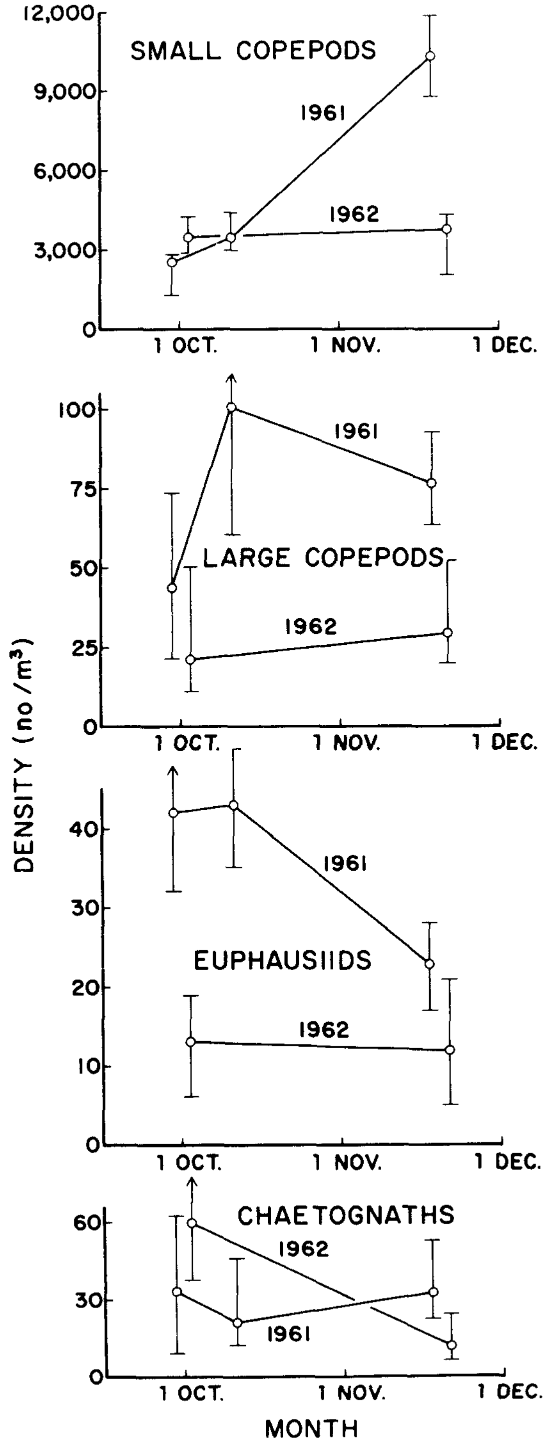

FIGURE 3.—The nighttime cruise medians for four species groups shown by cruise date. Vertical bars indicate the 95% confidence intervals.

TABLE 2.—Summary of density estimates (no/m^3) of 1.6-km samples by cruise, constituent group, and period of day.

	Mean	s	Median	Confidence limits[1] p = 0.95 Lower	Upper	Minimum	Maximum
			Cruise 1, September 26-28, 1961, N = 32 day, 40 night				
Small copepods:							
Day	2,569.7	987.4	2,275.5	2,023	2,552	1,210	5,233
Night	2,983.9	1,356.2	2,542.0	2,252	2,792	1,075	7,103
Large copepods:							
Day	6.4	16.0	1.0	0	5	0	83
Night	72.8	95.5	42.5	22	73	0	500
Euphausiids:							
Day	6.7	9.4	3.0	2	8	0	38
Night	52.2	37.1	41.5	32	57	10	172
Chaetognaths:							
Day	84.2	122.9	21.0	8	105	2	488
Night	123.6	244.2	33.0	10	63	2	1,153
			Cruise 2, October 9-11, 1961, N = 24 day, 40 night				
Small copepods:							
Day	3,379.0	1,773.1	3,034.5	2,217	3,527	1,550	7,532
Night	3,953.0	1,620.0	3,325.0	2,942	4,257	2,142	8,118
Large copepods:							
Day	47.3	104.5	1.0	0	17	0	440
Night	102.7	67.3	101.0	60	128	5	250
Euphausiids:							
Day	10.9	19.7	1.0	0	15	0	88
Night	48.2	31.7	42.5	35	50	7	145
Chaetognaths:							
Day	132.7	135.3	121.5	3	198	0	420
Night	51.8	61.9	21.0	13	47	2	280
			Cruise 3, November 16-18, 1961, N = 28 day, 40 night				
Small copepods:							
Day	8,679.0	3,969.7	7,381.5	6,107	10,208	3,752	19,868
Night	10,577.8	3,060.7	10,281.0	8,673	11,812	4,948	17,568
Large copepods:							
Day	18.3	21.1	10.0	5	18	0	92
Night	83.0	42.9	77.0	63	95	10	183
Euphausiids:							
Day	15.5	13.9	13.0	5	22	0	48
Night	39.5	50.8	23.0	17	28	2	243
Chaetognaths:							
Day	73.5	104.5	36.0	32	42	12	470
Night	44.5	38.8	32.5	23	50	3	188
			Cruise 4, October 1-3, 1962, N = 43 day, 26 night				
Small copepods							
Day	2,718.1	1,748.8	1,993.0	1,739	2,771	456	8,190
Night	3,524.1	1,087.1	3,504.0	2,854	4,179	1,477	5,560
Large copepods:							
Day	21.3	19.6	18.0	10	22	0	90
Night	33.6	29.5	21.5	11	50	3	99
Euphausiids:							
Day	8.2	9.1	4.0	3	10	0	39
Night	16.0	14.3	13.0	6	19	1	58
Chaetognaths:							
Day	116.7	164.6	57.0	35	133	9	993
Night	86.9	71.6	60.0	38	113	13	257
			Cruise 5, November 19-21, 1962, N = 32 day, 31 night				
Small copepods:							
Day	3,728.2	2,277.8	3,487.0	2,235	4,328	1,654	11,613
Night	3,505.3	1,962.1	3,750.0	2,054	4,223	796	9,476
Large copepods:							
Day	121.5	252.0	49.5	29	70	0	1,220
Night	41.1	35.6	30.0	19	52	1	154
Euphausiids:							
Day	9.8	11.0	6.5	1	13	0	48
Night	24.4	34.4	12.0	5	21	0	163
Chaetognaths:							
Day	32.2	20.8	28.5	19	41	3	94
Night	21.0	20.2	12.0	7	25	0	72

[1] Confidence limits are for medians (Tate and Clelland, 1957).

each successive cruise in 1961, and the median for the last cruise in this year was more than three times as high as any of the others. Median densities of the large copepods were two to four times as high for the last two cruises in 1961 as for the other cruises. Euphausiid medians were about twice as high for the first two cruises of 1961 than for the other cruises. The chaetognath median for the last cruise of 1962 was significantly lower than for the first cruise of that year, but no other differences can be distinguished.

In summary, the three crustacean groups showed real differences in density near the surface at night for the area as a whole. All showed differences of three to four times between the 2 successive years. The euphausiids and small copepods also showed real differences of about two and three times within the first of the 2 years.

VARIATION WITHIN THE AREA

The 1.6-km samples were taken in block clusters so that small-scale variability could be described in respect to variability over the entire area. The possibilities of comparison are limited, however, because parametric analyses were avoided. The necessary assumptions about frequency distribution of sample estimates could not be satisfied for the present data. Frequency distribution of block medians (or means) is variable between cruises.

FREQUENCY DISTRIBUTION OF BLOCK MEDIANS

Table 3 shows the frequency distribution of block medians for the day and night periods of each cruise. The distributions for each species group vary noticeably, but there are similarities

TABLE 3.—Frequency distribution of block medians by cruise and day (D) or night (N) period.

Class (no/m^3)	1D	1N	2D	2N	3D	3N	4D	4N	5D	5N
Small copepods:										
1-3,000	6	7	3	4	--	--	8	3	4	4
3,001-6,000	2	3	2	5	--	--	3	4	4	5
6,001-9,000	--	--	1	1	5	4	--	--	--	--
9,001-12,000	--	--	--	--	1	2	--	--	1	--
12,000-15,000	--	--	--	--	1	4	--	--	--	--
Category	1	1	2	2	3	4	1	2	2	2
Large copepods:										
0	3	--	3	--	--	--	--	--	--	--
1-50	5	5	2	3	7	1	11	5	6	7
51-100	--	3	--	2	--	7	--	2	1	1
101-150	--	1	--	3	--	2	--	--	--	1
151-200	--	--	--	2	--	--	--	--	1	--
201+	--	1	1	--	--	--	--	--	1	--
Category	1	3	1	4	1	4	1	2	3	2
Euphausiids:										
0	2	--	2	--	1	--	2	--	1	--
1-25	5	2	3	2	5	5	9	6	8	7
26-50	1	3	1	4	1	3	--	1	--	1
51-75	--	3	--	3	--	1	--	--	--	--
76-100	--	2	--	1	--	--	--	--	--	1
101-125	--	--	--	--	--	--	--	--	--	--
126-150	--	--	--	--	--	--	--	--	--	--
151+	--	--	--	--	--	1	--	--	--	--
Category	1	3	1	3	1	2	1	2	1	2
Chaetognaths:										
1-50	5	6	2	7	5	7	4	2	8	9
51-100	1	2	1	1	1	2	3	2	1	--
101-150	--	--	--	1	1	1	3	2	--	--
151-200	--	--	2	1	--	--	--	--	--	--
201-250	1	1	--	--	--	--	--	1	--	--
251-300	1	--	1	--	--	--	--	--	--	--
300+	--	1	--	--	--	--	1	--	--	--
Category	1	1	3	2	2	2	3	3	2	2

among them suggestive of trends with the general level of density. To define the trends, the distributions for each species group were pooled into three or four categories on the basis of the extent of concentration in specific frequency classes and the extent of dispersion over all classes. Category designations are indicated in the table, and percentage frequency histograms are shown for each category in Figure 4. Number of blocks, number of night and day periods, and the range of cruise medians (from Table 2) are given for each histogram.

The histograms suggest the same kind of trend for the three crustacean groups: a shift from distribution almost entirely restricted to the lowest classes when general area level is low, through distribution of greater positive skewness for intermediate levels of area density, to symmetrical distribution as blocks of low median value disappear at the higher levels of area density. The chaetognath distributions were more difficult to classify, but it appears that frequency distribution is appreciably skewed at all levels of area density for this group.

The differences in the trends for the four species groups are also illustrated by the extent of the overlap between the distributions for the highest and lowest categories in the figures. There is no overlap for small copepods, perhaps 50 to 75% overlap for large copepods and euphausiids, and complete overlap for chaetognaths. These differences suggest that when the overall area median is at one extreme, the possibility of blocks with medians at the other extreme is greatest for the chaetognaths, least for the small copepods, and intermediate for the large copepods and euphausiids.

The existence of such trends in frequency distribution indicates that, at least for the crustaceans, no one statistical distribution would satisfactorily fit all the data sets; nor would any single normalizing transformation be uniformly effective for the different data sets. Without normalized distributions, even the interpretation of coefficients of variation would be difficult in comparing cruise periods. It may be noted, however, that when all frequency distribution categories are pooled, the distributions for the four species groups show similar degrees of skewness. The total block array for each species group is approximately normalized by log transformation.

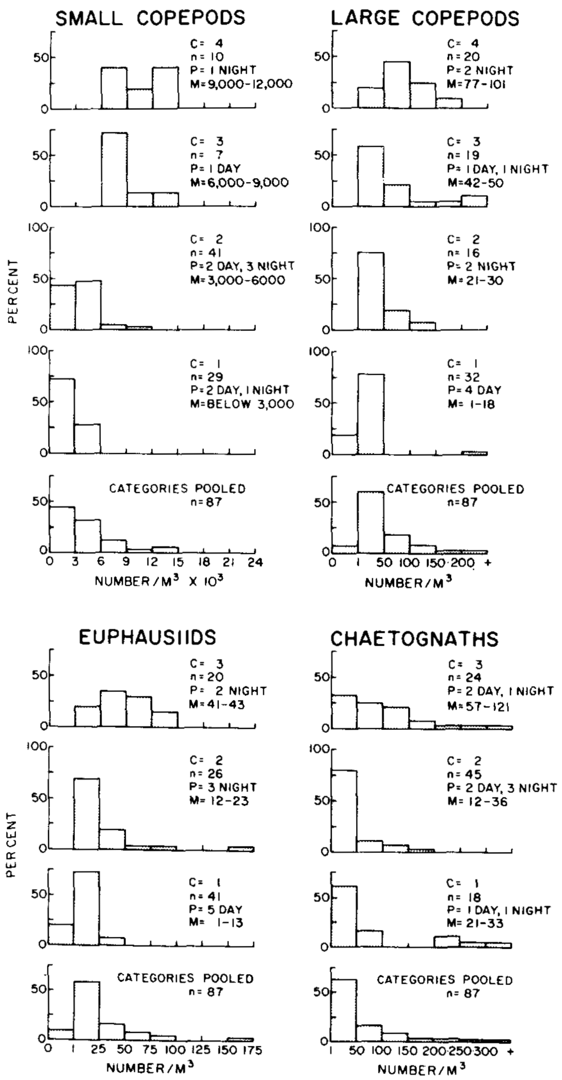

FIGURE 4.—Percent frequency distribution histograms for four species groups as pooled on the basis of similarity. Range of sample medians (M) (from Table 2), number of day and night periods (P), and number of sampling blocks (n) represented by each histogram category (C) is shown. The histogram at the bottom of each set shows the distribution of all block medians from all cruises.

RELATION OF RANGE TO MEDIAN IN SAMPLING BLOCKS

Within block variation is indicated for each species group and for all species groups together by regression $\log R = a + b \log M$ (Table 4), where R = block range and M = block median. The slopes, b, for the five equations do not differ significantly from each other ($p = 0.05$). All are significantly greater than 0 ($p = 0.01$), and all but that for small copepods are significantly less than 1.0 ($p = 0.05$). The intercepts are all significantly greater than 0, again except for the small copepods, but they do not differ significantly from each other ($p = 0.05$). In view of the similarities, the regression for all groups combined (Figure 5) is a satisfactory description of the average relation of block range to block median for each of the species groups.

TABLE 4.—Estimated coefficients for regressions of log block range on log block median for each species group and all species groups combined.[1]

Species group	N	a	b	s	r
Small copepods	87	—.18	.95**	.40	.53**
Large copepods	81	.51	.72**	.36	.74**
Euphausiids	79	.38	.72**	.30	.79**
Chaetognaths	86	.26	.87**	.33	.82**
Combined	333	.35	.80**	.35	.93**

[1] N = number of sampling blocks; a = intercept; b = slope; s = standard deviation about the line; r = correlation coefficient.
** p = 0.01.

The regression for all groups combined indicates that average block range increases with block median but not proportionately. The expected ranges for different medians are:

Median	1	10	50	100	1,000	10,000
Range	2	14	51	89	562	3,548

Thus range will tend to be greater than the median when the latter is below 50, but appreciably less than the median when the median is above 100. Small copepods are the only group with consistently high medians, and they also have the greatest standard deviation about the line. This suggests that, while the ratio of range to median is lower, on the average, for this group, it also tends to be more variable than for the other groups.

The relation of block range to the total variation within the area is suggested by the magnitude of block ranges relative to the class intervals of the frequency distributions shown earlier (Table 5). In the case of small copepods, block ranges only slightly exceed the size of class intervals for the two highest classes in the distribution. For the other three species groups, block ranges exceed the class intervals for all but the lowest class. Ranges tend to be spread over three or more class intervals for the upper halves of the euphausiid and chaetognath distributions. Even though the highest classes tend to be rare, it can be seen that ranges extending over two or more class intervals would not be uncommon for large copepods, euphausiids, and chaetognaths.

TABLE 5.—The number of class intervals encompassed by the range for the midpoint of each class interval in the frequency distribution for each species group. The 0-1 class is excluded and other classes are numbered consecutively.

Frequency class	Small copepods	Large copepods	Euphausiids	Chaetognaths
1	0.1	0.6	0.7	0.6
2	0.3	1.4	1.6	1.4
3	0.9	2.1	2.4	2.1
4	1.2	2.8	3.2	2.8
5	1.5	3.4	3.9	3.4
6	--	--	4.6	4.0
7	--	--	5.2	4.6

DIURNAL VARIATION

It is evident from the differences in day and night sets of data that density level near the surface is influenced by diurnal vertical movements, particularly for the larger crustacean groups. The pattern of change is indicated for each of the species groups by medians for 4-hr time intervals (Figure 6). A sequence of change is most apparent for the large copepods and euphausiids, the lowest medians occurring between 1000 and 1400 hr and the highest between 1800 and 0200 hr. The increase in the evening appears to be more rapid than the decrease in the morning for both groups.

The small copepods show a pattern similar to that for large copepods, but much weaker. The highest time interval median is almost 10 times the lowest for large copepods but less than 2 times the lowest for small copepods.

Chaetognaths show only slight evidence of diurnal change. The peak between 0600 and

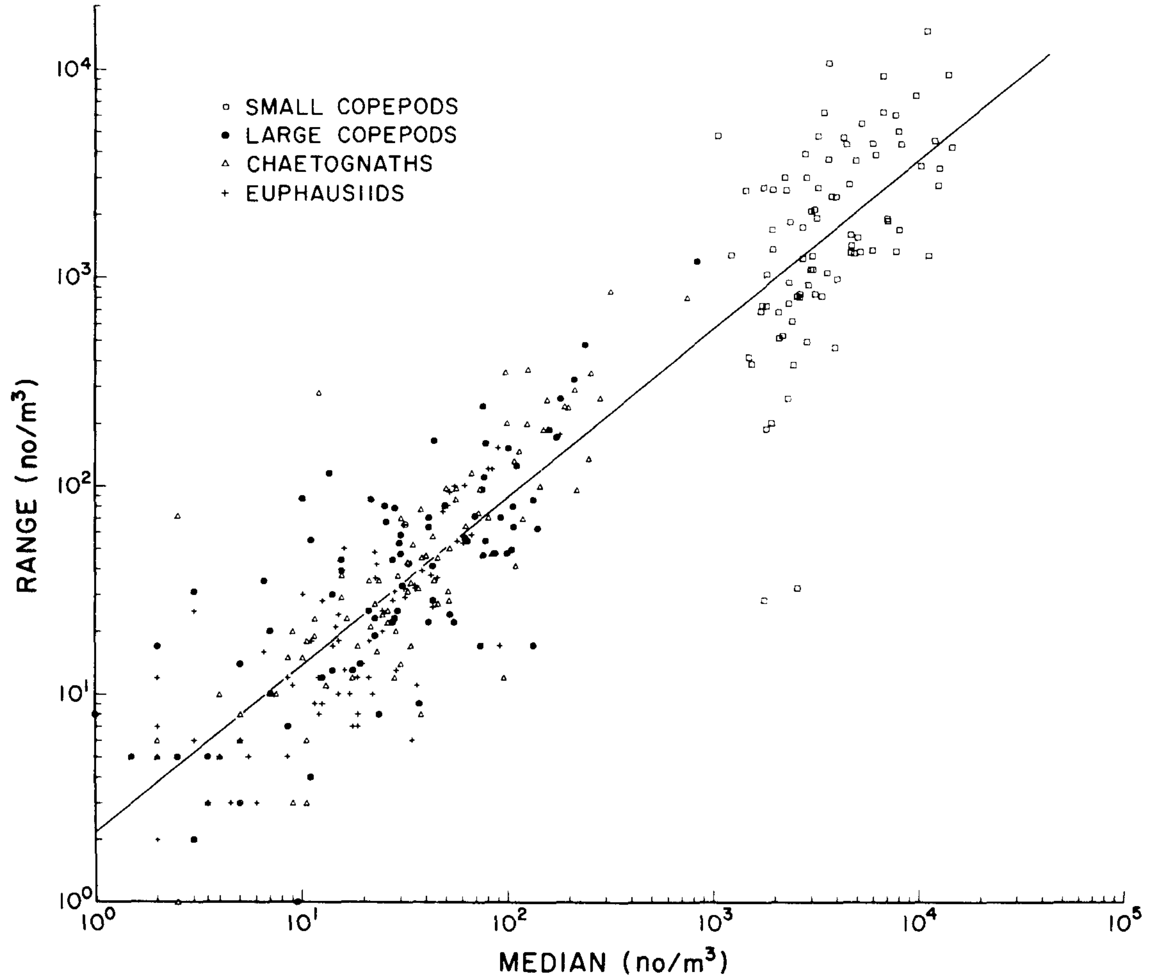

FIGURE 5.—The relation of sampling block range to sampling block median for the four species groups combined.

1000, which is obviously responsible for the generally higher day-period densities shown elsewhere, may indicate an upward and a downward movement in the morning.

The spread of block medians tended to be associated with the time-interval medians for euphausiids but not for the other species groups. The euphausiids showed both high and low block medians at night but only low medians during the middle of the day. Large copepods showed a similar distribution except that three of the highest four block medians in the series occurred between 1000 and 1800 hr. Small copepods and chaetognaths showed high and low medians in all time periods.

CORRELATIONS BETWEEN DENSITIES OF THE FOUR SPECIES GROUPS

The data were examined for association between the densities of species groups over the area by calculating rank-difference correlation coefficients (Tate and Clelland, 1957) for the nighttime block medians of each cruise (Table 6). Daytime blocks were excluded to reduce the component of correlation that would result from

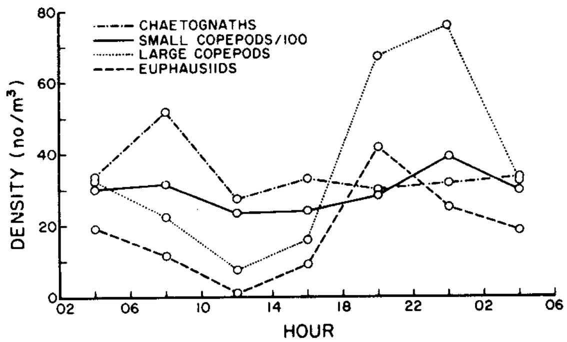

FIGURE 6.—The relation of median density to time of day for four species groups. The points are medians for block densities in 4-hr intervals. The small copepod medians were divided by 100 to put them on the same scale as the others.

TABLE 6.—Rank difference correlation coefficients for median block densities of four species groups for the night periods of five cruises.

	Cruise				
	1	2	3	4	5
Small copepods : large copepods	—.45	.31	.25	.71	.20
Small copepods : euphausiids	—.09	—.20	.59*	.14	.87**
Small copepods : chaetognaths	.26	—.36	—.43	—.42	.30
Large copepods : euphausiids	.10	.04	.71*	.14	.29
Large copepods : chaetognaths	.02	.29	.20	.21	.73*
Euphausiids : chaetognaths	.42	.12	—.23	.00	.53
Number of night blocks	10	10	10	7	9

* p = 0.05.
** p = 0.01.

the parallel patterns of diurnal change in the crustacean groups.

The coefficients for each of the six species group combinations varied widely among the five cruises, with only four of the entire 30 coefficients indicating significant correlations. It appears that, while occasional correlations can be expected to occur over the area, consistent trends of association in density do not occur among these four species groups near the surface at night.

DRY WEIGHT VARIATION

Dry weight concentrations are summarized by cruise period in Table 7 and by weight class for all cruises in Figure 7. Low and high values occur both night and day, but there is clearly a shift to higher values at night.

The sample concentrations may underestimate the true concentrations by as much as 15 or 20%. Ahlstrom and Thrailkill (1963) showed that for copepods dry weight decreased about 15% after Formalin preservation. Lasker (1966) showed that dry weight of euphausiids was about 35%

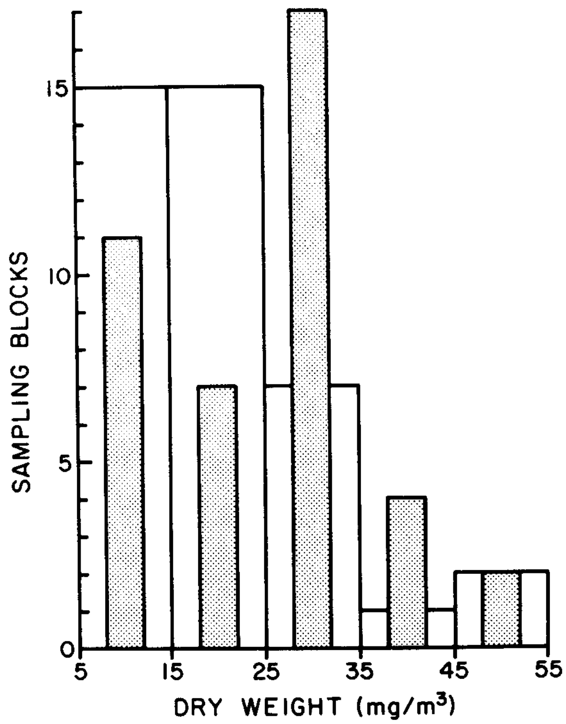

FIGURE 7.—Dry weight frequency distribution of all sampling blocks. The wide bars show day frequencies and the narrow bars night frequencies.

TABLE 7.—Summary of sample dry weight concentration (mg/m³) by cruise and day (D) or night (N) period.

	1D	1N	2D	2N	3D	3N	4D	4N	5D	5N
Mean	13.04	20.87	18.02	22.24	22.94	34.01	22.67	24.51	18.44	25.58
Median	15.00	18.32	14.51	21.03	22.76	31.80	15.24	24.72	15.27	23.23
Minimum	5.81	9.36	5.54	13.54	14.17	25.79	7.02	9.68	8.46	9.54
Maximum	20.85	34.00	43.74	30.57	30.42	49.59	56.90	34.62	32.11	52.42
Number blocks	7	9	6	7	7	9	11	7	9	9

lower for preserved than for fresh material. These groups were prominent in the pump samples, and dry weight determinations were made after long Formalin preservation. The pump samples undoubtedly contained a higher proportion of small copepod forms than the net samples of Ahlstrom and Thrailkill (1963), and it is possible that dry weight loss in Formalin is less for the smaller than for the larger individuals of this group.

As a basis for estimating the contributions of different species groups to dry weight concentration, dry weight factors were determined for large copepods, euphausiids, and chaetognaths by sorting known numbers of each from a few representative samples for drying and weighing. The resulting values are given in Table 8. The factor given for small copepods, which would have been difficult to separate in sufficient numbers and purity for a direct determination, was inferred from data given by Marshall and Orr (1955) for *Calanus finmarchicus* and *C. helgolandicus* in eastern Atlantic waters. They showed that *Calanus* stage V, at an average length of 2.5 mm, have a dry weight of about 300 mg/1000 organisms, and that according to Bogorov (1933) one stage V organism is equal in dry weight to two stage IV, 11 stage III, 42 stage II, and 60 stage I organisms. The average lengths of these stages are given as 2.1 mm, 1.65 mm, and 0.94 mm, and the average length of nauplii is given as 0.585 mm, which is the same as that of small copepods in the present study. Large copepods from the present study show an average length intermediate between those given for stages IV and III above,

TABLE 8.—Dry weight (DW) and ash weight (AW) determinations (mg/1000 organisms) for species groups in selected samples.

	DW	AW	AW/DW
	mg/1000	*mg/1000*	*%*
Small copepods	[1]2.5	--	--
Large copepods:			
Day	54.64	3.48	6.36
Night	49.88	2.94	5.89
Euphausiids:			
Day	42.03	3.29	7.82
Night	293.26	14.51	4.95
Chaetognaths	23.5	1.30	5.51

[1] Not determined by direct measurement. See text.

suggesting a ratio of six large copepods to one stage V, or a dry weight of 50 mg/1000 organisms, which is very close to the actual determinations. No dry weight equivalent is given by Bogorov for nauplii, but extrapolation of his series against average lengths suggests that 120 nauplii per stage V *Calanus*, or 2.5 mg/1000 nauplii, would be a conservative estimate.

Dry weight concentrations were calculated for each species group in each block from the dry weight factors and from the medians of numerical estimates for the blocks. The values for species groups were summed to produce a "calculated" dry weight concentration for each block. These are compared to the measured dry weight concentrations in Figure 8. All the data together tend to cluster around the line of equal value (slope 1.0), and each of the different

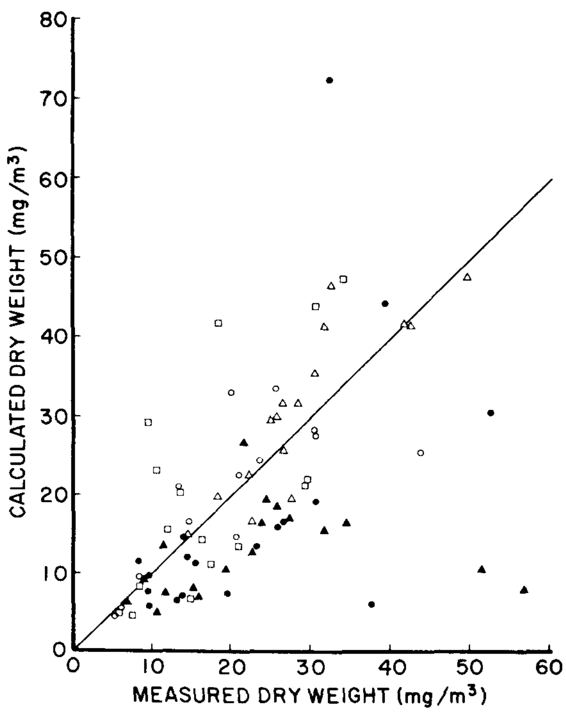

FIGURE 8.—The relation of calculated to measured dry weight concentration for all sampling blocks. Calculated dry weights were derived from species group density estimates and dry weight factors (Table 6). The line indicates equality of the two scales □ Cruise 1; ○ Cruise 2; △ Cruise 3; ▲ Cruise 4; ● Cruise 5.

cruise sets has slopes similar to the line. Variation is wide, but there are only four serious discrepancies. Whatever the reasons for these discrepancies, the four blocks were excluded from calculation of the relative contributions of species groups to dry weight concentrations for day and night cruise periods.

Table 9 shows the averages of dry weights calculated for each species group for each cruise period, and for all cruise periods pooled by day and night. "Calculated" sample concentrations, obtained by summing the values for the four species groups, are compared with the average measured concentrations for the cruise periods in the last two columns. Though the calculated concentrations are lower than the measured concentrations for all day periods, and higher than the measured concentrations for three of the night periods, the two sets show reasonably good agreement, as do the day and night averages for all cruises together.

The measured sample concentrations for all cruises pooled suggest that, on the average, dry weight was 31% higher at night than during the day. The calculated concentrations suggest that it was 48% higher. Calculated values for the species groups show that the dry weight increase at night is largely attributable to increases in the euphausiid group, with lesser increases in the large copepods and also the small copepods. Euphausiids were responsible for more than one-third of dry weight concentration at night, on the average, and small copepods for less than half of it. During the day, on the other hand, small copepods accounted for about three-fourths of dry weight concentration, with most of the remainder divided between large copepods and chaetognaths.

VARIATION WITH TEMPERATURE AND DISTANCE FROM LAND

The data for each of the four species groups, and for dry weight, were examined for possible relationships with the independent variables, temperature, miles from nearest land (including islands), and miles from nearest point on the mainland. Regressions were in the form log $Y = a + bX$, where $X =$ the independent variable and $Y =$ the dependent variable. Small copepods, large copepods, and dry weight showed significant trends with temperature, and chaetognaths showed significant trends with distance from land (Table 10). For euphausiids, night values alone, as well as day and night values together, were tested but neither demonstrated significant trends.

The two copepod groups and dry weight all show an inverse relation with temperature, but in all cases the trends are largely attributable to changes occurring in 1961, as a comparison of nighttime cruise medians with average cruise temperature shows (Table 11). The decline in

TABLE 9.—Calculated average dry weight fractions (mg/m^3) and percentages for species groups by cruise and day (D) or night (N) period.

	Small copepods		Large copepods		Euphausiids		Chaetognaths		Average sample dry weight	
	mg/m^3	%	mg/m^3	%	mg/m^3	%	mg/m^3	%	Calculated mg/m^3	Measured mg/m^3
1D	6.46	*70.9*	0.26	*2.9*	0.26	*2.9*	2.13	*23.4*	9.11	13.04
1N	7.70	*26.1*	3.49	*11.8*	14.88	*50.5*	3.41	*11.6*	29.48	20.87
2D	8.54	*61.4*	2.18	*15.7*	0.36	*2.6*	2.84	*20.4*	13.92	18.02
2N	9.29	*35.7*	4.08	*15.7*	11.83	*45.5*	0.79	*3.0*	25.99	22.24
3D	20.07	*88.3*	0.73	*3.2*	0.63	*2.8*	1.29	*5.7*	22.72	22.94
3N	25.74	*68.7*	3.70	*9.9*	6.99	*18.7*	1.03	*2.7*	37.46	34.01
4D	6.05	*62.6*	0.97	*10.0*	0.35	*3.6*	2.30	*23.8*	9.67	15.66
4N	8.88	*51.0*	1.50	*8.6*	4.95	*28.4*	2.07	*11.9*	17.40	24.51
5D	7.56	*66.4*	2.93	*25.7*	0.28	*2.5*	0.61	*5.4*	11.38	16.72
5N	8.52	*47.7*	2.09	*11.7*	6.86	*38.4*	0.41	*2.3*	17.88	24.09
Average D	9.74	*72.9*	1.41	*10.6*	0.38	*2.8*	1.83	*13.7*	13.36	17.28
Average N	12.03	*46.9*	2.97	*11.6*	9.10	*35.5*	1.54	*6.0*	25.64	25.14

TABLE 10.—Regressions of median block densities and dry weight concentrations on temperature and distance from land.[1]

Regression	*N*	*a*	*b*	*s*	*r*
Small copepods on temperature	83	5.38	−.105*	.23	.54**
Large copepods on temperature	78	3.23	−.101*	.52	.26*
Dry weight on temperature	78	2.46	−.067**	.22	.40**
Chaetognaths on distance to mainland	85	1.99	−.013**	.53	.31**
Chaetognaths on distance to nearest land	85	2.02	−.020*	.54	.22*

[1] *N* = number of sampling blocks; *a* = intercept; *b* = slope; *s* = standard deviation about the line; *r* = correlation coefficient.
* p = 0.05.
** p = 0.01.

TABLE 11.—Average temperatures, median copepod densities, and median dry weight concentrations for the night periods of each cruise.

Cruise date	Temperature	Small copepods	Large copepods	Dry weight
	° *C*	*no./m³*	*no./m³*	*mg/m³*
9/27/61	18.9	2,542	42	18
10/10/61	18.2	3,325	101	21
11/17/61	15.9	10,281	77	32
10/ 2/62	18.6	3,504	21	25
11/20/62	16.1	3,750	30	23

water temperature was approximately the same in both years. The copepod values and dry weight consequently show a strong inverse relation with temperature and date for 1961 but not for 1962.

The chaetognaths show inverse trends with distance from the mainland and from nearest land, but the former is the more significant of the two. The relationship with distance to nearest land includes many of the distance measurements to the mainland, of course, and it is possible that these are largely responsible for the significant relationship with distance to nearest land. The geographical distribution of all chaetognath block medians (Figure 9) shows that distance from the mainland is the more pertinent independent variable. Low densities occurred at all distances beyond 7 miles, whereas the highest densities did not occur farther offshore than 14 miles, with a single exception. It can be seen that density was far more variable near the mainland than offshore.

DISCUSSION

The food potential of plankton for pelagic fishes depends on the relation between the average density of some or all species groups over an area and the rate at which the fishes can feed on these species groups. Since median density of the more common species groups varies widely within the space of a few months for the area surveyed in this study, it is probable that food potential of near-surface plankton off southern California fluctuates appreciably within short time intervals. However, there were marked small-scale variations in the distributions of densities associated with the general area levels, and the general level would not be an appropriate index of food potential if fishes tend to orient to small-scale features of distribution.

Although the association of range with median for sampling blocks of 51.8 km^2 demonstrates that densities vary, sometimes widely, within the blocks, the medians of blocks of this or some similar size probably constitute a scale of sufficient resolution for assessing the food potential of plankton over a large area. Maximum values within the blocks are not likely to be impressively greater than the median. If the median of large copepods is 175/m^3, the block can be expected to have, on the average, a maximum density of 245/m^3 representing an area of 2.6 km^2 (1 square mile) within the block. If the median of euphausiids is 90/m^3, the block can be expected to have a maximum density of 130/m^3 for 2.6 km^2. Blocks with such medians are usually rare, and the medians, as well as the maximum values, are likely to be considerably higher than the densities in most blocks in the area. The medians would slightly underestimate the food potential of such blocks only if plankton feeding fishes tend to orient to the highest densities within the space of 20 square miles.

The distributions of sampling block medians, which were skewed unless general area level was very high, suggest that even under the poorest general conditions relatively high densities of organisms are likely to exist in some small portion of the survey area. Small copepods, for example, showed a few occurrences of blocks with medians above 6000/m^3, and one

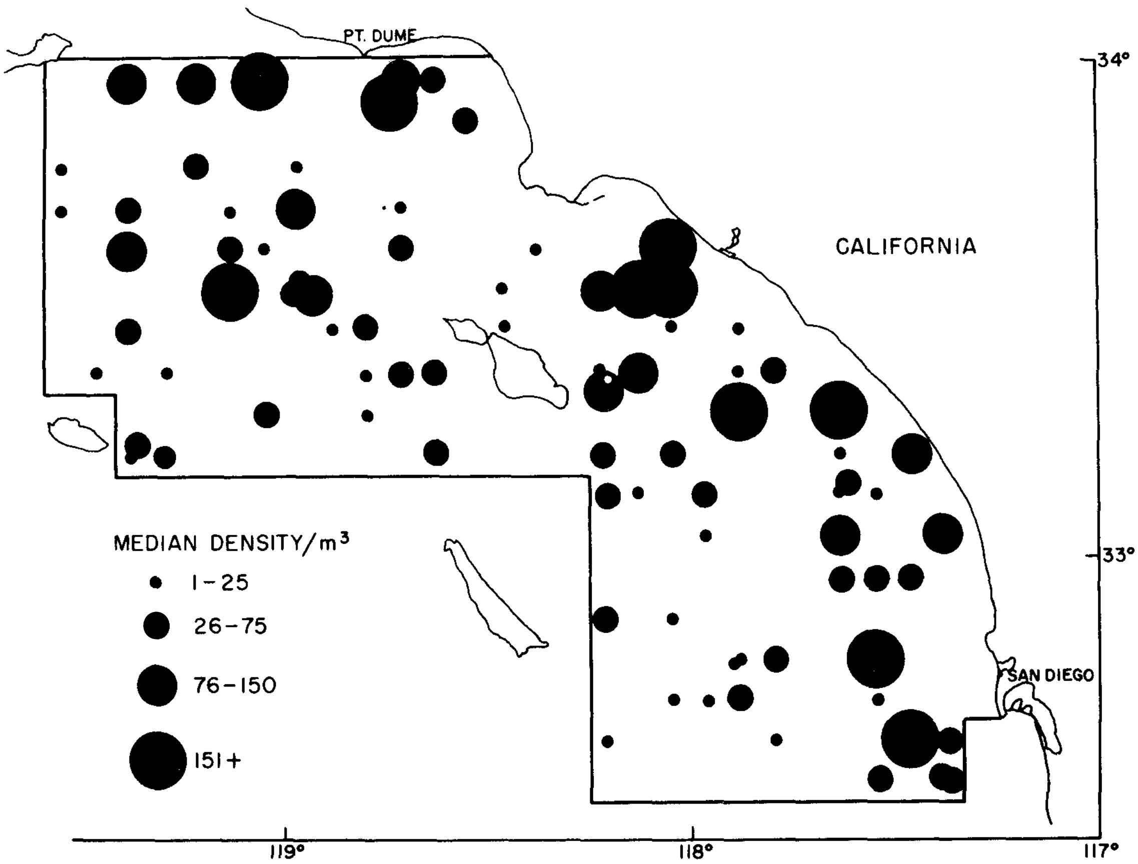

FIGURE 9.—Geographical distribution of chaetognath medians for all blocks on all cruises.

with a median above 9000/m³, when the general area median was about 3000/m³. Large copepods showed a few occurrences of blocks with medians well above 200 when the general area median was 50/m³ or less. Euphausiids showed occurrences of blocks with medians above 75/m³ when the general area median was between 25 and 40/m³. It seems probable, in other words, that high crustacean densities are always present somewhere in the area. At the lower general levels they would be scarce but perhaps as much as three times higher than densities over most of the area.

The data indicate that higher densities of chaetognaths are most likely to occur near the mainland, but they failed to demonstrate such trends for the three crustacean groups. They indicate only that the crustaceans, and dry weight, may sometimes be at higher levels where and when temperatures are relatively low. Regressions with temperature show, for example, that the density of small copepods was 6400/m³ in 15° C water, on the average, as compared with 2400/m³ in 19° C water, and that dry weight concentration was 29 mg/m³ in 15° C water, but only 15 mg/m³ in 19° C water. Since variation associated with these trends is wide, it can only be concluded that water of low temperature may sometimes, though not always, contain much higher standing crops of zooplankton than are likely to be found in warmer water in the survey area.

Dry weight factors were determined for the different species groups because it is impossible to estimate the relative nutritional value of such groups in the plankton on the basis of organism counts alone. In general, the near-surface zooplankton had a dry weight equivalent of about 25 mg/m^3 at night, which was approximately 30% greater than the average daytime level. Small copepods were the dominant fraction during the day and increased only slightly at night. Most of the nighttime increase in dry weight is attributable to the appearance of euphausiids, which were estimated to have a dry weight equivalent of 9 mg/m^3, on the average, as compared with less than 1 mg/m^3 during the day. There was some deviation from this general pattern among the five cruises. Differences between and within sampling blocks were not described in terms of dry weight. The general differences are enough to show that the nutritional potential of the plankton, in terms of dry weight for any set of samples, would depend on the extent to which fishes do or do not feed selectively.

However they are interpreted, it must be noted that the dry weight equivalents of the samples taken in this survey, aside from the possible loss of weight in Formalin preservation, may not represent the whole of the biomass utilized by some plankton feeding fishes near the surface. They contained almost no zooplankters smaller than 0.2 mm in length and relatively little phytoplankton. The comparison in Table 12 indicates that such smaller organisms may constitute a considerable fraction of the biomass.

Beers and Stewart (1967) sampled the euphotic zone with a towed pump on a line of stations off San Diego. Water was strained successively through 202-, 103-, and 35-μ cloths to estimate quantities below each cloth. Leong and O'Connell (1969) estimated from the resulting data

TABLE 12.—Comparison of dry weight values (mg/m^3) for different length ranges of planktonic organisms in two towed pump studies.

	Period	Group	Length range (mm)		
			<0.2	0.2-1.0	>1.0
Beers and Stewart (1967)	Day only	Phytoplankton	25.1	0	0
		Zooplankton	2.9	8.9	0
Present survey	Day	Crustacean	0	9.7	1.8
	Night	Crustacean	0	12.0	12.1

that phytoplankton and zooplankton passing through the 103-μ cloth represented average dry weight concentrations of 25 and 3 mg/m^3. The 103-μ cloth was approximately the same mesh size as the filtering screens used in the present survey. The material retained between the 103- and 202-μ cloths of Beers and Stewart is here judged to approximate the size range, 0.2 to 1.0 mm, and the numerical estimate for their innermost station, when converted to dry weight by the constant, 2.5 mg/1000 organisms, yields a concentration similar to the daytime average for crustaceans in this size range in the present surveys.

It appears that material smaller than that collected in the present survey might represent a dry weight approximately two to three times as great as that that was collected. Adjustment for the smaller organisms in questions of nutritional potential would depend on selectivity in the feeding of various fishes.

It is difficult to judge whether the dry weight values attributed to organisms larger than 1 mm in the above comparison fully represent the biomass of larger plankton organisms near the surface that can be utilized by plankton feeding fishes. Such fishes probably take crustaceans larger than collected by the pump when opportunity arises. It can only be restated that euphausiids larger than those sampled are relatively rare close to the surface. Five of the 1-m-mouth-opening-net tows taken by Ahlstrom and Thrailkill (1963) through the upper 100 m or so were composed largely of crustacean material. From the data given they were estimated to represent dry weight concentrations averaging 3.5 mg/m^3. The figure is in the range of day and night concentrations for the pump samples, but the comparison is uncertain because of differences in the location as well as the depth of sampling.

The above discussion implies that estimating the food potential of plankton for fishes must depend as much on information concerning the feeding behavior of the fishes as on information concerning the abundance and variability of the plankton. The data given here on plankton variability are intended as a basis for interpreting hypotheses that may arise from laboratory or field studies of feeding behavior.

LITERATURE CITED

AHLSTROM, E. H., AND J. R. THRAILKILL.
1963. Plankton volume loss with time of preservation. Calif. Coop. Oceanic Fish Invest., Rep. 9: 57-73.

ALVERINO, A.
1961. Two new chaetognaths from the Pacific. Pac. Sci. 15: 67-77.

BARNES, H., AND S. M. MARSHALL.
1951. On the variability of replicate plankton samples and some applications of "contagious" series to the statistical distribution of catches over restricted periods. J. Mar. Biol. Assoc. U.K. 30: 233-263.

BEERS, J. R., AND G. L. STEWART.
1967. Micro-zooplankton in the euphotic zone at five locations across the California Current. J. Fish. Res. Board. Can. 24: 2053-2068.

BODEN, B. P., M. W. JOHNSON, AND E. BRINTON.
1955. The Euphausiacea (Crustacea) of the north Pacific. Bull. Scripps Inst. Oceanogr. Univ. Calif. 6: 287-400.

BOGOROV, B. G.
1933. Modifications in the biomass of *Calanus finmarchicus* in accordance with its age. [In Russian, English summary.] Bull. State Oceanogr. Inst., Moscow, 8: 1-16.

BRINTON, E.
1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr. Univ. Calif. 8(2): 51-270.

CASSIE, R. M.
1959. Micro-distribution of plankton. N. Z. J. Sci. 2: 398-409.
1962. Frequency distribution models in the ecology of plankton and other organisms. J. Anim. Ecol. 31: 65-92.
1963. Microdistribution of plankton. Oceanogr. Mar. Biol. Annu. Rev. 1: 223-252.

CUSHING, D. H.
1951. The vertical migration of planktonic Crustacea. Biol. Rev. (Cambridge) 26: 158-192.

HOLMES, R. W., AND T. M. WIDRIG.
1956. The enumeration and collection of marine phytoplankton. J. Cons. 22: 21-32.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. (Translated from the Russian by Douglas Scott.) Yale Univ. Press, New Haven, 302 p.

KING, J. E., AND T. S. HIDA.
1954. Variations in zooplankton abundance in Hawaiian waters, 1950-52. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 118, 66 p.

LASKER, R.
1966. Feeding, growth, respiration, and carbon utilization of a euphausiid crustacean. J. Fish. Res. Board Can. 23: 1291-1317.

LEONG, R.
1967. Evaluation of a pump and reeled hose system for studying the vertical distribution of small plankton. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 545, 9 p.

LEONG, R. J. H., AND C. P. O'CONNELL.
1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). J. Fish. Board Can. 26: 557-582.

MARSHALL, S. M., AND A. P. ORR.
1955. Biology of a marine copepod. Oliver and Boyd, Edinburgh and London, vii + 188 p.

O'CONNELL, C. P., AND R. J. H. LEONG.
1963. A towed pump and shipboard filtering system for sampling small zooplankters. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 452, 19 p.

TATE, M. W., AND R. C. CLELLAND.
1957. Nonparametric and shortcut statistics. Interstate Printers and Publishers, Inc., Danville, Ill., ix + 171 p.