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Zooplankton Species Groups in the North Pacific

Co-occurrences of species can be used to derive groups whose members react similarly to water-mass types.

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Oceanic zooplankton are small animals which spend their entire life suspended in water. They are among the most abundant and widespread macroscopic organisms on earth. In general there are more species and more individuals per unit volume in the upper layers of the oceans than there are in the deeper waters. Although the individual species inhabit very large areas of the oceans, most of them have well-defined patterns of distribution and abundance. Many of these patterns show a remarkable similiarity to the patterns of distribution of water masses (*1, 2*). The latter are, however, defined by the temperature-salinity characteristics of the water below the depths that many zooplankton species inhabit. We have very little information to indicate what immediate environmental conditions determine the abundance and distribution patterns of zooplankton in the upper 150 meters.

Heretofore, most taxonomic and distributional studies of zooplankton have been concerned with the distribution of individual species. Large-scale sampling on three oceanographic expeditions in the North Pacific Ocean (Fig. 1) has provided data that make it possible to study groups of species. Study of the data by computer techniques has shown that certain species frequently occur together, and that these species groups characterize particular habitats, and it suggests that the groups are composed of species that have similar reactions to properties of the environment. The group characterizing the Subarctic Water Mass has been examined in detail in an effort to determine which of the usual hydrographic measurements of the physical-chemical properties of the environment are correlated with the overall abundance of the group. The results suggest that, for this group of species, the history of the water may be the most important property and that, from the standpoint of the biologist, the hydrographic properties usually measured on oceanographic expeditions may not be the right ones.

In this analysis only four kinds of zooplankton were studied: Chaetognatha, Euphausiacea, Heteropoda, and Pteropoda. However, they are among the more abundant members of the zooplankton community. The lack of data on the most abundant animals, the Copepoda, is a serious deficiency. Even for the zooplankton treated we have very little of the information that is basic to an understanding of zooplankton community and population dynamics. We need data on the food, feeding methods, and metabolic rates; the frequency of reproduction; the number of young produced; the causes and rates of mortality; and the relation of behavior to survival and selection of habitat. Nevertheless, the preliminary analysis has served to reveal relationships not readily observed in the untreated data and to indicate areas where more intensive work is needed.

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Materials and Methods

The three collecting expeditions were POFI-5 (1950), Transpac (1953), and Troll (1955). All were made during the summer months. Expedition POFI-5 (36 stations) covered two parallel north-south lines of stations, one line starting from Hawaii and going south to about 5°S and the other covering the same north-south range about 750 miles west of the first (*3*). Transpac (141 stations) crossed the Pacific from California to Japan on a track generally north of 40°N, came south along the coast of Japan, and returned by a more southern route, approximately between 20°N and 40°N (*4*). Troll [84 stations; zooplankton studied for only 24 stations, most of them south of 20°N (only these stations plotted)] started at Hawaii, went westward approximately between 5°N and 20°N and then, near the Philippines, turned northward toward Japan (*5*). The station positions for the three expeditions are shown in Fig. 1.

At all of the stations oblique net tows were taken to depths of 150 or 200 meters. The nets had a diameter, at the mouth, of 1 meter and were made of silk grit gauze with a mesh size of 0.65 millimeter. The amount of water filtered by each net was recorded by a flowmeter suspended in its mouth. The amounts ranged from 381 to 1943 cubic meters, but most were between 500 and 1200 cubic meters. After the organisms caught in these tows had been identified and enumerated, the numbers of individuals per 1000 cubic meters were calculated. Hydrographic measurements were made at the same stations.

Chaetognaths were identified by Bieri and (one species) Alvariño; euphau-

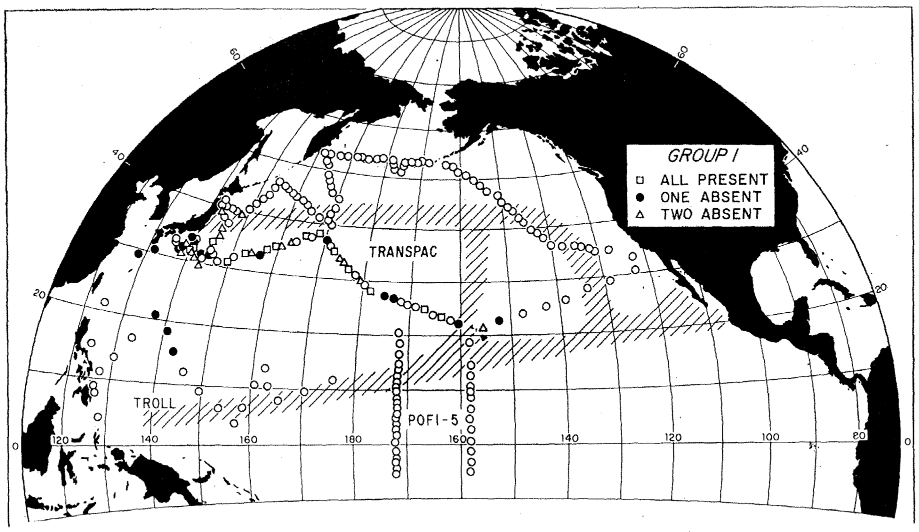

Fig. 1. Distribution of zooplankton group I in the North Pacific. The three expeditions from which material was obtained are indicated by name. The locations of all stations are shown, even those (open circles) where no group I species were found. (Shaded areas) The approximate boundaries of water masses [after R. Bieri (*1*)].

sids, by Brinton; and heteropods and pteropods, by McGowan (*6*). All species used in this study satisfy the following criteria: They occurred with high frequency in some of the regions of the North Pacific sampled during the expeditions; their vertical ranges fall within, or overlap to a considerable degree, the depth of sampling; their taxonomic status is clear.

The method which was used to determine recurrent groups of these species has been described (*7*). The index of affinity between species originally proposed does not follow the hypergeometric distribution exactly (*8*). It has, therefore, been replaced by the geometric mean of the proportion of joint occurrences, corrected for sample size:

$$[J/(N_A N_B)^{\frac{1}{2}}] - 1/2(N_B)^{\frac{1}{2}}$$

where J is the number of joint occurrences; N_A is the total number of occurrences of species A; N_B is the total number of occurrences of species B; and species are assigned to the letters so that $N_A \leqq N_B$. Pairs of species for which this expression was equal to or greater than 0.50 were considered to show affinity; those for which the values were lower were considered not to show affinity. This breakpoint was chosen because it was felt that species should be found together in somewhat more than "half" their recorded occurrences if they are to be grouped together. The grouping procedure, based on this dichotomy, leads to definition of the largest groups within which all possible pairs of species show affinity. All species within a group are, therefore, rather frequent members of each other's environment. Because of this, the groups appear to be particularly appropriate units within which to examine interspecific relationships.

Calculation of the affinities and the preparation of the incidence matrix on the basis of the dichotomy and the grouping procedure have been programmed for the CDC 1604 computer (*9*). The operation is at present limited to 150 species; slight modifications should make it possible to increase this number to somewhat over 200 species.

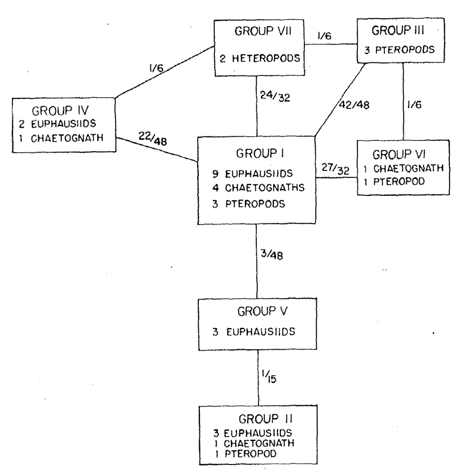

Fig. 2. Composition of zooplankton groups and interrelationships between the groups (see Table 1). Fractions are the ratios of the number of observed species-pair connections between groups to the maximum number of possible connections; for example, there are six possible intergroup species pairs between groups IV and VII but only one of these pairs showed affinity at the "significance" level used.

Species Groupings

Of the 48 species of organisms used in this study (euphausids, 20 species; chaetognaths, 9 species; pteropods, 11 species; heteropods, 8 species), 34 could be arranged in seven groups; five others had affinities with some, but not all, of the members of one or the other of the groups; and nine species had no affinities with any of the others (see Table 1 and Fig. 2). Six of the nine species without affinities were heteropods; the remaining three belonged to the other taxonomic groups, each to a different group.

The first group (I) obtained in the analysis consisted of 16 species (Table 1)—nine euphausids, four chaetognaths, and three pteropods. Three additional species [*Hyalocylix striata* (P), *Limacina trochiformis* (P), and *Euphausia brevis* (E)] had multiple interspecific connections with some but not all of the members of this group (affinities with 14, 12, and 8 of the 16 species in the group, respectively). All of the smaller groups, except II and V, also had many interspecific connections with group I (see Fig. 2).

The second group (II) was an assemblage of five species: three euphausids, one chaetognath, and one pteropod (Table 1). It had connections with only one other group in the analysis; out of 15 possible species pairs, it was connected with group V through a single pair. It was equally sharply separated geographically. Two species [*Thysanoessa inermis* (E) and *Sagitta scrippsae* (C)] had four affinities and one affinity, respectively, with members of this group. The case of *Thysanoessa inermis* is particularly interesting because it could be substituted for *Tessarabrachion oculatus* to form an alternate group of five species. This alternate group, however, did not appear to be as homogeneous in its relation to the environment, to judge by the agreement in relative abundances of the species.

Group V, which was composed of three species of euphausids (Table 1), appeared to form a connecting link between groups I and II, but the connections were limited (3 of 48 possible interspecific connections to group I and 1 of 15 possible connections to group II), and the group seems quite distinct.

Groups III, IV, VI, and VII consisted, respectively, of three pteropods; two euphausids and one chaetognath; one pteropod and one chaetognath; and two heteropods (Table 1). Each of these groups had numerous interspecific connections with group I (42 of a possible 48, 22 of a possible 48, 27 of a possible 32, and 24 of a possible 32, respectively; see Fig. 2). None were connected with any other group by more than one species pair.

Among the 34 species which could be arranged in the seven recurrent groups, species within each genus show considerable morphological similarity, and this implies functional similarity. As the groups were formed on the basis of frequent co-occurrence of the animals, one would, therefore, expect them to be as generically diverse as possible, if functionally similar species tend not to occur together (*10*). In order to test this expectation, a program was written for the CDC 1604 computer which formed all possible arrangements of the 34 species into groups of the same composition (above the level of genus) as the observed groups—all possible sets of nine species of euphausids, four species of chaetognaths, and three species of pteropods for group I, and so on. The sets were drawn from the species lists, only the genera being taken into account. For example, the seven species of *Euphausia* were considered equivalent, the five species of *Nematoscelis* were considered equivalent, and so on. There were 2,227,680 different arrangements. For each arrangement the number of congeneric pairs within each group was calculated. For example, in group I the maximum number of congeneric pairs would be observed if the nine euphausids consisted of the seven species of *Euphausia* and two species of either *Nematoscelis* or *Stylocheiron* or *Thysanoessa* (22 congeneric pairs); the four chaetognaths were all in the genus *Sagitta* (six congeneric pairs); and the three pteropods were all in the genus *Limacina* (three congeneric pairs). The numbers of congeneric pairs were summed over the seven groups. The maximum total of congeneric pairs for the seven groups was 37, the minimum was 10, and the value for the groups as formed from the zooplankton data was 15. Of the more than 2 million different arrangements, 73,044 had a total of 15 or fewer congeneric pairs. If all arrangements are assumed to be equally likely, the probability of the observed value, or a smaller value, is .0328. This constitutes evidence of considerable selection against congeneric pairs within the recurrent groups.

Distribution Patterns of Groups

Certain patterns appear when the stations at which the groups occurred are plotted on a chart of the North Pacific (Figs. 1, 3, and 4). In all cases the group patterns are consistent with the individual species patterns arrived at independently by Bieri, Brinton, and McGowan (*1, 2*), although some of the individual species within the groups have more extensive ranges of occurrence than the groups do.

Table 1. Species composition of recurrent groups. C, chaetognath; E, euphausid; H, heteropod; P, pteropod.

Species
Group I
Euphausia hemigibba (E)
Euphausia mutica (E)
Euphausia recurva (E)
Euphausia tenera (E)
Nematoscelis atlantica (E)
Nematoscelis microps (E)
Nematoscelis tenella (E)
Stylocheiron carinatum (E)
Stylocheiron suhmii (E)
Pterosagitta draco (C)
Sagitta enflata (C)
Sagitta hexaptera (C)
Sagitta pacifica (C)
Creseis virgula (P)
Limacina bulimoides (P)
Limacina inflata (P)
Associated:
Euphausia brevis (E)
Hyalocylix striata (P)
Limacina trochiformis (P)
Group II
Euphausia pacifica (E)
Thysanoessa longipes (E)
Tessarabrachion oculatus (E)
Sagitta elegans (C)
Limacina helicina (P)
Associated:
Thysanoessa inermis (E)
Sagitta scrippsae (C)
Group III
Cavolinia inflexa (P)
Clio pyramidata (P)
Styliola subula (P)
Group IV
Euphausia diomediae (E)
Nematoscelis gracilis (E)
Sagitta robusta (C)
Group V
Euphausia gibboides (E)
Nematoscelis difficilis (E)
Thysanoessa gregaria (E)
Group VI
Limacina lesueuri (P)
Sagitta pseudoserratodentata (C)
Group VII
Atlanta lesueuri (H)
Atlanta turriculata (H)
No affinities
Euphausia paragibba (E)
Sagitta ferox (C)
Cavolinia longirostris (P)
Carinaria japonica (H)
Oxygyrus keraudreni (H)
Protatlanta souleyeti (H)
Pterosoma planum (H)
Pterotrachea hippocampus (H)
Pterotrachea minuta (H)

The distribution of the major water masses of the North Pacific is also shown in Figs. 1, 3, and 4. Comparison of this with distributions of the groups makes it evident that each group is confined to, or occurs much more frequently in, a specific water mass. Group V is an exception, for it mainly occupies an area which is hydrographically transitional between two water masses.

Perhaps the most interesting pattern is that shown by group I (Fig. 1). The 16 individual species comprising this group are widely distributed in the Equatorial and Central water masses of the Pacific. The group, however, had a more restricted distribution, being found largely in the Central Water Mass and in the Kuroshio and its extension. This was true no matter whether only samples from those stations where all members of the group were found were considered or whether samples from stations where all but one or all but two of the species of the group were found were added (see Fig. 1). When samples from the 47 stations where 14, 15, or 16 species of the group were found were considered, the group was found west of the 180-degree meridian much more frequently than expected [the expected ratio of occurrences, based on the west-east ratio of all samples taken between 10° and 40°N, was 27/20; the observed ratio was 39/8; χ^2 (1 degree of freedom) = 11.51, $p < .001$]. This discrepancy was due, at least partially, to an increase in the abundance of its members in the Kuroshio extension, where the waters appear to be "enriched" along the southern boundary of the Subarctic Water Mass.

Group II consists of five species which have been termed "Subarctic" (*1, 2*) because of their approximate limitation in the Pacific to the Subarctic Water Mass. The group was found almost exclusively north of 40°N (Fig. 3); the observed numbers of occurrences east and west of the 180-degree meridian in this region did not differ from the numbers expected on the basis of the west-east ratio for all samples taken in the area north of 40°N. Group II's only areal overlap with other groups occurred at two stations on the southern border of the subarctic region. This group has the most coherent distribution of any of the seven groups, the euphausids, chaetognath, and pteropod in it being frequently part of each other's biological environment over a very large geo-

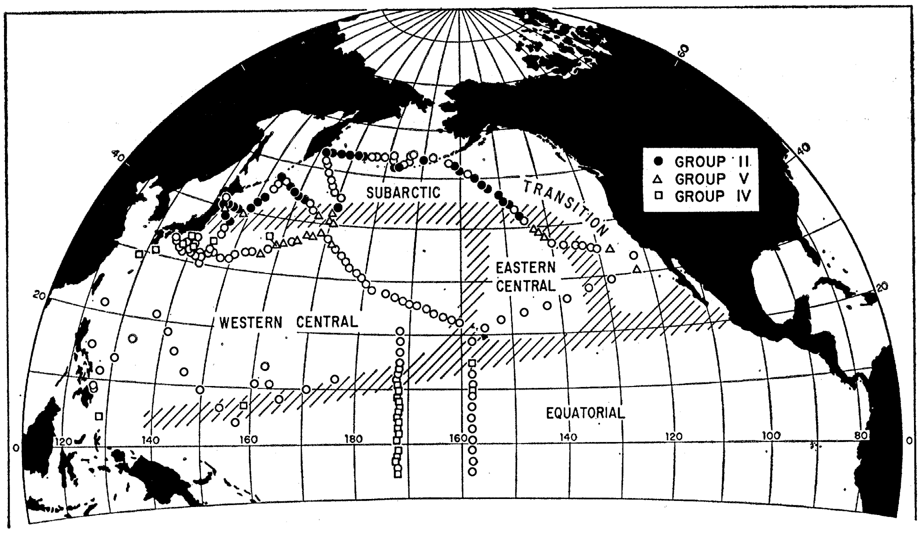

Fig. 3. Distribution of zooplankton groups II, IV, and V in the North Pacific. The water masses are indicated by name. The locations of all stations are shown, even those (open circles) where no group II, IV, or V species were found. (Shaded areas) The approximate boundaries of water masses [after R. Bieri (*1*)].

graphical range of waters with considerable hydrographic similarity.

The three euphausids comprising group V were found in an area that is hydrographically transitional between the Subarctic Water Mass to the north and the Central Water Mass to the south (Fig. 3). As would be expected, its areal overlap was greatest with groups I and II, although still quite limited. This, in conjunction with the weak, but essentially equal, interspecific connections with these groups marks group V as a transition-zone group. Several species in the other taxa are also thought to be transition-zone species. However, they occurred too infrequently in this series of samples to appear in the groupings. There was some indication that group V occurred west of the 180-degree meridian more frequently than expected, but the observed distribution of occurrences differed from the expected distribution only at the 25-percent level.

Group IV was found only in the Equatorial Water Mass (mostly south of 10°N) and in the Kuroshio (Fig. 3). Most of its areal overlap with group I was in the latter region. It may have been somewhat more frequent east of the 180-degree meridian, but the evidence is not very strong ($p \sim .30$, on the basis of all samples taken south of 10°N).

Over 50 percent of the occurrences of groups III, VI, and VII were in samples which also contained group I; the overlap among the three smaller groups was noticeably less (21 to 39 percent). On the basis of the overlap with group I and the multiple interspecific connections with it (see Fig. 2), they might be considered subgroups. However, groups III and VI are formed of species which are known to be limited to the Central Water Mass. Keeping these groups separate serves to emphasize their status as additions which alter the expression of the main group in certain localities. By contrast with findings for group I, the west-east distribution (in relation to the 180-degree meridian) of samples containing group III (23 samples) or group VI (31 samples) was found to be almost exactly that expected (expected west-east ratios, 13.2/9.8 and 17.8/13.2 for groups III and VI, respectively; observed ratios 13/10 and 18/13). Apparently these species of the Central Water Mass differ from the species of group I in their lack of response to the "enrichment" near the boundary between the Central and the Subarctic water masses. The distribution of group VII, on the other hand, parallels that of group I so closely [significantly more frequent west of the 180-degree meridian ($p < .01$)] that it is probably best to consider it a subgroup.

Abundances of Groups

The initial groupings were based entirely on the presence or absence of species and did not take account of the wide ranges of abundance of the various species. If it is assumed that species are most abundant in areas that they find most suitable as habitats, and least abundant in those areas within their range that are least suitable, then the relative abundances between samples can be used to determine whether each group as a whole shows agreement among its component species as to the "best" and "worst" habitats (*7*). For this purpose, the abundances of each species were ranked over the set of samples within which the group occurred, the ranks for each sample were then summed, and these sums of ranks were used as a basis for calculating concordance (strongly positive correlation of species relative abundances) within the group.

The 16 species of group I showed very significant concordance ($p < .005$, on the basis of data for the 47 stations at which 14, 15, or 16 of the species occurred together). The "best" habitats for these species were clustered in the core of the Kuroshio and in its extension eastward; the "worst" habitats were near the northern boundaries of the group's area of distribution. In this case the "best" habitats for the group were in its region of most frequent occurrence. As the individual species comprising the group are much more widely distributed in the Central and Equatorial water masses than the group seems to be, one might conclude that the apparent general abundance and high frequency of occurrence of the group in the area of mixing is an artifact resulting from the grouping procedure or from limitations in the station pattern or from our inability to collect species where they are uncommon. It seems unlikely, however, that there would be such very strong agreement in relative abundances if the group did not have some biological reality, at least in the sense of similarity of reactions of the species to environmental conditions.

The five species of group II also showed very significant concordance ($p < .005$, on the basis of data for 34 stations at which all five species were found). For the species of group II, the "best" habitats were in the eastern sector of the Subarctic Water Mass, just north of the southern limit of the group range; the "worst" habitats were on the southern edge of the group range, both immediately adjacent to the "best" areas and off Japan. The west-east distribution of "best" habitats was strongly biased toward the east, although, as already noted, the group

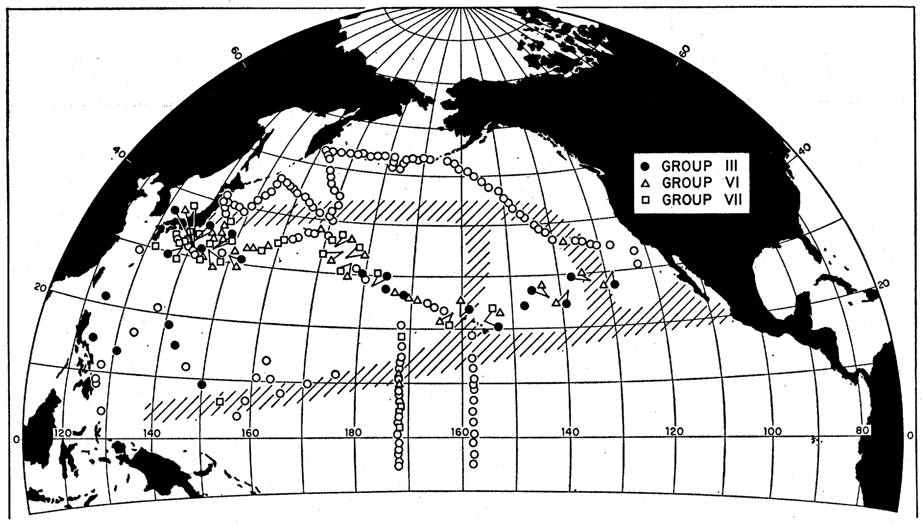

Fig. 4. Distribution of zooplankton groups III, VI, and VII in the North Pacific. The locations of all stations are shown, even those (open circles) where no group III, VI, or VII species were found. (Shaded areas) The approximate boundaries of water masses [after R. Bieri (1)].

showed no bias in frequency of occurrence east and west of the 180-degree meridian.

For the three species of group V there was a certain amount of agreement on the "best" and the "worst" habitats ($p \sim .15$, on the basis of data for 19 stations at which all three species occurred), but there was no consistent pattern of distribution of "best" and "worst." In fact, of the four "best" and the four "worst" samples, in two cases a "best" and a "worst" sample were immediately adjacent to each other.

The three species in group IV also showed some degree of concordance ($p < .10$, on the basis of data for 26 stations at which all three species were found). The distribution of samples taken in the Equatorial Water Mass was such that no certain idea of the west-east distribution of "best" and "worst" samples can be obtained. There was, however, a clear north-south difference; the "worst" samples occurred along the northern boundary of the area occupied by the group, and the "best" samples were taken in the southern part of the area covered by the expeditions. This is what would be expected of a group of Equatorial Water Mass species.

Groups III and VI did not show significant agreement on what were the "best" and "worst" habitats. The three species of pteropods comprising group III showed some positive correlation of abundances ($p = .35$, on the basis of data for 23 stations at which all three species occurred); the abundances of the two species that made up group VI (one pteropod, one chaetognath) were somewhat negatively correlated ($p = .40$, on the basis of data for 31 stations at which both species were found). In contrast to this, the abundances of the two species of heteropods which formed group VII were very strongly positively correlated ($p < .001$, on the basis of data for 30 stations at which both species occurred); the "best" samples were all located in the region of the Kuroshio off Japan and in its eastward extension, and the "worst" samples were in the southern and eastern parts of the area occupied by the group. The distribution of group VII thus agrees with that of group I not only in general extent and in regions of greatest frequency but also in detail in regard to the location of the "best" habitats.

Group II and Its Environment

Because group II was a particularly well defined, coherent entity in terms of its very few interspecific connections with other groups and its geographic distribution, a more detailed analysis of the group was attempted. Its characteristics, as developed so far, are briefly as follows. It consists of three euphausids, one chaetognath, and one pteropod. It occurs generally across the North Pacific, north of 40°N, being largely confined to the Subarctic Water Mass. There is strong evidence of agreement among the species in regard to "best" and "worst" habitats; in terms of the relative abundance of the group as a whole, the "best" localities were east of the 180-degree meridian and near the southern border of the group range, the "worst" were on the southern border.

Table 2 gives some statistics for the individual species. The estimates of frequency, abundance, average rank, dominance, and dispersion are based on the data from samples taken at 62 stations considered, from their hydrographic properties, to be in the Subarctic Water Mass. The two relative measures, average rank and dominance, reflect relations among the five species only and do not take into account the other organisms in the samples. The information under the column headings "Fidelity" and "Vitality" is drawn from general knowledge of the species.

Tessarabrachion oculatus, which has the most restricted general distribution, was found in only 40 percent of the shallow (0 to 150 m) samples; however, it was present in the deeper tows at a number of additional stations. The other four species of Table 2 were found in about 90 percent or more of the samples. *Tessarabrachion oculatus* was also the least abundant species; the median number of individuals per 1000 cubic meters in those samples in which the species occurred was 8. The median abundances of *Thysanoessa longipes*, *Euphausia pacifica*, and *Limacina helicina* were about equal, at about 370 individuals per 1000 cubic meters. The first two of these species were also similar in average rank, and both were definitely above *L. helicina* in this characteristic. Of the five species, *Sagitta elegans* had the highest frequency, abundance, and average rank. This species is a predator; the other species in this group are not. Its relative position emphasizes the limited nature of the data so far available. Clearly, not all of its prey are included.

The measure of dominance used indicates with what frequency a species was the most abundant, or one of the more abundant, of the five species. In 52 of the 62 samples, one species contributed 50 percent or more of the individuals of the five species; in the remaining ten samples, two species were needed to make up 50 percent or more of the individuals. Again, *Sagitta elegans* had the highest rating, but *Euphausia pacifica* was not far below it; *Thysanoessa longipes* and *Limacina helicina* were definitely secondary species, while *Tessarabrachion oculatus* was never dominant. The use of numbers of individuals instead of weight could obscure the real relationship. A consideration of the size range of individuals of the five species in these samples, however, suggests that this is not a problem. The individuals of *Limacina helicina* are, on the average, smaller than individuals of the other four species, which are all about the same size. Changing numbers to weight would, therefore, have little effect except to move *L. helicina* somewhat further toward *Tessarabrachion oculatus*.

The changes in order of the species, particularly the three intermediate species, that occur as the statistic examined is changed indicate that no one measure is likely to be completely satisfactory as a criterion of the position of a species in a community.

For all the species the ratio of variance to mean is above the value (1.0) expected for a random (Poisson) distribution by 2 to 4 orders of magnitude. This indicates that all the species have highly clumped distributions, even within this geographic area where conditions are, presumably, everywhere within their tolerance ranges. Such inflated variances might arise from the presence of a few excessively large or small values, or it might be a general property of the distributions. An indication of which of these factors is the cause can be obtained from the ratio of the calculated variance to a percentile estimate of the variance, $(P_{84} - P_{16})^2/4$, based on the value below which 16

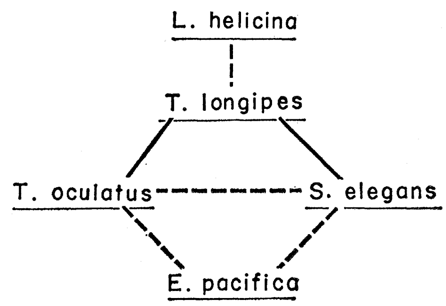

Fig. 5. Interrelationships among members of zooplankton group II. (Solid lines) Strong positive correlation of abundances ($p < .005$); (dashed lines) weaker positive correlation of abundances ($.03 < p < .07$).

percent of the values fall (P_{16}) and that above which 16 percent of the values fall (P_{84}). Extreme values in the tails of the distribution are thus not included. If the ratio is not far from 1.0, these distributions, although flat-topped, are probably more or less symmetrical; if the ratio is large, a few outsize values have contributed to inflation of the variance.

For *Thysanoessa longipes, Euphausia pacifica*, and *Sagitta elegans* the ratios were 3.5, 4.4, and 1.2, respectively; for *Tessarabrachion oculatus* and *Limacina helicina*, the ratios were 329 and 406. The first three species seem to have, generally, non-Poisson distributions; for the latter two species the main cause of the large values of the variance appears to be the presence of a relatively few samples containing unusually large numbers of individuals.

Only one of the species, *Tessarabrachion oculatus*, occurs almost wholly in the Subarctic Water Mass. The others can be listed in a series, with more and more extensive ranges outside of this region: *Thysanoessa longipes, Euphausia pacifica, Sagitta elegans, Limacina helicina*. The extensions are both south along the west coast of North America in the California Current, which is made up partially from subarctic water, and north across the Arctic Ocean into the North Atlantic. Therefore, although these five species can be considered members of a subarctic community within the area studied, it is evident that in other areas they would be members of communities composed of other species. However, the geographic region within which they occur together is very extensive, and it is important to understand their interrelations within it.

Because almost all growth stages of the species were found in the tows, it seems reasonable to assume that they breed successfully in this region of the North Pacific. Little can be said about seasonal changes in abundance, for the samples available were taken only during the summer season. However, Beklemishev (*11*) has shown that *Limacina helicina* is present during the winter in this area.

The area within which group II occurred may be divided into sectors on the basis of the dynamic topography (*12*); such a division gives a system of gyres and currents. For the purpose of this article, these may be designated the Oyashio-West Bering Sea gyre; the center portion of the North Pacific-Gulf of Alaska gyre; the

Table 2. Statistics for the five species of zooplankton that comprise the Sub-Arctic group (II): *Tessarabrachion oculatus, Thysanoessa longipes, Euphausia pacifica, Sagitta elegans*, and *Limacina helicina*.

Species	Frequency*	Abundance†	Average rank‡	Dominance§	Dispersion (aggregated)‖	Fidelity¶	Vitality**
T. oculatus	25/62	2–744 (8)	1.24	0/62	430	Aleutians S to 40°N in Pacific	All stages present
Th. longipes	59/62	4–9,784 (413)	3.35	13/62	2,275	Arctic Ocean S to 40°N in Pacific	All stages present
E. pacifica	55/62	4–22,278 (345)	3.36	23/62	6,950	60°N in Bering Sea, S to 25°N in Calif. Current to 35°N in Central Pacific	All stages present
S. elegans	60/62	17–7,900 (1,405)	4.15	29/62	1,830	N. Atlantic, Arctic Ocean, S to 40°N in Pacific	All stages present
L. helicina	58/62	20–75,770 (360)	2.90	7/62	52,400	N. Atlantic, Arctic Ocean, S to 30°N in Calif. Current to 35°N in Central Pacific	All stages present

* Proportion of samples in which the species was found (total number of samples, 62). *T. oculatus* occurred in deeper tows at nine additional stations. † Range and median (in parentheses) of numbers of individuals per 1000 cubic meters in samples in which species was found. ‡ Species were ranked within each sample on the basis of numbers of individuals. Ranks for each species were averaged over the 62 samples (1, least abundant; 5, most abundant). § Proportion of samples in which the species was among those making up 50 percent of the individuals; summation in each sample was begun with the most abundant species. ‖ The ratio of variance to mean; the expected value for a random (Poisson) distribution is 1.0. ¶ Degree of restriction to the Subarctic Water Mass. ** Proportion of life lived in the Subarctic Water Mass.

periphery of the North Pacific-Gulf of Alaska gyre; and the North Pacific Drift. The expected frequencies of occurrence in these sectors were calculated on the basis of frequencies observed in sampling the sectors. The observed distribution of frequencies of occurrence of the group did not differ significantly from expectation. This finding is in agreement with the earlier calculation which suggested that there was no west-east trend in frequencies of occurrence. However, with respect to the relative abundance of the group as a whole, the abundance in samples taken in the sector designated "periphery of the North Pacific-Gulf of Alaska gyre" was much greater than expected and the abundance in the sectors designated "North Pacific Drift" and "Oyashio-West Bering Sea gyre" was much less than expected. [According to the Kruskal-Wallas one-way analysis of variance by ranks, $p < .01$ (*13*).]

It has already been pointed out that the five species comprising the group showed very significant concordance in their relative abundances in the 34 samples in which all occurred. The rank correlations between relative abundances for all possible pairs of the five species (ten pairs) were examined in these samples. Even though this procedure raises the question of multiple tests of interrelated data, the correlation coefficients can still be used as qualitative indicators of the direction and strength of relationships. All the correlations were positive. Those between *Thysanoessa longipes* and *Tessarabrachion oculatus* and between *Thysanoessa longipes* and *Sagitta elegans* were very significant ($p < .005$). Four others were significant at about the 5-percent level: *Sagitta elegans* and *Tessarabrachion oculatus, Limacina helicina* and *Thysanoessa longipes, Sagitta elegans* and *Euphausia pacifica*, and *E. pacifica* and *Tessarabrachion oculatus*. None of the other four pairs showed significant correlation. These relations are shown in Fig. 5. They suggest that the three species *Thysanoessa longipes, Tessarabrachion oculatus*, and *Sagitta elegans* may be alike in their response to environmental conditions. Further evidence for this is the fact that it is just these three species which have distributions with a definite southern limit at 40°N in the Pacific; the distributions of the other two species, *Limacina helicina* and *Euphausia pacifica*, extend appreciably further south along the west coast of North America (see Table 2).

The sums of the ranks of abundances of the individual species in the 34 samples, used in calculating the concordance, were also used as the dependent variable in a multiple regression analysis. Hydrographic and other data taken at the same 34 stations were treated as the ten "independent" variables; it is evident from the list given below that some of these "independent" variables are more or less correlated.

1) Difference in shape of the temperature-salinity (T-S) diagram from that of the "best" station. A planimeter was used to determine the area enclosed by the T-S diagram of Transpac station 18 (the "best" station), the T-S diagram of the station being considered, and two straight lines, one connecting the bottom points of the two diagrams, the other connecting their top points. The T-S diagrams were plotted from depths of 50 to 1000 meters (*14*).

2) Depth of thermocline, estimated from bathythermograph cards.

3) Time of day of sampling, measured in hours from the nearest midnight on the assumption that effects due to vertical migration would be symmetrically distributed around midnight.

4) Depth at which the O_2 concentration fell to 2 milliliters per liter, estimated by linear interpolation between adjacent measured values.

5) Temperature at 10 meters, estimated by linear interpolation between adjacent measured values.

6) Temperature at 100 meters, estimated by linear interpolation between adjacent measured values.

7) Salinity at 10 meters, estimated by linear interpolation between adjacent measured values.

8) Salinity at 100 meters, estimated by linear interpolation between adjacent measured values.

9) Latitude, measured in degrees, with decimal equivalents of minutes and seconds.

10) Longitude, measured in degrees, with decimal equivalents of minutes and seconds; longitudes for stations west of 180° were expressed in terms of 180° + number of degrees west of 180°; for example, 159°E = 180° + 21° = 201°.

The depths for temperature and salinity were chosen to represent conditions near the shallowest and the deepest levels through which the net tows were taken.

The overall regression was significant ($p < 0.05$; standard error of estimate, 24.365). It accounted for about 56 percent of the variability of the dependent variable. Only two of the individual "independent" variables had significant regression coefficients; greater relative abundances were associated with T-S diagrams having shapes more like that of the "best" station ($p < .01$) and with lower salinities at 10 meters ($p < .05$). Both of these associations appear to indicate a property, or properties, related to the history and quality of the water; probably neither change in the shape of the T-S curve nor change in salinity is, of itself, the cause of the observed changes in relative abundance of the group.

This is particularly true of the salinity at 10 meters, for it seems unlikely that the observed small differences in salinity could have such an effect on the abundances of the species. More probably, the lower salinities indicate water which came from a region with higher precipitation than evaporation—that is, from the Oyashio or the Gulf of Alaska. Although the other regression coefficients were not significant, they are interesting as indicators of possible trends. Greater relative abundances were associated with greater depth of thermocline; with times farthest from midnight; with greater depth at which the oxygen content was reduced to 2 milliliters per liter; with higher temperature at 100 meters and lower temperature at 10 meters; with lower salinity at 100 meters; and with the more southern and western locations. Many of these associations suggest that more thorough vertical mixing creates more favorable conditions for these organisms.

Discussion

It is evident that multispecies groups occur in the zooplankton and that these groups can be identified by the procedure used in our study. If samples are taken in such a way that each contains animals from a single environment, the groups can be examined for evidence of interspecific relations, for all species within a group will be frequent members of each other's environment. The details of group composition may change with more extensive sampling in the North Pacific, but it seems likely that the changes will represent finer resolution and not fundamental alterations. For example, some of the species placed in group I seem to have stronger connections with the Central Water Mass, while others have stronger connections with the Equatorial Water Mass. With further sampling, therefore, group I might be split into Central and Equatorial groups.

The difficulties introduced by the sampling pattern become evident when the patterns of distribution of the samples representative of each group are considered in terms of frequency and abundance. Again, group I provides an example. The samples available indicate that the group was both more frequent and more abundant west of the 180-degree meridian, in particular off the coast of Japan. It is, however, known that many of the individual species in the group are more abundant toward the northern edge of their range and less abundant in the center. The southern track of the Transpac expedition started near the northern edge of the range of group I, off the coast of Japan, and then went south and east to Hawaii. The observed greater frequency of capture of the complete group and the greater relative abundance of the group at the stations off the coast of Japan may, therefore, represent the effects of the pattern of sampling, which seems to have made a north-south gradient in abundance appear to be an east-west gradient.

This possibility serves to emphasize the need for supplementary information on the individual species, for caution in interpretation, and for more extensive sampling, but it should not be allowed to overshadow the usefulness of the grouping procedure as a means of summarizing, of picking out groups of species which share a habitat, and of getting a preliminary idea of the geographic distribution patterns of the groups.

The strong evidence for group selection of water masses and the frequent strongly positive correlation of species relative abundances within groups suggest that the groups are composed of species with similar reactions to properties of the environment. The regression analysis of the relative abundances of group II was disappointing in that it indicated that many of the usually measured properties of the water—temperature, thermocline depth, oxygen content, and so on—were not closely related to the differences in abundance. Instead, the results suggest either that the organisms are reacting to a complex of factors, including the history of the water, or that the usual hydrographic procedures are not measuring the right things from the standpoint of the biologist. It will be important to examine the boundaries between groups in greater detail, to attempt to correlate other properties of the water—physical, chemical and biological—with abundances, and to supplement these field observations with laboratory studies of the effect of changes in various environmental parameters on the animals and their functions. Thus, we may get an understanding of the causes of the evident, and often sharply defined, patterns of zooplankton distribution and abundance (*15*).

References and Notes

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