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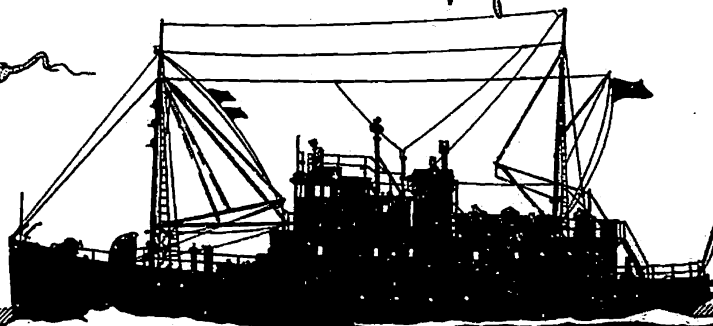
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January 1966

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ON THE VERTICAL DISTRIBUTION OF ZOOPLANKTON IN THE SEA, by K. Banse. Pp. 55-125 in Progress in Oceanography, vol. II (Mary Sears, ed.). Pergamon Press, London. 1964.

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SYNONYMS OF PROTODORVILLEA EGENA (EHLERS) (EUNICIDAE, POLYCHAETA), by K. Banse and G. Hartmann-Schröder. Proceedings of the Biological Society of Washington, 77:241-242. 30 December 1964.

Technical Report No. 138

THE INFLUENCE OF VARIABLE DEPTH ON STEADY ZONAL BAROTROPIC FLOW, by Gene H. Porter and Maurice Rattray, Jr. Deutsche Hydrographische Zeitschrift, 17(4):164-174. 1964.

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## ON THE VERTICAL DISTRIBUTION OF ZOOPLANKTON IN THE SEA

K. BANSE

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# ON THE VERTICAL DISTRIBUTION OF ZOOPLANKTON IN THE SEA\*

K. BANSE

**Abstract.** The effects of some factors on the vertical distribution of marine zooplankton are examined: temperature, water masses and transport, stratification, dissolved oxygen, pressure, seasonal and ontogenetic movements, and diurnal migrations.

Distributions of species and biomass of holopelagic animals in deep water are reviewed. There are indications of a relation between species or community distribution and water masses in deep water. A homology between distributions of radioactive fallout and zooplankton in the surface layers is suggested; convection and advection, rather than animal movements, may best explain observed distributions. Zooplankton sampling should not be made at standard depths, but at hydrographically meaningful depths.

The biomass of net plankton at great depths depends on surface production. There are indications that in the deep-sea the amount of nanoplankton is smaller than the amount of net plankton. Biological evidence of vertical divisions in the pelagic domain is not yet comparable to that for the provinces of zoogeography. Lack of knowledge of plankton near the sea floor is emphasized.

Oceanographically, diurnal migration of holopelagic species may not be as important as implied by autecological studies. Diurnal migration seems to be weak or absent among pelagic larvae of bottom animals.

\* Contribution No. 253 from the Department of Oceanography, University of Washington, Seattle 5, Washington. The paper is based on an unpublished review with the same title, presented at the symposium on "Zooplankton Production" sponsored by the International Council for the Exploration of the Sea, in Autumn 1961. The preparation of the review was supported by Contract Nonr-477(10), Project NR 083-012 with the Office of Naval Research. The participation in the symposium was made possible by Grant No. G-19227 of the National Science Foundation. I am indebted to these agencies for their support, and to my colleagues for criticism and advice.

## I. INTRODUCTION

Since the review, *The vertical distribution of plankton in the sea*, by RUSSELL (1927), which concentrated on zooplankton, the amount of published data has grown considerably, making it difficult to gather all relevant observations. Therefore, I will not offer a full account of the knowledge on the vertical distribution, but will select some aspects of the subject. Emphasis is placed on outlining features common to *all* oceans, and little is contributed to a better understanding of *particular* seas. Features of the general vertical distribution are considered first. Ontogenetic and seasonal vertical migrations, and relations to horizontal distribution are discussed. The subsequent treatment of diurnal vertical migrations of holopelagic animals includes remarks on the Deep Scattering Layer, although the layer appears to be mainly composed of nektonic animals. Finally, observations on the vertical distribution of larvae of bottom-living animals are reviewed. In bringing together existing knowledge, I have attempted to point out areas where large deficiencies exist, and to suggest means which may help to improve the situation.

## II. GENERAL VERTICAL DISTRIBUTION OF HOLOPELAGIC ANIMALS

### a. *Submergence and Distribution Related to Water Masses*

1. *General observations.* In section IIa, emphasis is given to discussing the vertical distribution of plankton below the surface layer. There appears to be little vertical uniformity even at great depths where the environment is more uniform than in the upper layers. Visual observations during bathyscaphe dives demonstrate a very marked uneven vertical distribution of plankton (predominantly Copepoda) and nekton (Fig. 1). In most cases, an identification has not been possible. It is not known whether the maxima of animals in Fig. 1 represent layers or swarms of a spherical shape. The observed distribution must be quite ephemeral with the Myctophidae which participate strongly in diurnal migrations. Earlier, BERNARD (1955) had noted, during another deep dive in the Mediterranean, that in the fairly poorly populated intermediate and bottom strata (average density, 4-7 organisms seen per sec, varying between 0 and 20) there are 1 to 5 m thick intervals devoid of anything recognizable as animals. These intervals, if significant, may represent layers, but again, nothing definite is known. COOPER (1961) has suggested widespread occurrence of hydrographic stratification in the deep-sea, with sharp boundaries between layers. He explained the stratification with

advection of water interleaving at the appropriate density between resident water masses, and has pointed to its possible biological significance. In the deep parts of the Bay of Biscay, layers of resident water of varying origin seem to be several score (up to a few hundred) meters thick, separated by

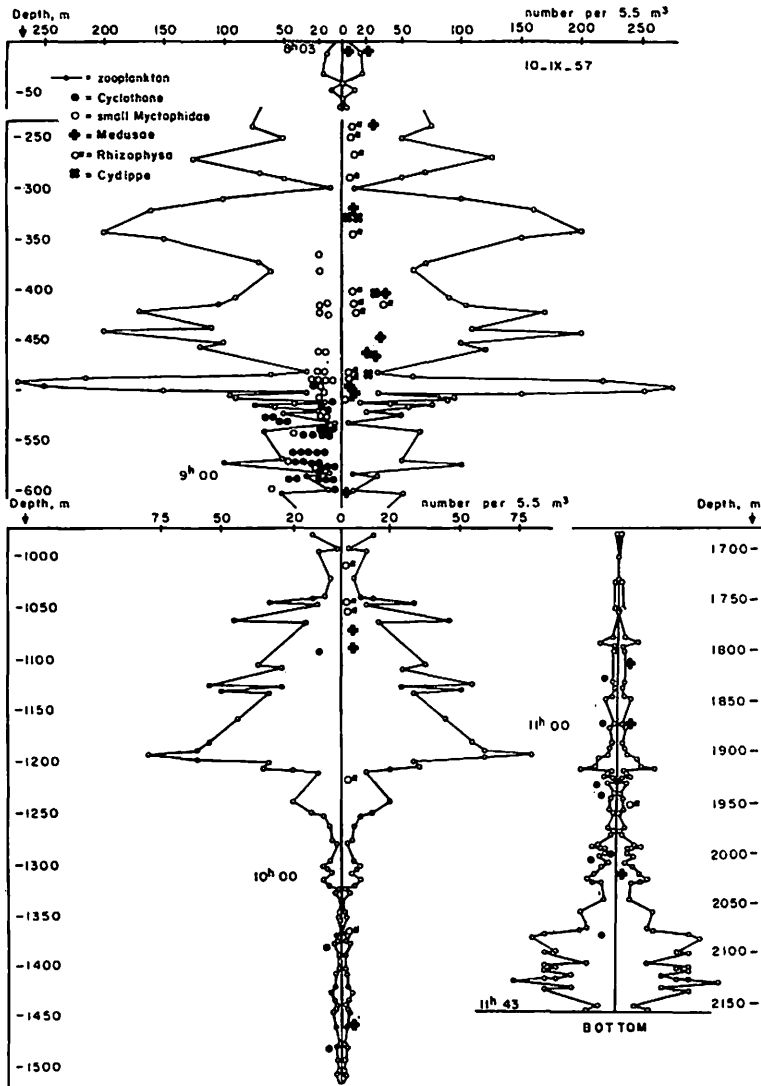


FIG. 1. Zooplankton and nekton observed during a bathyscaphe dive in the Mediterranean, off Toulon. The scale on the abscissa changes at 1000 m (Modified from BERNARD, 1958).

Intrusions a few meters high. The vertical extent of the latter can be expected to depend on the size of the water source and its history prior to interleaving. Additional observations have been presented by COOPER *et al.* (1962).

VINOGRADOV (1959a) has pointed out that in the north-western North Pacific the vertical range of many deep-living species seems to be quite limited. This is particularly so with representatives of pelagic Decapoda and Chaetognatha, which are not as diversified in feeding habits as are Copepoda or Amphipoda. Vertical maxima of the former groups are often made up of one species only, which reduces interspecific competition considerably. The same has also been shown for Chaetognatha in the upper 1000 m of Antarctic seas (DAVID, 1958). VINOGRADOV (1959a, b) has found in the north-western North Pacific that even in vertical hauls through layers of 1000 m, one species can contribute a large fraction of the total biomass: The chaetognath *Eukrohnia hamata* may represent 20, 30 or even 40 per cent, species of *Hymenodora* among the Decapoda 16 to 20 per cent, and *Calanus cristatus* among the Copepoda on the average 18 per cent, maximal 30 per cent. If these animals were concentrated in layers of 100 to 200 m they would indeed predominate. Observations by LEAVITT (1938) in the Atlantic indicate similar conditions.

At present, it is unknown whether the occurrence of certain species at fairly limited, specific depth ranges is characteristic for these forms in a particular area, or whether it is accidental. Too few seasonal surveys in deep water are available, and too often vertical hauls over large depth intervals were made which obscure the details of the distribution within the layer. Several phenomena discussed below may cause the vertical distribution of plankton.

2. *Submergence.* When describing the meridional distribution of the Radiolaria collected by the *Valdivia*, HAECKER (1904) coined the term *submergence* which referred to the presence of high latitude surface species, in low latitudes, at depths where the appropriate temperature prevails. This phenomenon was known previously from studies of benthic organisms. MURRAY and HJORT (1912) discussed several observations made in the pelagic zone and more data on equatorial submergence of boreal or polar forms were gathered by EKMAN (1953). RUSSELL (1927) summarized older observations on plankton which show that not only temperature but also light can make subpolar animals stay in deeper layers in temperate latitudes (also MARSHALL, 1954). Another contribution to the subject of submergence was given by LEAVITT (1938) for the North Atlantic. Among the many recent studies of submergence in the North Pacific, the papers by BOGOROV and VINOGRADOV (1955) and by BEKLEMISHEV (1961) may be mentioned. Detailed investigations of cold-water cosmopolites in lower latitudes show that an

*equatorial emergence* can be superimposed on the general submergence (BIERI, 1959, for *Eukrohnia hamata* and other cool-water Chaetognatha. For *E. hamata*, see also DAVID, 1958). The oceanic circulation results in lifting of the isotherms below the divergences in low latitudes so that species can occur at shallower depths than at lat. 20° or 30°. *Sagitta minima* emerges into the upper 200 to 300 m at 10°N, for the same reason.

There is also *polar submergence* when warmer water is found below polar water. Examples from the Weddell Sea of northern plankton which occurs south of the Antarctic Convergence only below the halocline, have been reviewed by EKMAN (1953). Of 67 species, mostly Copepoda, studied by ØSTVEDT (1955) in the Norwegian Sea, 19 species were found at intermediate depths only, between 100 and 600 m, where Atlantic water prevails. All species are Atlantic forms which are usually not regarded as occurring north of the Iceland-Faroe-Shetland ridge.

Before elaborating on these types of distribution, brackish water and seasonal submergences may be mentioned. In positive estuaries with little or no tidal mixing, as well as at the entrances to large brackish water basins, the deeper layers consistently have a higher salinity than the surface water. The term *brackish water submergence* (originally coined for benthic organisms) denotes the occurrence at depth of organisms which are unable to tolerate the low salinity near the surface. Examples of this type of plankton distribution have been given for the area between the North Sea and the Baltic Sea: by KRAMP (1915) for the Great Belt, by KÄNDLER and WATTENBERG (1940) for Kiel Bay, and by HESSE and VALLIN (1934) for the Baltic Sea itself. Brackish water submergence of plankton animals is difficult to distinguish from passive transport in water of high salinity, and the term seems to be more useful in studies of the benthos.

The term *seasonal submergence* refers to the seasonal disappearance of species from the surface as long as a certain temperature is exceeded. NIKITINE (1929) has given examples from the Black Sea; the seasonal vertical distribution of plankton could be described by distribution of isotherms. Because the depth of isotherms, and particularly of the thermocline, varies according to the circulation pattern, the upper distribution limit for a species during summer may be found on hydrographic cross-sections at different depths (PETIPA *et al.*, 1960, for the same area). This is analogous to the equatorial emergence discussed earlier. Other observations can be found in RUSSELL (1927). In contrast to active seasonal migrations (section II d), the term *seasonal submergence* should be restricted to a random spreading of a population within a certain temperature range if it is caused by temperature distribution. However, in practice it will often be difficult to distinguish, without many observations, whether seasonal submergence, in the strict sense, or seasonal migration is present.

3. *Distribution related to water masses. The concept.* A more closely worked-out example of an apparent submergence of a subarctic animal towards the equator was presented by MCGOWAN (1960), who found that the highest catches of the pelagic worm *Poebobius meseres* are obtained at 150 to 300 m depth in the Kurile-Kamchatka area of the North Pacific. The abundance declines towards the south and the east, although there are some records from the California Current. Only very few animals have been caught, and only at greater depths, equatorward of the polar front in the mid-Pacific, south of roughly 45°N. Even in the subarctic water in the north-eastern

Pacific, many hauls reaching to only 400 m failed to collect specimens. MCGOWAN did not regard this distribution as submergence caused by temperature but suggested that the species is bound to the Subarctic Water Mass as physically defined by SVERDRUP *et al.* (1942). There is some indication that the animals occur also in the North Pacific Intermediate Water. New records for this worm were mentioned by BEKLEMISHEV and LUBNY-GERTSKY (1959) from the north-eastern North Pacific, off America but not very close to the coast, down to 20°N; particulars are not available to me.

The first large-scale attempt to relate the distribution of deep-living pelagic animals to physically defined *water masses*, and not to temperature alone, was that for the cephalopod, *Vampyroteuthis infernalis* (PICKFORD, 1946; 1952). This species appears to live in the upper Deep Water of the tropical and subtropical oceans, the Indian Equatorial Water, and the lower Atlantic Central Waters. The salinity range it inhabits varies from ocean to ocean. Thus, merely tabulating either the salinity or temperature range of the species does not describe the situation adequately. Other pertinent papers are the treatments of the stomiatoid fish genus *Chauliodus* (HAFFNER, 1952) and the melamphaid fish genus *Melamphaes* (EBELING, 1962).

The point made for the four examples just cited is that the animals occur only with certain combinations of salinity and temperature, although the same range of salinities and temperatures is also found elsewhere in the particular oceans. The combinations apparently represent bodies of water large and continuous enough to permit development and maintenance of their own faunas. The distribution of the species mentioned is not so much determined by salinity and temperature as such but by the horizontal and vertical circulation maintaining the water masses. Mixing within these water masses is more intense than across the borders so that there is biological isolation. The importance of this approach to animal geography is to give an understanding of the three-dimensional distribution of zooplankton. A species bound to a water mass follows the vertical and horizontal movement of that water mass, and vertical and horizontal distribution can be explained in the same terms. Additional observations are given on p. 62.

Before discussing possible conclusions on this subject, two explanatory remarks should be made.

(a) When plotting salinity against depth for a station where Intermediate Water is present, a minimum salinity is found at the depth where the original quality of the water is best preserved, that is, where the center or the *core layer* of the Intermediate Water occurs. In the *T-S*-diagram, this core layer would show as a bend in the curve. Stations far from the region of origin will exhibit the minimum less clearly than stations near to it, because the core layer is eroded by mixing with more saline water above and below. If a species is bound to the Intermediate Water (as *Poebius* may be in the North Pacific), the greatest number of animals would be expected in the core layer as long as other factors, such as light, do not influence their vertical distribution.

(b) Using the *T-S*-relation, SVERDRUP *et al.* (1942) have described *water masses* between

core layers in the upper subsurface waters, approximately down to the 4°C isotherm, that is, in the mesopelagic and bathypelagic zones according to BRUUN (1957, also p. 89). Most water masses are believed to acquire much of their character at the surface. The Indian and Pacific Equatorial Waters, however, seem to be formed at depth by mixing of the layer of the intermediate salinity maximum of subtropical origin, with the Intermediate Waters (of subpolar origin) below; these core layers are several hundred meters apart. The mixing maintains uniform hydrographic characteristics over large areas of the Indian and Pacific Oceans.

Stimulated by the arguments put forward by WYRTKI (1962) concerning the usage of the term *water mass*, it should be pointed out that it is not known whether the greater number of species present in the Equatorial Waters (and for that matter, in the Central Waters as well) have their centers of vertical distribution *in* these water masses, or in the core layers above and below. If the Central and Equatorial Water Masses of the Pacific were entirely due to mixing between the core layers above and below as implied by WYRTKI, it would be difficult to understand that there seem to be Euphausiidae bound to the geographic regions of either water mass but not occurring elsewhere, or that there are species occurring in and above the Central Waters of the North and South Pacific but not in the region of the Equatorial Water as reported by BRINTON (1962). BRINTON'S material is not ideally suited for deciding physical problems, owing to the diurnal and ontogenetic vertical migrations of Euphausiidae. To arrive at a rational biogeography of the mesopelagic and bathypelagic zones, it may be useful to investigate more closely the alternatives: distribution according to core layers or water masses *sensu* SVERDRUP *et al.* Suitable methods will be mentioned at the end of this section.

The abyssopelagic zone could also be studied biologically with core layers in mind, as is common in discussions of oxygen or salinity distributions. There is not enough information to describe the distribution of plankton in the indicated terms, because divided hauls have only been made over very large depth intervals, and at standard depths. Also, the few horizontal hauls were made mostly without depth gauges and closing devices so that the depths of capture given are only approximate. The understandable tendency of expeditions to sample macroplankton and nekton mainly during the night, skews the apparent vertical distribution and makes interpretation even more difficult. It may be that the distribution of the greater number of pelagic species is determined by temperature, light or food, and not at all by the genesis and maintenance of water masses. However, if a relation of species distribution to water masses can be established, the distribution in biologically poorly known areas could be predicted. Physically unclear situations in biologically well-known regions could be determined in a manner similar to that for indicator species in surface waters where physical characteristics for tracing the origin of waters are obscure.

4. *Other observations.* There are additional studies suggesting a more widespread connection between water masses and animal distribution. Much of the treatment of the Antarctic Chaetognatha by DAVID (1958) and the arguments used by BEKLEMISHEV (1960, see section IIe) show, or imply, a connection between the vertical distribution of animals and core layers. The spreading of Bering and Chukchi Seas species into the Beaufort Sea and adjoining parts of the Arctic Basin is apparently limited to the geographic distribution of the intermediate layer of Bering Sea water (GUDKOVICH, 1955, quoting BRODSKY; JOHNSON and BRINTON, 1963). Many records in the literature of submergence of subpolar species towards the equator may be better explained in terms of water masses than of isotherms once more collections become available. An Atlantic example for a species bound to Arctic water may be *Calanus glacialis*; the related *C. helgolandicus* spreads from the core layer of the Mediterranean outflow into the Atlantic to the north-east (JASHNOV, 1961a). The distribution of the latter also shows how important knowledge of seasonal migration (life history) is in understanding the geographic distribution. Some of the distribution patterns recorded by HAFFNER (1952) may indicate that the Equatorial and Central Waters are populated throughout (*Chauliodus sloanei sloanei* in the Indian Equatorial Water, *Ch. s. dannevigii* in the western South Pacific Central Water). The population of these fishes are thus not derived from the core layers above and below. It must be realized that even if the Central Water masses harbor a fauna of their own, the fauna may not occur uniformly throughout the water masses. Water masses are so large that environmental factors other than salinity and temperature can vary considerably and limit some species. HAFFNER has suggested that the distributions of *Chauliodus sloanei sloanei* and *Ch. danae* in the North Atlantic Central Water, and the limited distribution of *Ch. sloanei schmidti* in the Atlantic may be caused by varying tolerance to the oxygen content of the water, and interspecific competition. BRINTON (1962) believed that some mesopelagic Euphausiidae do not occur in the Eastern Pacific Equatorial Water because of low oxygen concentration. EBELING (1962) has suggested that the availability of food may restrict the distribution of species within a water mass and has mentioned the high primary productivity of the eastern tropical oceans.

Further, there are species with a geographical distribution limited by surface convergences. The convergences often can be considered in the first approximation as the surface projections of the borders of the water masses below. TEBBLE (1960) has given examples for pelagic Polychaeta in the South Atlantic. Many of the species, however, not present south of the Subtropical Convergence have been caught as adults not only in the warm surface waters but also in the South Atlantic Central Water, in the Antarctic Intermediate Water, and even in the Deep Water, that is, at depths where temperatures

lower than 4°C are common. Apparently, such species are not warm water forms as might be expected from their surface distribution. The reason why these species do not occur south of the convergence in cool surface water might then be sought in the subsurface waters, that is, the layer of the intermediate salinity maximum, or the Central Water below. Too few data on life histories and the quantitative distribution of developmental stages are available to allow more definite guesses (see also *Japetella*, p. 80). It could also be that the animals at depth are doomed individuals which will not reproduce and not return to the surface layers (*expatriates*, according to EKMAN, 1953).

Evaluating the geographic distribution of Chaetognatha, Euphausiidae, Heteropoda, and Pteropoda in the upper 150 m of the Equatorial and North Pacific, FAGER and MCGOWAN (1963) found recurrent groups of species. The distribution of the groups is similar to that of the water masses described by SVERDRUP *et al.* (1942). The reasons are not clear because the water masses are largely subsurface phenomena. More physical and biological research is needed, but vertical distribution patterns of the species are likely to be one cause of the relationship. The approach by FAGER and MCGOWAN is particularly interesting because pelagic communities are established statistically, and unwieldy species lists are replaced by ecological groups which may be a more desirable basis for animal geography than the species themselves (see also p. 91).

It is not likely that the vertical distribution of all pelagic species can be described in terms of physically defined bodies of water. HAECKER (1908) suggested for the Aulacanthidae among the Radiolaria that some species seem to be bound to the same depth ranges in cool and cold water below tropical and antarctic seas. The distribution of many species which perform marked diurnal vertical migrations may be better related to the distribution of light in deeper layers. MOORE (1952) has suggested a mechanism for distribution for the Euphausiidae of the North Atlantic feeding at night in the surface layers, which is very different from the water mass concept. Although vertical distribution is primarily regulated by illumination, each species can live only within a certain temperature range. At night, the animals must reach the feeding grounds but cannot go beyond a certain warm temperature so that they are excluded from certain regions. If the surface temperatures are too low the feeding rates may become too low to maintain the species so that it is also excluded from these regions. During the day, the animals have to compromise between temperature and illumination at depth. Too low temperatures at the depth with optimum illumination exclude a species from an area; too high temperatures may result in further downward swimming, and the diurnal range of migration may become so large that the species cannot be maintained either. On this basis, MOORE suggested that the horizontal

distribution of North Atlantic Euphausiidae can be predicted by considering relative values of underwater illumination and the degree of departure of temperatures from the optimum value at night when the animals are near the surface, and during the day when they are at depth. Most species appear to have two temperature optima, one related to the night depth, the other related to the day depth of the species. It is not yet possible to say whether this explanation of vertical and horizontal distribution will hold elsewhere, and for other pelagic animals.

Another vertical distribution pattern has been mentioned by VINOGRADOV (1959a). In the north-western North Pacific, the greatest amount of plankton is often found in the zones where hydrographic gradients are greatest, that is, in the mixing zones or discontinuity layers, not in the centers of bodies of water (see also p. 101). On the other hand, in the equatorial Pacific HIDA and KING (1955) did not find an accumulation of zooplankton in the thermocline underlying the surface layer.

Regarding the distribution of the weak swimmer *Vampyroteuthis infernalis*, discussed earlier, it may even be that it is not related to water masses at all but is limited to the density range of  $\sigma_{-t}$  27.4 to 27.8 which happens to occur in the water masses listed on p. 60, as pointed out by PICKFORD (1946). Yet, only part of this density range is populated (PICKFORD, 1952).

5. *Notes on field methods.* As indicated in section IIa1, there is at present no reason to believe that the subsurface and deep-sea net plankton\* is evenly distributed vertically through thick layers at a given station. Vertical hauls, then, not only pass through a range of depth, salinity, and temperature, but also capture animals which may have no relation to one another. The observations from a bathyscaphe (Fig. 1) when integrated are exactly like a haul with a vertically towed net. It seems to me that with our present taxonomic knowledge of the oceans, the collection of a limited number of a few ecologically unambiguous samples for which the environmental conditions are known is more desirable than a large increase of the number of samples which result only in new dots of records on world maps. To investigate the distribution of pelagic animals rationally, I believe that it is advisable to abandon the net hauls executed at, or between, standard depths. The oceanographic knowledge of much of the oceans is advanced enough that on research vessels, if not on survey ships, a suitable depth can be chosen beforehand or on the basis of temperature observations while on station. The lowering of recording instruments to great depths will greatly enhance recognition of layering in the deep-sea. It may even be wise to abandon vertical hauls and fish horizontally in core layers, determined from the *T-S*-relation, and midway between them.

\* Refers to plankton caught by a net as opposed to other devices. The same usage occurs throughout this paper.

The relation of plankton to discontinuity layers can be studied by adding levels of observations. Only metered closing nets, having the same mesh throughout, equipped with depth recording devices, should be employed, and the horizontal towing distance should be kept short. There may be patchiness in the layers but it is better to obscure this than to mix the animals from different layers in a single haul. Probably, in the near future, the use of conductor cables will permit monitoring the environment during the haul. This is desirable when towing near discontinuity layers. In order to obtain an unskewed picture on the ecology of diurnally migrating organisms, the number of day and night hauls should be the same. The need for seasonal coverage has been touched upon earlier, but obviously it is feasible only in a very few localities.

The idea of voluntarily skipping most of the water layers situated between the levels of the horizontal hauls may seem strange to the taxonomist, thinking in terms of the early collecting expeditions. However, even if all vessels would now start surveys of the kind just proposed the number of hauls which would become available during the next half decade would provide much more material than the existing taxonomists can cope with in a reasonable time. The ecologist should aim at samples of the community taken from a well-defined depth, and sacrifice full vertical coverage. (In any case, the community is incompletely sampled by nets due to the selectivity of the mesh-size.) Data collected, as proposed, would be suitable for many ecological studies; they are not only suited to prove or disprove the very important question of the relation of plankton to the water masses of physical oceanography. Another suggestion which will be made again when discussing the near-surface plankton (section IIc) is that it is too difficult to relate integrated samples (such as vertical hauls through a water column of a few hundred meters) to the information on the environment which is derived from samples obtained at particular points.

#### b. *Influence of Oxygen Content and Water Pressure on Distribution*

A very low oxygen content and changes in hydrostatic pressure may also influence the vertical distribution of zooplankton. In this review, the influence of vertical changes in the aeration of the water on vertical migrations will not be considered; only the effect of a low oxygen content on the average vertical distribution will be examined.

SCHMIDT (1925) reported particularly rich catches of net plankton from the intermediate oxygen-minimum layer of the tropical Eastern Pacific. The values were well below 10 per cent saturation (down to 0.1 ml/1. of O<sub>2</sub>), quite small when compared with most parts of the ocean. There are also Deep Scattering Layer observations from this region (KANWISHER and

EBELING, 1957). VINOGRADOV and VORONINA (1961) and VINOGRADOV (1962a), however, found in intermediate layers of the northern Arabian Sea that the biomass of the net plankton becomes abnormally low when the oxygen content falls below approximately 0.15 ml/l. (2 to 3 per cent of saturation). VINOGRADOV and VORONINA pointed out that this is particularly true at the depth of the nitrite maximum which lies near the upper border of the oxygen minimum, and suggested a connection of low biomass with very small amounts of  $H_2S$  reported by IVANENKOV and ROZANOV (1961). Below this zone, but still at quite low oxygen values, the net plankton increases to a secondary maximum.

Usually the variations in the oxygen content in the open ocean will not affect the vertical distribution of the biomass of the net zooplankton because oxygen values as low as those reported are rare. This can be different on the species level: For the open sea, HAFFNER (1952) showed that there are fish species which avoid water layers with less than 50 per cent oxygen saturation. Similarly, PARIN (1961) suggested that faunistic differences of the upper bathypelagic fish fauna between the north-eastern and the north-western North Pacific may be due to the lower oxygen content in the former. VINOGRADOV and VORONINA (1961) gave examples of the distribution of Copepoda for the upper 500 m of the Arabian Sea. In the area where very low oxygen values prevail below 100 or 200 m depth, certain species are restricted to the water layers above that depth; whereas at neighbouring stations with a greater oxygen content, the species occur down to 500 m. Some species are found even in almost deoxygenated water, and living stray specimens of those which generally avoid these layers are also caught there. The observations by WOODMANSEE and GRANTHAM (1961) of Copepoda migrating diurnally into oxygen-free water in a shallow lake may be mentioned here.

The paper by VINOGRADOV and VORONINA also contains an example of the bearing of populations at mid-depths on surface occurrence. In the areas with an oxygen content below about 0.5 ml/l. at depth, *Neocalanus gracilis* is absent not only at those depths but also in the better aerated layers above. Elsewhere, it occurs in the surface layers and at depth. The influence of low oxygen content on the horizontal distribution of mesopelagic Euphausiidae as observed by BRINTON (1962) has already been mentioned on p. 62.

Observations on the low oxygen content of water influencing vertical distribution were also made in neritic seas. NIKITINE and MALM (1934) compared field and experimental data on the lower oxygen limit and the distribution of common Black Sea neritic species. Although the resistance of species varied, it was found that many can live slightly below 5 per cent saturation (about 0.3 ml/l. of  $O_2$ ). Experiments by ZEUTHEN (1947) with larvae of bottom animals from the Kattegat showed that respiration rates may be

affected by oxygen saturation values below 25 to 30 per cent. Similar results were reported for *Calanus finmarchicus* by MARSHALL and ORR (1955). However, data reviewed by BANSE (1956b, 1959) indicated that the vertical distribution of the common zooplankton species and bottom larvae in the area between the North Sea and the Baltic is scarcely, if at all, affected by oxygen saturation above 10 per cent.

Since the experiments by HARDY and BAINBRIDGE (1951), pressure has been studied as a possible factor regulating vertical distribution in groups other than fishes (see BAINBRIDGE, 1961). It has been shown that some crustacean species migrate upwards with an increase of water pressure; others, including *Calanus finmarchicus*, do not. Larvae of Decapoda respond to pressure differences of 10 cm of water (KNIGHT-JONES and QASIM, 1955). RICE (1961) studied pressure responses of marine Mysidae and found that these animals also tended to move upward with an increase in pressure. He suggested that the response may be connected with tidal migrations of shallow-water Mysidae (see also p. 75). For distributions found in the field, MOORE (1955; also MOORE and CORWIN, 1956) suggested an influence of pressure on the daytime depth of plankton in the Florida Current in an area with sloping isotherms. BANSE (1955) indicated that Copepoda and larvae of bottom animals in the Great Belt did not adjust to the vertical displacement of water caused by internal waves. This was perhaps caused by the slight stratification of the water; diurnal vertical migrations did not occur either. The many studies of the early days of the evolutionary theory begun at the upwelling sites near Messina and other places in the western Mediterranean, also show that zooplankton can be carried vertically by the water and imply that the Kiel Bay case may not have been a special situation (see, however, LOHMANN, 1910). SCHRÖDER (1962) observed that freshwater zooplankton was carried up or down under the influence of internal waves. It did counteract by swimming when the vertical displacement became too great. Areas with internal waves of periods other than 24 hr seem to be most suitable for field observations on the effect of pressure changes on vertical distribution.

The search for pressure registering organs in Crustacea has not been very successful. In a preliminary report on work with the prawn *Palaemonetes varians* and the freshwater *Daphnia pulex*, DIGBY (1961b) suggested that the mechanism for registering pressure changes may be negatively charged surfaces of the animals where a very thin hydrogen gas layer develops. Pressure sensitivity of experimental animals was reversibly destroyed by surface-active, positively charged, complexes. Model studies were presented in support of the suggestion. ENRIGHT (1962) has objected to the validity of the model and has argued for a non-gaseous sensory mechanism.

c. *Plankton in the Surface Layer and Near the Sea-Bed*

In most regions of the sea, the water above the main discontinuity layer is regarded as vertically stirred either by wind-induced or convective mixing. However, the occurrence of oxygen maxima in the wind-mixed layer indicates that biological activity often proceeds at a more rapid rate than physical processes, and pronounced intermediate phytoplankton maxima have been observed in a physically homogeneous water column. Observations from

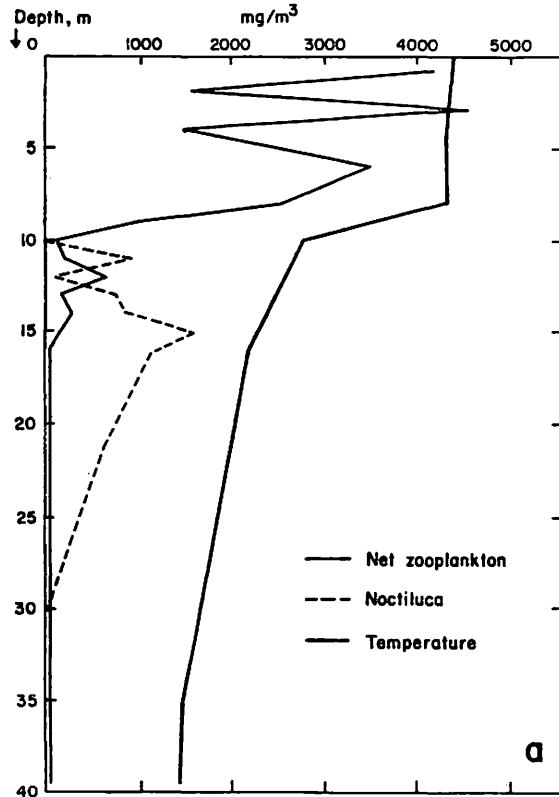


FIG. 2 (a)

coastal waters show that zooplankton can also be distributed vertically in a very uneven manner (KUSMORSKAJA, 1954; BANSE, 1955, 1959), although short-term, active, vertical movements may not be involved. Even in the surface layer the numbers of specimens were found to vary commonly by 100 per cent in 1–2 m depth intervals with holopelagic species, and up to 1000 per cent with meropelagic forms. Figure 2 shows an example for the biomass distribution of individual species as well as for the total net zooplankton from the Black Sea. The samples had been taken by a water bottle.

The distribution shown in Fig. 3 had been observed in fairly open waters using a plankton pump. The upper 10 m were physically nearly homogeneous.

Because diurnal migration was absent in Kiel Bay, even in the surface layer (Fig. 3), it is also likely that Fig. 2 does not represent a "snapshot" of a vertically moving population, in view of the similar hydrographic regime in

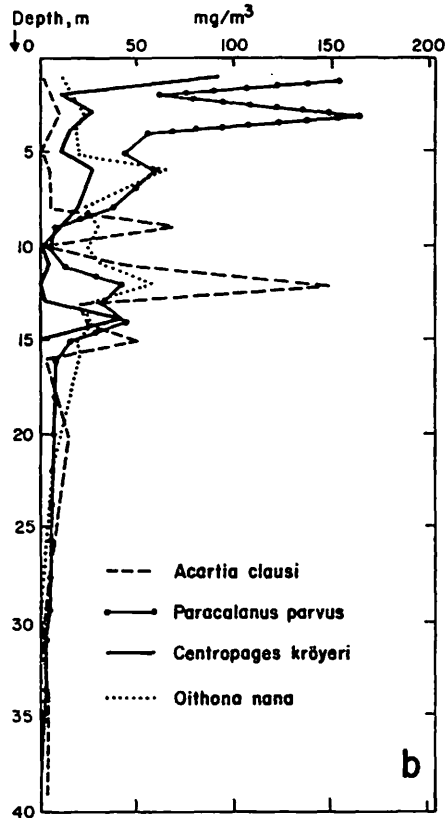


Fig. 2 (b)

FIG. 2. Vertical distribution of zooplankton biomass at two stations in the Black Sea (From KUSMORSKAJA, 1954).

the Black Sea; it will be shown in section IIIa that diurnal migrations are not as common, particularly with smaller species of Copepoda in neritic areas, as sometimes believed. Obviously, the fine structure of animal distribution near the surface will be altered if not destroyed by strong wind. Convective mixing, however, may not homogenize the surface layer and the plankton distribution, but may result in vertical displacement of large water parcels. Small plankton may be rearranged accordingly. Studying the distribution of

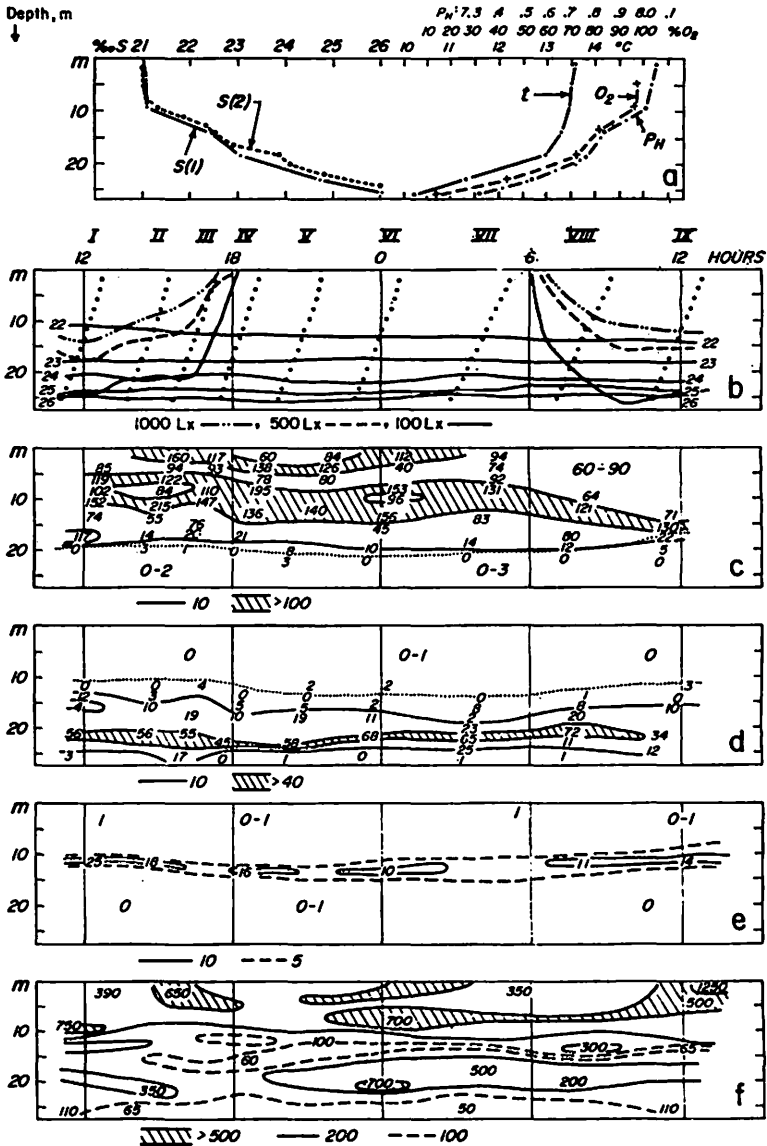


FIG. 3. Observations on an anchor station in the Bay of Kiel.  
 a. Hydrographical observations prior to series III. 1: salinity from Nansen bottles. 2: salinity from pump samples. b. Time and depth of plankton samples, salinity from pump, and illumination. c. Adult females of *Paracalanus parvus*. d. Adult males of *Pseudocalanus elongatus*. Dotted lines in panels b and c are borders of water masses, from T-S-relation. e. Larvae of *Pisone remota* (Polychaeta). f. Juveniles of *Sagitta elegans* and *S. setosa* (Modified from BANSE, 1955 and 1959).

strontium-90, and referring to other studies on tritium distribution in the open ocean, BOWEN and SUGIHARA (1957) tentatively suggested that convective mixing in northern waters may be conceived "... as occurring by the transport of large boluses of water of equal density, coming quickly to equilibrium with respect to components supplied at the surface ... but retaining their identity with respect to some components for which there is no source of rapid supply". The same authors (1958) brought forward more evidence, and suggested that the water parcels extend for distances of 1 to as much as 5 km, and 30 to 50 m vertically. In warm-water regions (south of 38°N), the distribution pattern of the isotopes was found to be considerably more uniform, emphasizing that the non-homogeneity of isotope distribution in northern waters may indeed be due to the mechanism of convective overturn.

It is suggested here that if there are no diurnal vertical migrations, relatively slowly growing zooplankton may be distributed in the mixed layer like the isotopes. Evidence for Kiel Bay had been presented when discussing the distribution shown in Fig. 3 (BANSE, 1959; also BANSE, 1956b). In marginal seas, where slight salinity gradients often influence the density distribution, water boluses would probably be thinner than indicated by BOWEN and SUGIHARA. It had been shown for Kiel Bay that diurnal migrations were absent, and that meroplankton and small species of Copepoda did not compensate for vertical displacement of water. Thus, the convective mechanism proposed by BOWEN and SUGIHARA could vertically rearrange zooplankton up to the size of small Copepoda. It was pointed out that, in Kiel Bay, swarms of meroplankton and clouds of phytoplankton, turbidity, and yellow substance have about the same horizontal dimension, a few hundred to a few thousand meters, as have swarms of Copepoda. It was implied that similar dimensions were due to the same cause, the physical non-homogeneity within water, uniform by the standards of physical oceanography. It was suggested that maxima in population density of species at one station, as shown in Figs. 2 and 3, were not due to the seeking of optimum levels by parts of the population being in different moods, but to interleaving of water layers with a different biological content. This holds even for the surface layer (Fig. 3). At a given station, the vertical distribution of the studied species of Copepoda would not reflect, then, the reaction of the animals to

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Explanations to Fig. 3, observations on 25-26 September 1953: After a Nansen-bottle cast, 500 l. samples were pumped from 2 m above sea bed to 2 m below surface, and the water filtered through a net with a mesh aperture of about 110  $\mu$  (no. 12). The salinity of the water was determined in order to check the depth of the intake; light was measured without a cosine collector and filter (panel *b*). On 25 September, wind strength was 1 on the Beaufort scale, on 26 September, 3 on the Beaufort scale. Current measurements showed the surface, intermediate, and bottom water to move quite independently of each other. Animal numbers in panels *c* and *d* are for 250 l.; in panels *e* and *f* for 500 l.

the actual conditions of life but would be attributable to former conditions at other places. If similar physical processes are at work in the open ocean, as indicated by the strontium and tritium distribution, it can be concluded that the accidental character of zooplankton patchiness within the surface layer on occasion might not be due to biological events, like grazing by a school of herring, but to the occurrence of discrete parcels of water, with different biological histories, transported to the site of observation by physical forces. Direct proof of this thesis is possible by large-scale tagging of water.

The same explanation, referring to mixing processes of an order of some 10 kilometers, had been advanced for the large-scale distribution of Copepoda in the Bay of Kiel, which is 20 to 40 m deep (BANSE, 1959). It was shown that the *major* features of vertical (and horizontal) distribution in the Bay were determined by advection, but not by active movements of the animals. However, vertical maxima were much more frequent in discontinuity layers between water masses than to be expected by chance from the number of samples taken in zones with strong gradients of environmental conditions (p. 101). Copepodids and adults did not leave the water masses in the Bay of Kiel in spite of the tendency to accumulate in the discontinuity layers. "Seeding" of unpopulated water masses was accomplished by mixing of water, by sinking of eggs, and by active vertical movements of nauplii through pronounced salinity and temperature gradients (BANSE, 1959).

It is not yet known how long the water boluses of BOWEN and SUGIHARA retain their identity in the open ocean. Without going into the limnological literature concerning patchiness of plankton distribution, observations from Lago Maggiore may be mentioned which indicate that over a fairly long time the lake is not well mixed horizontally: BALDI *et al.* (1949) found appreciable biometric differences in a copepod species sampled near the surface at the same day at eight locations a few kilometers apart. TONOLLI (1949) had shown for the species in the same lake that this did not hold for samples taken a few meters apart. The results suggest that plankton swarms retained their individuality long enough to produce statistically different mean individuals. The situation was complicated, however, by changes of body dimensions of the animals towards depth. Slightly different patterns of vertical migrations, caused by varying depth of the water, would have resulted in different size distribution patterns at the surface, even if there had been fairly effective horizontal mixing within the surface layer (BALDI *et al.*, 1949). Also here, repeated sampling in tagged water would be desirable. It must be emphasized that plankton in the ocean can be distributed like the isotopes only in the absence of diurnal migrations or other marked vertical movements.

BOWEN and SUGIHARA (1958) have indicated that the pattern of convective mixing may be different in temperate waters from that prevailing in warm seas, producing a more uneven distribution of radio-isotopes in the former zone. It was implied earlier that this may hold for plankton as well. CUSHING (1962) has pointed out that differences in the degree of patchiness might be expected also because the environmental conditions, which affect the reproduction strongly, are less stable in temperate waters than in subtropical

or tropical areas. From TONOLLI and TONOLLI (1958), it can be seen how important it is to consider the mode of reproduction in treating distribution patterns. In the same fresh-water locality, Rotifera and Cladocera, generally reproducing parthenogenetically, were found randomly distributed, whereas Copepoda were clumped. LANGFORD (1938) had made similar observations in a Canadian lake where Cladocera were found to be randomly distributed more often than Copepoda.

Some observations are available on the vertical distribution of plankton near the very surface. HASLE (1950) collected autotrophic Dinoflagellatae at 0, 25, 50, 100 and 200 cm depth in a sheltered part of the Oslo Fjord. A marked biological stratification was found in physically stratified water; diurnal migrations were present. Sampling in good weather at every decimeter of the upper one meter in the Mediterranean, DELLA CROCE and SERTORIO (1959) found vertical changes in population density exceeding 100 to 300 per cent per decimeter, particularly for Copepoda. With new material at hand, DELLA CROCE (1962) pointed out that there seemed to be regular changes in animal distribution at about 50 cm depth. It is not known how much active movement of the animals was involved. ZAITSEV (1961) studied the 5 to 6 cm below the sea surface in the Black Sea where peculiar conditions of illumination, temperature, and aeration prevail, causing an increased growth of phytoplankton. ZAITSEV found considerably more zooplankton there than in the four 20-cm intervals below, even with waves up to 2 m high. He stated that much of the development of the larvae of fish species with pelagic eggs takes place in the upper 5 cm, and coined the term *hyponeuston* for the association. The enrichment of the surface layer with phosphate by bursting air bubbles which carry with them a film of surface-active organic phosphate compounds (BAYLOR *et al.*, 1962), contributes to increased fertility at the sea surface. HEINRICH (1960a) observed that in the open tropical Pacific, the upper decimeters of the water are distinguished day and night by species of Copepoda, family Pontellidae, which are almost absent in deeper layers, and ZAITSEV (1961) tentatively suggested an ecological relationship between the hyponeuston and the pleuston in this area.

Distribution patterns as in Figs. 2 and 3 cannot be sampled with a vertically towed net because one cannot determine at what depth the animals were caught. Also, the population density obtained from a haul with a metered net may hardly occur along the path of the net. Even in the open ocean, with a possibly more uniform vertical distribution, it is doubtful whether a horizontally towed net could give as much information as a point sample (water bottle or pump). Furthermore, because all environmental data including phytoplankton samples are taken from distinct points, it is very difficult to relate them to the results from analyses of integrated samples (to compare net hauls with bathythermograph readings is difficult enough). Also, samples from a well-defined environment are better suited than integrated samples for posing experimental questions which are to verify the conclusions from

field observations. It is, therefore, stressed that not only pumps, but large water bottles (5- to 25-l. capacity), can be employed for collecting zooplankton (HANSEN and ANDERSEN, 1962). It may be remembered that the only available and often reproduced map of zooplankton distribution in the surface waters of the South Atlantic (HENTSCHEL, 1932) was based on 4-l. samples. Collecting with water bottles or pumps has an additional advantage in that the plankton is separated from the environment on board ship. Very fine nets can be used even during phytoplankton blooms, because clogging cannot influence the amount of water filtered, and most measurements of the environment can be performed on the water strained through the plankton net.

Zooplankton work in the surface layers is likely to become directed more and more towards productivity studies. The future investigators thus will be interested in the common forms which make up most of the catch. For this purpose, the amount of water strained by a tow net is unnecessarily large, and it seems better to study a sample small in the beginning, rather than to count a subsample representing 1/100 of the net haul. There are, of course, situations where large water samples must be strained either because rare forms are studied, or because a few large animals, like Euphausiidae, contribute most of the biomass of the net plankton, so that even a pump may not be satisfactory. In these cases it may be better to make two short hauls than one very long tow, since small replicate samples are to be preferred over replicate subsamples of large samples. Statistical analysis of part of the duplicate samples will show how much effort must be spent on counting the remaining samples in order to get a result of a specified quality, and great savings in time and man-power can result.

To avoid a very large increase in the number of samples to be counted, it is not advisable to take point samples "blind" at standard depths (see also section IIa5). Rather, sampling depths should be chosen after recording instruments have shown the vertical distribution of temperature, salinity, oxygen, or beam transmission. Investments in these instruments will quickly pay off in saving time when working-up the collections.

The importance of giving attention to hydrographic conditions may be seen from the following examples: The sharp break in population density at about 8 m in Fig. 2a was due to the thermocline. The dotted lines in panels *c* and *d* of Fig. 3 were physically defined borders of water masses of different origin. In spite of patchiness of distribution, there were sharp border zones separating populated from unpopulated areas. HANSEN (1960) showed for the upper 50 m of the Norwegian Sea that catches through the layer above the summer thermocline yield two to three times as much biomass per unit volume of water strained as do catches from 50 m to the thermocline.

The vertically towed net is useful when the amount of diurnally migrating animals under the unit surface must be known. Certainly, it would be futile

to look in samples from water bottles for a relation between zooplankton and phytoplankton if the mass of the zooplankton migrated diurnally. However, it will be shown in sections IIIa and IIIb that quite commonly less than one-half of the zooplankton biomass does so, except at the very surface. The remainder feeds and digests in the same water. Particularly in neritic waters, there are situations where there is no migration.

Little is known about the distribution of zooplankton in the last 10 to 100 m above the sea-bed. First, observations in comparatively shallow water may be mentioned. RUSSELL (1928b) occasionally found, during the daytime, very large numbers of *Sagitta* sp., while using a net designed for catching plankton 15 to 45 cm above the bottom. The animals supposedly were kept close to the sea-bed, at about 35 m, by the high light intensities prevailing in the upper water layers. BEYER (1958) who used an epibenthic closing dredge in the Oslo Fjord, stated that several common holopelagic species "... can be found in very much higher concentrations in the immediate vicinity of the sea-bed ..." than in the free water. This might have been due in part to the hydrography of the locality where the deepest water may be most favourable for the particular species. In my material from Kiel Bay, there was not a clear trend of numbers of specimens or plankton settling volumes when pump samples taken 1 to 2 m above the sea-bed were compared with those taken 3 to 4 m from the bottom. Many of the lowest samples contained very few specimens of holopelagic animals; others contained considerably more than the next sample above. A relation with the hydrographic factors, including the oxygen content and the pH, was not apparent. Echo sounder observations of pronounced plankton accumulations in layers (Copepoda and Cladocera) in fresh water did not indicate changes of plankton distribution where the layers touched the slope of the beach (SCHRÖDER, 1961).

As a matter of course, plankton hauls near the bottom contain bottom-dwelling animals like Cumacea and Amphipoda. BOSSANYI (1957, with earlier references) noted that in shallow water the night plankton near the sea-bed is very different from that found during the day, and depends on the nature of the bottom. WATKIN (1941), among others, showed for tidal flats, that owing to the nocturnal rise of sublittoral bottom animals into the upper layers, nocturnal tides bring in a plankton quite different from that of the daytime. ELMHIRST (quoted from RICE, 1961) has called these species *tidal migrants*.

The number of observations on the near-bottom plankton from very shallow localities is quite small. Usually, the studies were undertaken in connection with investigations on the benthos. In an abstract on work in a tidally influenced estuary, MARSHALL (1962) points out that the gradients of chlorophyll and diatom cell counts in the last centimeters above the bottom are very steep, and suggests "... that some of the most critical ecological exchanges

which take place in an estuary involve these gradients between the bottom and the overlying waters ...”.

BEYER (1958), like some earlier authors, held that the holoplankton found very close to the sea-bed is a functional member of the benthic community and may form, together with nektonic species, the *hyperbenthic* subdivision of the benthic biocoenosis. In analogy to the terms *endopelos* and *epipelos* of REMANE, he introduced the term *hyperpelos* for the animals living just above the mud. The terms are mentioned here because in situations like that in the Oslo Fjord, holoplankton like *Calanus hyperboreus* can join the community (*tychobenthos*, BEYER, indicating the rather accidental character of the relation). Also, members of groups commonly thought to be pelagic appear to be permanent members of the hyperpelos: BEYER has described a bottom-living Trachymedusa from the Oslo Fjord. Mr. D. M. DAMKAER has advised me that MATTHEWS (1961) collected *Mesaiokeras nanseni* in western Norway with the dredge designed by BEYER. The species "... appears to be a true bottom-living calanoid, probably closely associated with loose detritus on a muddy bottom. In the laboratory, it was observed to swim just over such detritus, into which it burrowed when disturbed ..." (MATTHEWS). Earlier, Clarke (1934b) had observed *Calanopia americana*, a pelagic calanoid, known to perform diurnal migrations, burrowing into mud in the laboratory. The species apparently does the same in its natural environment, in shallow water in Bermuda. Several common pelagic Mediterranean calanoid Copepoda were observed by BERNARD (1961) to be able to take up food from the bottom of aquaria. Also BERNARD suggests that there may be more benthic Calanoidea than previously thought which only make excursions into the pelagic zone.

Recently, observations on zooplankton distribution near the sea-bed became available from deep water. HARTMAN and EMERY (1956) found off southern California that of 138 specimens of Medusae, present on about 5000 film exposures taken between the surface and the sea-bed down to almost 1800 m, 112 occurred within 100 m from the sea-bed. The visual observations from the bathyscaphe dives to the sea-bed at 1000 to 2000 m in the western Mediterranean and off Dakar vary in this respect. An increase in numbers of larger animals is quite frequent, in approximately the last 200 m above the sea-bed (Fig. 1). BERNARD (1958) notes that part of the increase is due to supposedly benthic animals, like Gammaridae and Caprellidae among the Amphipoda, and Polychaeta. On the other hand, during two dives off Toulon to 1040 m and 1350 m, PÉRÈS and PICARD (1956) did not see representatives of *Gnathophausia* among the lophogastrid Mysidae in the last 40 to 50 m above the bottom.

Animals are quite rare in the last few meters above the sea-bed (BERNARD, 1958). This is also emphasized by PÉRÈS (1958a) for the same area, who stated that nekton avoids the last one or two meters above the sea-bed.

According to PÉRÈS (1958b), this holds for Copepoda, *Sagitta*, etc., as well. BROUARDEL and VERNET (1958) have shown, for depths between 100 and 2000 m in this area where the bottom current is slight, that the oxygen content decreases by about 10 per cent in the last one meter or so above the bottom but still is above 50 per cent saturation (see also the measurements of the Swedish Deep Sea Expedition as reproduced by BRUUN, 1957). All observers in the bathyscaphes have described "snow" made up of Radiolaria, filaments of about 50  $\mu$  to 1 cm length, and other small particles, occurring throughout the water column. Because the particles were observed in an illuminated cone at approximately right angles, even small ones were discernible. Near Toulon PÉRÈS and PICARD (1956; see also BERNARD, 1955) reported a decrease in the numbers of these particles in the last few meters, or perhaps even in the last few 10 meters above the bottom, until the last decimeters appeared crystal clear. This was also seen at other places. Perhaps, benthic suspension feeders help to remove particles. On the other hand, TRÉGOUBOFF (1959 and earlier) working off Villefranche-sur-mer, in the western Mediterranean area, known for its relative richness of plankton at the surface, reported quite large amounts of "microplankton" in the bottom layer. After discussing the visibility of particles near the sea bottom (PÉRÈS and PICARD, 1956), PÉRÈS (1958b) has considered his earlier observations as erroneous. Certainly, there is no uniformity of the near-bottom particle content, as also seen from the measurements of Tyndall-scattering in samples taken in the tropical deep-sea at about 4, 10, 16, 25 and 150 m above the sea-bed (JERLOV, 1953). There is almost always a strong optical layering present, the scattering more often than not increasing toward the bottom. Of course, the conditions for particle suspension in the very bottom layer can differ, and the plankton distribution is not necessarily affected by increases of those particles (whirled-up sediment) which contribute most to the scattering measured.

For studying the nanoplankton distribution near the sea-bed of the South Atlantic between 2150 and 5700 m, HENTSCHEL (1936) had at his disposal ten samples, either from the water above the sediment of a corer sample, or from SIGSBEE water bottles attached above the corers. However, the variations in cell counts were too large to permit a conclusion as to whether or not the plankton content immediately above the bottom is usually different from that of the free water.

#### d. *Seasonal and Ontogenetic Vertical Movements*

In section IIa2, reference has already been made to vertical movements other than diurnal migrations and passive transport by water. These movements are frequently called seasonal migrations, although they very often are intimately connected with the life cycles of individuals. However, ontogenetic

migration of annual species cannot be well separated from seasonal vertical movements. Probably, only a few of these vertical movements can be considered as migrations in the strict sense. Usually, we are concerned with "... more probably a gradual upward drift of the optimum distribution level with the seasonal ..." or ontogenetic "... change, rather than an active, oriented, and persistent directional swimming ..." (BAINBRIDGE, 1961).

Earlier studies have been mentioned by RUSSELL (1927). New observations may be discussed only for the widely known examples of "overwintering" of Copepoda of temperate and higher latitudes in depths of several hundred meters, even below 1000 m. Reference is made to the study of the zooplankton at weathership "M" in the Norwegian Sea by ØSTVEDT (1955) and to the monograph on *Calanus finmarchicus* by MARSHALL and ORR (1955). It appears that temperature and light, the most obvious seasonally changing environmental factors at the surface, are not the reason for the onset of migrations of *C. finmarchicus* and other Copepoda, particularly of the upward migration in early spring. MARSHALL and ORR point out that in *C. finmarchicus*, the moulting of stage V into the adults begins at depth in both the Clyde Fjord (about 56°N) and in East Greenland (at about 71°N) in December to January. Upward movements follow. It is difficult to understand how the animals should recognize seasons at great depths, and it seems probable that the onset of moulting and upward migration is internally regulated. The term *ontogenetic migration* is applicable.

For *Calanus hyperboreus*, CONOVER (1962) has presented respiration measurements in relation to the life cycle and has shown that profound metabolic changes accompany the migration. In the north-western North Atlantic, the species stays at the surface about three months where development to stages IV and V takes place during the time of phytoplankton growth. The rest of the year is spent at a depth of about 200 m or more where the food supply must be limited; the animals presumably depend mostly on their stored fat. This is possible because the respiration rate is reduced seasonally by two-thirds when food becomes scarce. It was shown that this is not related to temperature, but is a true adaptation.

The widespread change of depth ranges for occurrence of developmental stages of meso- and bathypelagic animals is generally taken as a step in the life history of the species, and not as a response to seasons. A reviewing table has been compiled by VINOGRADOV (1959b; see also MARSHALL, 1954). Active as well as passive vertical movements may be involved. In the greater number of species investigated, the young stages live in upper layers, or even near the surface. BERTELSEN (1951) has pointed out that among ceratioid fishes, which presumably live several years, rising from about 2000 m to the depth of spawning, and the occurrence of larvae in the upper layers, is seasonal (also, RASS, 1959). Again, it is difficult to see how the animals could

recognize a change of seasons at these depths, except by a seasonal change in food supply. Observations to this effect are not yet available. Seasonal food supply may be absent under the tropical oceans but is to be expected below temperate and polar seas with their pronounced seasonal production of phytoplankton and zooplankton at the surface. Benthic abyssal species seem to breed at any time of the year (MADSEN, 1961).

Conversely, there are species living as adults in the upper layers which spawn or undergo some development at depth. HAECKER (1906), when discussing reproduction in the Challengeridae among the Radiolaria, pointed out that about a dozen individuals with two nuclei or with two central capsules were found by the *Valdivia*. Apparently dividing, they occurred at great depths, whereas at smaller depths, members of the same species have only one nucleus. The larva of *Veleva*, a pleustonic Siphonophore, sinks to about 1000 m as reported by WOLTERECK; for *Pyrosoma*, sinking of juvenile stages to great depth has been tentatively suggested (both observations quoted from STEUER, 1910). Larvae of pelagic Decapoda sinking up to 4000 m have been reported in 1951 by BERNARD (quoted from VINOGRADOV, 1959b). DAVID (1958) has shown that species of Chaetognatha, important in the upper layers in the Antarctic, migrate to below 750 m, and even 1000 m for spawning. This is not so with *Sagitta scrippsi*, a predominantly mesopelagic species from the Pacific. Young stages are mostly found in the upper 100 m (ALVARIÑO, 1962). HEINRICH (1962a) mentions for the small-sized race of *Calanus plumchrus* living in the Bering Sea and off southern Kamchatka that it spawns at depths greater than 200 m; the growth of the species occurs at the surface.

Seasonal and ontogenetic migrations may be important to animal biogeography. In the Antarctic, west of Drake Strait, two species of Copepoda and one Chaetognatha species contribute much more than half of the biomass caught by nets in the upper 1000 m. MACINTOSH (1937) stressed the role of seasonal vertical migration in maintaining the distribution area of these species in the Antarctic. Because the drift of the Antarctic surface layers has a northward component, whereas the drift of the water below has a strong southerly component, seasonal downward migration to a few hundred meters was thought to hinder transport out of the area of distribution. Without denying the beneficial effect of this type of animal navigation, I believe that a small seeding stock should be maintained even for non-migrating plankton bound to the surface layer, including phytoplankton. The species listed by MACINTOSH as Group III may be taken as examples for the Antarctic Ocean. The distribution area of a pelagic species is always large enough to allow for more than a strictly one-directional current system, so that maintenance is accomplished by semi-enclosed circulation in a horizontal plane. Certainly, the proposed mechanism would be more important for zooplankton species with a slow reproductive rate than for the phytoplankton.

An example showing the role of ontogenetic migrations for the geographic distribution of species has been given by THORE (1949). The adults of the pelagic cephalopod *Japetella diaphana* live in the bathypelagic and upper abyssopelagic regions, but the geographic distribution can be best described by the 10°C isotherm at 200 m. The species is particularly frequent in the regions circumscribed by the 10 and 15°C isotherms at this depth. The young are found only in, and just below, the tropical discontinuity layer, and THORE suggests that the geographic distribution of the species is determined predominantly by temperature which governs the distribution of the young stages in the mesopelagic region.

Seasonal downward migration, and reappearance of a fairly large number of grazers, has an important bearing on the annual cycle of the phytoplankton (BEKLEMISHEV, 1957; HEINRICH, 1961a, 1962a; STEEMANN NIELSEN, 1962). In higher latitudes, the beginning of phytoplankton development in spring is governed by the mean illumination in the mixed layer, and varies from year to year with the weather. The authors show that the timing of phytoplankton development in relation to the appearance of a sizeable crop of grazers determines whether or not a phytoplankton bloom will occur. For *Calanus finmarchicus*, the main grazer in the temperate and subarctic North Atlantic, the onset of breeding and number of eggs produced depend on the amount of food available. STEEMANN NIELSEN notes that during some years, the final stabilization of the water column is preceded by a period of changing conditions, with small pulses of phytoplankton development interrupted by heavy mixing (see observations by RYTHER and HULBURT, 1960). In these years, the zooplankton stock can begin to increase early, and after the final stabilization the phytoplankton will not really "bloom" because too many grazers are already present. As a result, the production process will be more balanced. There are also regular latitudinal variations of the upward migration of *C. finmarchicus* which may modify the classical picture of annual phytoplankton distribution. HEINRICH (1962a) points out that in other oceans, the dominant grazers can reproduce independently of the phytoplankton, using their fat reserves, as is the case with *Calanus cristatus* and *C. plumchrus* of the temperate North Pacific and parts of the Bering Sea. The species live as adults at depths greater than 200 m, exhibit limited diurnal migrations only, do not feed and reproduce in winter. The offspring, which grazes on phytoplankton, is in the early copepodid stages and near the surface when the abiotic environment becomes favorable for the phytoplankton. *Eucalanus bungii*, the third important species, spends the winter in the later copepodid stages. Consequently, the phytoplankton in that area normally does not reach a marked peak in spring; a slightly higher standing stock of algae may occur in fall when the effective grazers have left the surface layers.

For the subarctic North Pacific, it may be noted that owing to the halocline at 100 m or somewhat deeper, the mixed layer never becomes as deep as in the North Atlantic. Therefore, at the same latitude, the light conditions can rarely, if ever, become so unfavorable for the phytoplankton as in the North Atlantic, as pointed out by STEEMANN NIELSEN (1962). The nauplii of the winter-breeders find food prior to the time the "spring bloom" is due, and can grow early to an effective age. Thus, in the North Pacific during winter and spring, abiotic and biotic factors both tend to suppress the spring bloom of phytoplankton.

For the Bering Sea, HEINRICH (1962b) has shown that a balanced phytoplankton production due to grazing being distributed evenly through the year leads to considerably higher annual zooplankton production in the upper 500 m than is found with a seasonally unbalanced phytoplankton production of the same size. As a result of the greater importance of active transport of particulate organic matter into the deep-sea, over passive sinking (section IIe, p. 88), one would expect a relatively large biomass in the deep-sea under an area with balanced plant distribution but no observations are yet available.

Seasonal and ontogenetic migrations to deep water transport organic matter downwards. Estimates of the importance of this mechanism can be made for 1950-1951 for the layer of 600 to 2000 m at weather ship "M" in the Norwegian Sea based on observations by WIBORG (1954) which were used by BEYER (1962). For the Subantarctic and Antarctic regions (the seas north and south, respectively, of the Antarctic Convergence), the data of FOXTON (1956) give information for the layers between 500 and 750 m, and 750 and 1000 m. The observations relate to volumes of net zooplankton exclusive of larger animals like Medusae, Salpae, etc. (According to a personal communication from Mr. F. BEYER, Chaetognatha also were not included in WIBORG's data). At weather ship "M", the ratio between the highest and lowest monthly means is about 3:1. Copepoda contribute about one-third of the volumes in both cases. In the Subantarctic, the corresponding ratios for both depth intervals are 2:1 to 3:1 and in the Antarctic 3:1 to 4:1. Instead of monthly means, BEYER (1962) has given individual observations for weather ship "M" for 1948-1949, made under the direction of ØSTVEDT (1955). They indicate that the above estimates may be crude.

BEYER (1962) has pointed out that in crustacean plankton, the consideration of volumes as representative of annual distribution of the organic matter may be misleading even in the same species because growth and increase in organic matter content are not parallel. The animals increase their volume ("grow") by uptake of water immediately after moulting and add organic matter between moults. BEYER maintained that the constancy of zooplankton volume, when taking the whole water column into account (as reported by FOXTON, 1956, and others), was at least partly due to this effect. Also, the mesh size used for collection must have led to dampening of seasonal fluctuations of biomass because the juvenile stages of small species can be missed although the adults are retained. However, I believe that the ratios for deeper layers given in the preceding paragraph can only be slightly affected by these errors. Most juvenile stages are found at the surface only, and the maximum and minimum monthly means fall presumably at the beginning of, and the time after, the stay of the overwintering population at depth. Apparent growth by water uptake would have taken place between these dates.

e. *Vertical Distribution of Biomass in Deep Water*

The early work on zooplankton in the deep ocean was dominated by describing species and outlining the depths of their occurrence. For understanding the distribution of organic matter in the oceans and its relation to the inorganic environment, knowledge about the amount, size composition, and turnover rates of particulate organic matter including the living fraction is required. Information about zooplankton growth and decay rates are extremely scarce, and the discussion must be restricted to the vertical distribution of the standing stock.

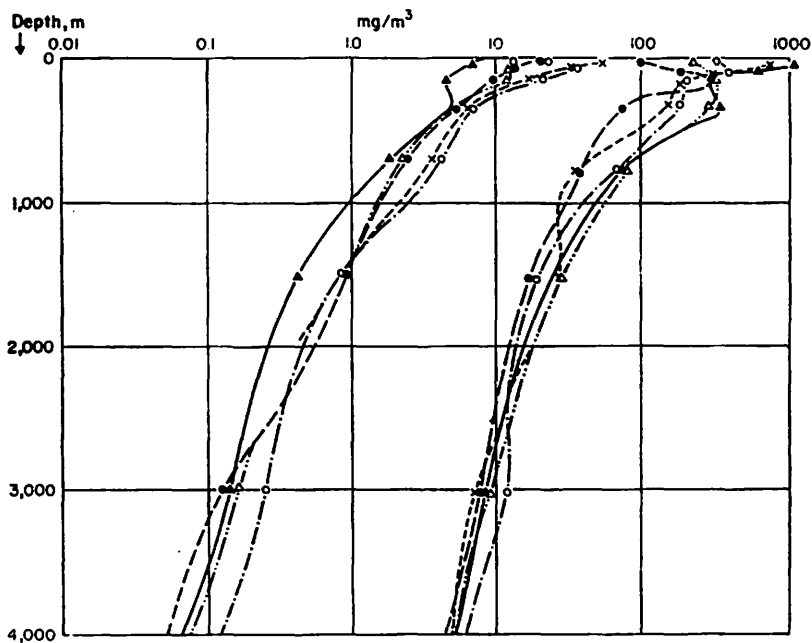


FIG. 4. Vertical distribution of net plankton biomass (wet weight) in the Pacific, from divided hauls. The right family of curves is for stations off the Kurile Islands. The left family is for tropical stations (---●--- = average of two stations). (Modified from VINOGRADOV, 1961a).

Generally, the amount of the plankton retained by nets decreases with depth, but large deviations from this trend may be found in the upper water layers. On the average, however, the biomass in the western North Pacific (May to October) and tropical Pacific has been found to decrease from the surface to 1000 m by 1 to 1½ orders of magnitude, and from 1000 to 4000 m by another order of magnitude (VINOGRADOV, 1960, 1961a; Fig. 4). In the North Indian Ocean, about the same amounts of plankton as in the tropical Pacific are found (VINOGRADOV, 1962a). The biomass of the deep-sea plankton

is high where the surface plankton is rich, and low where the latter is poor. At the same depth, the biomass in the tropics is 1 to  $1\frac{1}{2}$  orders of magnitude smaller than in the subarctic Pacific; in the tropics, the decrease towards depth may be slightly more rapid than in the higher latitudes. The biomass of net plankton in Pacific deep-sea trenches also seems to reflect changes of plankton abundance in the surface layers, so that in trenches in lower latitudes very little plankton is found (VINOGRADOV, 1961a). This differs from the situation with the benthic biomass at the greatest depths, which primarily reflects the distance of the trench from the shore (see table on p. 126 in BELYAEV and SOKOLOVA, 1960).

Values on net zooplankton biomass from the North Atlantic south of  $43^{\circ}\text{N}$ , collected from August to November, have been published by JASHNOV (1961b). Even though nets of different mesh size were used, which apparently does not matter too much in this size range,\* the Atlantic data are fairly close (roughly within 100 per cent) to those from the Pacific. During summer, BRODSKY and VINOGRADOV (1957) have found about the same amount, or slightly less, of plankton as in the north-west Pacific, in the upper 500 m of the Indian sector of the Antarctic Ocean. The data of JASHNOV (1961b), and of MENZEL and RYTHER (1961) for autumn in the Sargasso Sea are also rather close. Particularly for deeper ocean water, Fig. 4 may thus give a fairly general picture of zooplankton biomass retained by nets of medium mesh size, hauled vertically with 0.5 to 1 m/sec speed.

For the higher latitudes, the discussed observations do not cover the winter, or may be restricted even more seasonally. The investigations by BSHARAH (1957) in the Florida Current, McALLISTER (1961) in the subarctic Pacific, and by WIBORG and ØSTVEDT in the Norwegian Sea (as figured by BEYER, 1962), show for the upper 1000 m that the seasonal change at a given depth can be considerable (see also previous section, p. 81). In the Subantarctic and Antarctic regions, FOXTON (1956) found the maximum of net plankton during winter below 500 m depth. In all observations, however, the maximal and minimal amount of plankton collected at one depth differed less than one order of magnitude, except in the very surface layer, and less than half an order of magnitude below 500 m (with the exception of observations during June 1949 in the Norwegian Sea, BEYER, 1962). Thus, global

\* The nets employed by JASHNOV had 38 strands/cm (slightly less than 0.2 mm mesh aperture), whereas in the Pacific and in the Indian Oceans, nets with 15 strands/cm (approximately 0.5 mm mesh aperture) had been used. VINOGRADOV (1961a) found in tropical waters that the finer net collected 1.5 to 1.8 times more biomass than did the net with coarser gauze. According to a comparison between nets with about 0.37 mm and 0.24 mm mesh aperture in the Sargasso Sea, the difference can be even smaller (MENZEL and RYTHER, 1961). By comparing the catches by oblique hauls from 200 m to the surface on three stations in the central tropical Pacific, KING and HIDA (1957) found that a net with a mesh aperture of 0.31 mm yielded  $1\frac{1}{2}$  to  $1\frac{3}{4}$  times as much plankton volume as the same net with a mesh aperture of 0.65 mm.

differences are not obscured by seasonal changes, although locally the vertical pattern of distribution can change considerably.

Other anomalies of vertical distribution may be mentioned: JESPERSEN (1935) in the Gulf of Panama, and LEAVITT (1938) in the western North Atlantic, also found subsurface maxima for the large net plankton. The maximum observed by LEAVITT occurred at about 800 m, and might correspond to the accumulation apparent at 700 m in the mean annual distribution as given by BSHARAH (1957). A marked secondary minimum layer of net plankton is present throughout the year in the cold water at the top of the halocline, in depths of 100 to 200 m, in the subarctic Pacific (BOGOROV and VINOGRADOV, 1955; MCALLISTER, 1961). This is true for the Bering Sea and Sea of Okhotsk as well (BRODSKY, 1955).

It is not known how much of the total heterotrophic biomass (Metazoa, Protozoa, Bacteria and Fungi) is represented by the zooplankton caught with nets of roughly 0.5 mm mesh aperture. On the average, the numbers of nanoplankton specimens (which far below the euphotic zone are chiefly animals) seem to decline with depth in a manner similar to the net plankton. Following LOHMANN, HENTSCHEL (1936) found that in the great depths of the South and Equatorial Atlantic, the nanoplankton distribution reflects the surface distribution pattern, rather than being related to the currents of the deep-sea. Relatively high values occur at depth where the surface concentrations are high. According to HENTSCHEL, the presence of currents, or the occurrence of Intermediate Water, only modify, but do not basically change, the distribution at depth. This is also indicated by the distribution in sediments of pelagic constituents like diatom frustules, which are not very conspicuous far beyond the limits of heavy growth of pelagic diatoms at the surface. Away from the land, the amount of bottom fauna is by and large rich where the surface productivity is high, and poor where the latter is low (ZENKEVITCH *et al.*, 1960).

The net plankton values discussed above may be compared with the amount of particulate matter, containing protein which is obtained by filtering a few liters of water through filters of less than 1  $\mu$  pore diameter. A similar comparison for surface waters had been presented by BANSE (1962). It was shown that nets of about 0.33 mm mesh aperture retain amounts of protein ranging from one-thirtieth to the same as that collected by fine filters. It is not known how much of the fraction lost by nets is living matter. SUSHCHENYA (1961) demonstrated for surface waters of the south-western Black Sea and the Aegean and Ionian Seas that, on the average, the dry weight of net zooplankton is one-fourteenth to one-seventeenth per cent of the ash-free, oxidizable particulate matter. Assuming a low chlorophyll content of about 1 per cent of the organic matter of phytoplankton, I estimate that the plants contributed one-quarter to one-half of the organic matter not retained by the nets.

The averages of net plankton collections on the seven stations of VINOGRADOV (1960) near the Kurile Islands (44° to 49°N, 149° to 159°E, May to October) as given in the right part of Fig. 4 are compared with collections of particulate matter by MCALLISTER *et al.* (1959; 50°N, 145°W, July and August) and by PARSONS and STRICKLAND (1962; 49° to 51°N, 133° to 145°W, July and August). The data (Table 1) have been expressed as protein (albumen equivalents) by means of the analyses of KREY (1958). In the Gulf of Alaska a consideration of the carbon content would be biased by the cellulose

TABLE 1. COMPARISON OF NET PLANKTON AND SUSPENDED MATTER CONTAINING PROTEIN IN THE NORTH PACIFIC AND NORTH ATLANTIC OCEANS (in mg/m<sup>3</sup> protein)\*

m	100	200	300	400	500	1000	1400	1500	2000
VINOGRADOV (net plankton)	-12.4-   — 10.8 —   —2.8—   —1.0—								
MCALLISTER <i>et al.</i>	48 <sub>2</sub>	38 <sub>2</sub>	34 <sub>2</sub>	—	—	—	—	—	—
PARSONS and STRICKLAND	—	—	60 <sub>1</sub>	—	73 <sub>2</sub>	—	—	54 <sub>3</sub>	—
KREY	10 <sub>28</sub>	9 <sub>17</sub>	10 <sub>7</sub>	7 <sub>7</sub>	7 <sub>4</sub>	—	6 <sub>10</sub>	—	—

\* The biomass of net plankton as given by VINOGRADOV is converted into protein (albumen equivalents) by using the factors of KREY (1958): dry weight, 14 per cent of wet weight; organic matter, 92 per cent of dry weight; albumen equivalents, 37 per cent of organic matter. Because MCALLISTER *et al.* (1959) standardized their measurements against egg albumen, their values are used as reported whereas the data of PARSONS and STRICKLAND (1962) have been reduced taking the albumen equivalents as 60 per cent of 6.25 times the nitrogen content found by the KJELDAHL method (KREY, 1958). From pigment analyses, interference by plant matter is estimated to be of the order of 10 to 20 per cent of protein in the upper layers. Subscripts give the number of samples.

fibers present also at depth (MCALLISTER *et al.*, 1960). The size ranges collected by nets and water bottles do not overlap because MCALLISTER *et al.* strained the water sample through a net with 0.15 mm mesh aperture in order to remove large animals.

It is seen from Table 1 that in the subarctic Pacific, the net plankton contributes little to the total suspended protein. The difference is not likely to be due to the loss of small Metazoa: In the South Atlantic below 700 m, HENTSCHEL (1932) usually took nanoplankton samples of 0.5 l. The number of Metazoa was one or two, if any were present. Assuming that these were of a size which could slip through meshes of 0.5 mm aperture (nauplii of Copepoda, stage I copepodids of small genera such as *Pseudocalanus*, or older stages of *Oithona* spp.) they would each contribute 0.2 or maximal 0.3 µg/l.

protein when the wet weights given by BOGOROV (1957) are converted by the factors of KREY (1958).

The difference between net plankton and total protein may be due in part to the loss of true nanoplankton, but the available data indicate that there may be less nanoplankton than net plankton in the deep layers. For the tropical Indian Ocean, BERNARD and LECAL (1960) have estimated the volume of nanoplankton at a depth of 1000 m to be about 0.5 mm<sup>3</sup>/l. which roughly corresponds to 0.5 mg/l. biomass. This is one-tenth to one-quarter of the net zooplankton found by VINOGRADOV (1962a) in approximately the same area. From the values reported by HENTSCHEL (1932) for all latitudes of the South Atlantic, it would appear that the biomass of the nanoplankton may be very low and insignificant at great depth, as compared to the net plankton. It may be noted that for depths of several hundred meters in the area off West Africa, the nanoplankton figures reported by HENTSCHEL for February–March are about 10<sup>3</sup> times smaller than those found by BERNARD (quoted from BERNARD and LECAL, 1960) during June. Farther north, the time of pronounced upwelling near the African coast is in the spring and summer (SCHOTT, 1935; WOOSTER and REID, 1963), and the difference may be entirely due to seasonal effects. The biomass of bacteria and other heterotrophic micro-organisms near the Kurile Islands during the summer, below 100 m is so small (KRISS, 1959, Table 95) that it contributes far less than 1 µg/l. protein. Thus, it might be that the difference between net zooplankton and total protein at depth in the subarctic Pacific is due to a large loss of protein-containing detritus.

In Table 1, unpublished data from the northern Atlantic (40° to 55°N, 25° to 50°W, March to May, filters of 1–2 µ pore-size) are added which have been kindly sent by Prof. J. KREY. The protein content found in small water samples from the Atlantic is much lower than that reported from the subarctic Pacific, even though the large plankton had not been strained off. Because the difference in pore size of the filters is so small that only very fine detritus can have been lost, no satisfactory explanation can be given. It was indicated earlier that the zooplankton data of VINOGRADOV as given in Fig. 4 and Table 1 should be fairly representative for all oceans. Most of the zooplankton data of JASHNOV (1961b) have been collected farther south in the Atlantic, so that a comparison with the observations of KREY does not seem justified. The amounts of plankton collected by LEAVITT (1938) are very small owing to the mesh size of the nets, so they too cannot be used for the present purpose. In the example from the Atlantic there seems to be only a moderate loss of particulate protein by the nets used. Because of the different chemical methods employed, I feel that a conclusion on the relation between net zooplankton and total suspended protein, or on differences between oceans in this respect, is not warranted at present. It is clear, though, that

below 100 m the total organic particulate matter decreases with depth much slower than do net zooplankton, nanoplankton and bacteria. The problem of the vertical distribution of the total community should be kept in mind.

The size composition of the biomass is of great interest when studying the nutrition of deep-sea plankton. The geographical distribution of net plankton and of benthic animals in the deep-sea, away from the continents, indicates that the main source of food material is autotrophic production at the surface, and the zooplankton living from it. It does not seem likely that the main food source for the nutrition of the deep-sea zooplankton, and the zoobenthos as well, is the heterotrophic production from dissolved organic matter in the water, although PARSONS and STRICKLAND (1961) suggested that the contribution may be sizeable. The examples of secondary maxima of bacterial biomass at depth given by KRISS (1959) show that, in this respect, there is a certain autonomy of the deeper layers. If, however, the net zooplankton and the bottom fauna did not depend directly on the surface production, their meridional distribution would be difficult to understand. By and large, their biomass in the open ocean is high where the surface production is high, and vice versa. On the other hand, the dissolved organic matter in the deep-sea has so far not been shown to be distributed horizontally according to the primary production at the surface. KROGH (1934) pointed out that the amount of dissolved organic matter in the sea is so large, as compared with the annual primary production, that it must be distributed fairly evenly throughout the ocean, similar to a conservative property. New figures indicate an organic matter content corresponding to about  $1 \text{ g C/m}^3$ , or slightly less, and an annual gross production of phytoplankton of  $100 \text{ g C/m}^2$  or less. Assuming that 10 per cent of the latter goes into solution, which may be a high estimate, and taking the average depth of the oceans of almost 4000 m into account, it is seen that 400 yr would be needed to accumulate the dissolved organic carbon present even if there were no decay. In view of decay, 4000 yr seem a more realistic estimate. Therefore, it is not likely that the dissolved organic matter content in the deep-sea is markedly higher below areas of high production near the surface even if there is vertical convection in winter. The fact, that there is so much more net plankton, and also zoobenthos, below these areas can be understood only if this life depends directly on the surface production. It appears likely at present, that the active downward transport of organic matter by migrating animals is a major food source for the deep-sea as pointed out by VINOGRADOV (1962b, and earlier).

To judge from the cell counts in the Atlantic (HENTSCHEL, 1932), the nanoplankton at depth may not contribute much to the nutrition of the larger zooplankton, although BERNARD and collaborators have found quite sizeable

nanoplankton volumes in the Mediterranean and other areas (BERNARD and LECAL, 1960), as pointed out on p.86. It may be noted also that HAECKER (1904) stated that the large Radiolaria living between 2000 and 5000 m are often filled with diatom shells, although the closing nets very rarely contain diatoms with plasma below 600 m. Recently BEKLEMISHEV (1961) reported from the eastern North Pacific that some protoplasm is still present in algae collected between 2000 and 3000 m depth (pill-box shaped diatoms of the genus *Ethmodiscus* which can be larger than 1 mm, and cells of *Halosphaera* of the Heterocontae which often have a diameter  $>0.1$  mm). He stated, however, that epipelagic Foraminifera and Pteropoda have no protoplasm at depths of 500 to 1000 m. VINOGRADOV (1961b) reported the same for *Ethmodiscus rex* and for Pteropoda from the Indian Ocean. Further, KROGH (1934) found in the *Challenger* narrative the remark "... that deep-sea sponges are often filled with diatoms and radiolarians, although the bottom at these stations was not a diatom or a radiolarian ooze ..."; he says, however, that "... even in the face of this statement I find it very hard to believe that sufficient food in the shape of micro-organisms can arrive directly from above".

The suspended bacteria of the deep-sea are not likely to be accessible to the pelagic filter feeders among the Crustacea because of their small size, although they may be eaten by Protozoa, Salpae, and Appendicularia. This seems to be true also for much of the detritus, although nothing definite is known about its size. Recent observations in the upper layers, down to 200 m, show that some of the detritus may occur as very loose aggregates, like snow flakes, of more than 1 mm diameter (NISHIZAWA and RILEY, 1962). As a consequence of the scarcity or unavailability of small food particles, the relative importance of pelagic filter feeders at depth decreases in favor of carnivorous species (VINOGRADOV, 1962b). In that review, VINOGRADOV again emphasized that the main source of food for the deep-sea far from the continents cannot be the sinking of surface plankton (nor of zooplankton feces), but must be the active downward transport by vertically migrating animals. VINOGRADOV mentioned a number of species which graze in the surface layers and return daily to depths of 2000 m and more. They represent the majority of the filter feeders at those depths. In addition, non-diurnal movements like ontogenetic migrations supply food to the deep-sea. BRUUN (1957) has suggested that between about 2000 and 6000 m there may be less than a full link in the food chain, because these layers are so thinly populated. This would result in a very efficient downward transport, but nothing definite is known. MENZIES (1962), on the other hand, favored sinking of dead plankton over active transport. VINOGRADOV (1959b) stated that vertical movements beyond 6000 m, that is into the trenches, have not yet been observed.

BEKLEMISHEV (1960, also VINOGRADOV, 1961a) has stressed the importance of the lateral transport of food by the Intermediate and Bottom Waters. He has used slightly higher catches of net plankton in intermediate layers as evidence for retention of organic matter, in the form of zooplankton, over several thousand kilometers. He has pointed out, however, that the layers are poorly explored, due in part to the prevailing use of vertical hauls at standard depths. Long periods of transport would be involved. In the absence of full species lists, I speculate that a very far-reaching influence of lateral transport may be felt, not so much in the amount of total biomass but in the species composition. If these species happen to be fairly large, the change in species composition may lead, in the Intermediate Waters, to an increase of the net plankton biomass, but does not necessarily reflect an increase of the total. BEKLEMISCHEV (1960) has given two examples for the bearing of water mass distribution on species distribution (see also p. 59). It may be noted that HENTSCHEL (1936) found in the Antarctic Intermediate Water of the Atlantic south of the equator, a slight decrease of nanoplankton relative to the average distribution, and not an increase.

#### f. *Vertical Divisions of the Pelagic Domain*

When more data on the vertical distribution of pelagic organisms have been collected than are available now, and a better understanding of the reasons for the distribution patterns has been achieved, the recognition of natural divisions of the water column of the oceans may be facilitated. There is not yet universal agreement on this point. Recent schemes have been explained by BRUUN (1957), HEDGPETH (1957a) and VINOGRADOVA *et al.* (1959, with a tabulation of previous attempts). BRUUN has used the distribution of temperature for dividing the realm below the *epipelagic* zone; this zone is essentially lighted and produces food. Neglecting the trenches for a moment, BRUUN distinguishes the *mesopelagic*, *bathypelagic* and *abyssopelagic* zones. The mesopelagic zone is the region above the 10°C isotherm, and thus in and above the main discontinuity layer of the tropical and subtropical oceans. The term bathypelagic is used in a narrower sense than by previous authors and refers to the zone between the 10 and 4°C isotherms. The latter isotherm was chosen because it was known that true deep-sea benthic animals usually do not occur above it. The abyssopelagic zone, or the deep-sea proper, reaches down to about 6000 m. The transition to the abyssopelagic zone is put by many workers at about 2000 m although BRUUN, when using the 4°C isotherm, pointed out that much argument about the depth of the transition may be due to the fact that this isotherm is found at 1500 or even 1000 m in certain areas, particularly in the Indian and Pacific Oceans. Many divergent opinions about the subdivisions of the upper 1000 m, as well, are the results

of varied experiences from different areas, and the coarse partitioning of the water column by divided hauls over a great vertical range. Most scientists, though, agree that the upper 200 m should be kept separate from the rest. On the other hand, the study of the Pacific Euphausiidae by BRINTON (1962) shows that the division is not satisfactory for these strongly migrating animals: the vertical distribution of apparently epipelagic species reaches deep into the mesopelagic zone, down to about 700 m in the subtropical gyres.

The meso- and bathypelagic zones do not yet seem to be clearly distinguishable from each other. In the waters of the Kurile area, Copepoda dominate the net plankton in terms of biomass in both zones, i.e. in the upper 2000 m. Owing to diurnal vertical migrations (Deep Scattering Layer), and seasonal migrations, the connection of both with the epipelagic zone is marked. Diurnally migrating mesopelagic and bathypelagic animals (Myctophidae among the fishes, squids and Crustacea, in particular Amphipoda) can constitute a sizeable part of the food of cod and salmon in the upper layers (ANDRIEVSKAYA and MEDNIKOV, 1956; MEDNIKOV, 1958); one myctophid species alone was reported to contribute 20–23 per cent of salmon food. Off Japan, Myctophidae can constitute up to 80 per cent of the food of seals (RASS, 1959). The relative importance of transparent species declines in the mesopelagic zone due to an increasing number of reddish or dark and even black species. The depth of appearance of the latter forms is greater in clear water like the Sargasso Sea, than in less transparent water as found by HJORT (in MURRAY and HJORT, 1912; also EKMAN, 1953). Animal luminescence is very common in the mesopelagic and bathypelagic zones, whereas it is quite rare below 2500 m (GÜNTHER and DECKERT, 1950). KRAMP (1957) has listed seven Anthomedusae, mostly from the Atlantic, as predominantly bathypelagic (including the mesopelagic zone) which indicates that there is meroplankton in these layers.

In the abyssopelagic zone, Chaethognatha, Decapoda and Mysidae seem to be more important than Copepoda. Reddish and orange colored animals dominate but more and more whitish species occur (VINOGRADOVA *et al.*, 1959). Even this zone is biologically connected with the surface layers, not only by diurnal migrations of a few species but also by ontogenetic migrations of a number of species (see section II d).

The Mediterranean, the Red Sea, the Sea of Japan, the Arctic Ocean, and other smaller deep basins present special situations or even lack a deep-sea fauna proper owing to high submarine sills which separate them from the deep-sea of the open ocean, causing a peculiar hydrography.

Agreement seems to prevail on the separation of the pelagic fauna of the trenches, below about 6000 m, from the abyssopelagic fauna. The terms *ultra-abyssopelagic* or *hadopelagic* fauna have been proposed which correspond to the ultra-abyssal, or hadal community of the benthic domain

(WOLFF, 1960). Endemic Copepoda and Amphipoda have been described. Little is known about common biological characters of the plankton at these depths. The animals are whitish (VINOGRADOVA *et al.*, 1959). Exchange by vertical migrations with the pelagic fauna above has not been observed so far. It may be interesting to investigate what the vitamin D content of hadal animals is. The vitamin should originate close to the surface.

The picture presented is not completely satisfactory. BRUUN had based his classification on the situation in the tropical ocean. Particularly in the upper layers, other climatic belts may deviate from this situation, and even within one climatic belt, a scheme may be modified by variations in physical oceanography, like varying depths or thickness of intermediate water layers. A classification on biological grounds may be more convincing than using temperature or depth alone as pointed out by EKMAN (1953) and others, although temperature is of enormous importance in regulating the distribution of marine organisms. Also the benthic domain can now be divided on the basis of species distribution (VINOGRADOVA, 1958, quoted from VINOGRADOVA, 1961) as it is practised in animal geography. Preferably, biological typology of the oceans should be based on several groups of organisms; ideally, it should not be based on species but on ecological units (HEDGPETH, 1957b).

New data have confirmed previous observations mostly from temperate and polar seas (see MURRAY and HJORT, 1912; EKMAN, 1953) that the greatest number of pelagic species does not occur at the surface but at depth. In the north-western North Pacific, the number of about 1000 known species at 2000 to 3000 m depth is about three times that at the surface, contrary to the situation on the sea-bed (ZENKEVICH and BIRSTEIN, 1956). The amount of plankton at these depths is only 1 to 10 per cent of that found at the surface (Fig. 4, p. 82), presumably due to the scarcity of food. Although the tropical surface layers are much richer in species than temperate and polar waters, a subsurface maximum still seems to be present (MURRAY and HJORT, 1912; SEWELL, 1948). It seems surprising that there should be more ecological niches below the photic zone even though the abiotic environment becomes quite stable and probably less diversified. It may be noted that the importance of carnivorous species in the plankton increases greatly with depth (VINOGRADOV, 1962b); comparing temperate with tropical surface waters, an increase in total number and in relative importance of carnivorous species in the tropics is noticed as well. Greater climatic stability over the ages is regarded by FISCHER (1960) as the main reason for the high number of species in the tropics, including the pelagic domain. One may speculate whether the lower bathypelagial and the upper abyssal also are geologically more stable habitats, that is, older than the temperate surface waters (see also ZENKEVICH, quoted from HEDGPETH, 1957b). Age must more than balance the trend to

slow evolution in the deep-sea due to stability of environment and lack of isolation (save by distance). The problem has been briefly treated by CARTER (1961). Commenting on the large number of species, FRIEDRICH (1955) had already suggested that for the deeper layers and the tropical epipelagic region, biological factors like competition must be most important for selection and evolution because of the small fluctuations in the abiotic environment. Concerning the great number of pelagic organisms in general, HUTCHINSON (1961) may be consulted.

It is useful to keep in mind that species are not equally abundant. COE (1946) has listed striking examples for the great numerical dominance of very few species between 1000 and 2000 m near Bermuda where very many net hauls had been made under the direction of BEEBE. This point was well documented for fresh water zooplankton by PENNAK (1957). Marine data for the dominance of a few species in terms of biomass have been given on p. 58, where the bearing of this fact on interspecific competition was pointed out. Further examples of mutual vertical exclusion of related species can be found in the discussion of biogeography in deep water by MARSHALL (1954). Other ways of reducing competition in the deeper layers may be specialization in prey, differences in diurnal migrations, or presence or absence of ontogenetic vertical movements. Very little is known about seasonal fluctuations of abundance in water below 1000 m because deep-sea research is usually done along itineraries of expeditions, and stations are not revisited.

### III. DIURNAL VERTICAL MIGRATIONS OF HOLOPELAGIC ANIMALS

#### a. *Vertical Range and Occurrence*

Diurnal vertical migration occurs in all phyla with planktonic representatives and has received much attention. Early observations were reviewed by RUSSELL (1927). Recently, data on the migration of deep-sea zooplankton were summarized by VINOGRADOV (1959b). Because there are two new reviews on migrations of Crustacea available (CUSHING, 1951; BAINBRIDGE, 1961), it is not necessary to discuss the basic pattern in detail. From BAINBRIDGE (pp. 444-445), the main conclusion on diurnal migration of Crustacea, likely to hold to a large degree for other animals, may be quoted: "A rise occurs in the late afternoon which is a positive swimming toward a source of weak or decreasing light intensity. This is continued into or through the night with an orientation dependent upon gravity and is replaced either by a station-keeping behavior or by sinking as a result of inhibition of activity. With the increase of light at dawn the station-keeping or sinking may be followed by upward movement which may be kinetic at the low intensities involved. Later this is superseded under the rapidly increasing intensity by a

downward movement away from the light. At the day depth this is in turn replaced by an exploratory hop-and-sink behavior which keeps the animal within a zone of optimum illumination. With advancing afternoon the upward part of this hop-and-sink activity must become gradually extended until finally a continuous upward swimming takes place again as a directional taxis toward the rapidly dimming light. This cycle of behavior can be markedly affected to the extent of complete distortion by many factors including effects of the phytoplankton, pH, temperature, and apparently also by various known and unknown features of the animal's physiological state."

As pointed out by HARRIS and WOLFE (1955), CLARKE and BACKUS (1956), and SIEBECK (1960), light adaptation may influence the depth where species are found, the animals tending to rise slightly during the course of the day. RINGELBERG (1961) has put forward new objections to the theory of an optimum light intensity as the means of depth control. He has suggested that the relative change in illumination is the stimulus for upward migration in *Daphnia magna*, and possibly also in other organisms. The role of gravity as a means of orientation has been re-emphasized (SCHRÖDER, 1959; SIEBECK, 1960); gravity is important not only for those deep-living species which continue their upward migration during the early night, but also for surface forms. Many authors have pointed out that the upper members of a migrating population behave differently from the lower ones, so that some sorting of the populations must occur (MOORE and O'BERRY, 1957). HARRIS (1963) has reviewed older observations on endogeneous activity rhythms manifested in pelagic animals of several phyla in continuous darkness or light, and has reported new experimental evidence that an endogenous 24 hr cycle of locomotory activity can occur (*Daphnia magna* and *Calanus finmarchicus*). One of the effects of the cycle may be a false "dawn rise" observed occasionally, long before kinetic movement due to dim light can be expected. In *C. finmarchicus*, the periodicity was found to be absent during the winter months, when the species usually does not migrate diurnally. One of the examples for modifying influences in the basic pattern has been given by MOORE and CORWIN (1956). According to them, the vertical arrangement of four species of Siphonophora in the Florida Current can be described statistically using illumination, temperature, and pressure (see also MOORE and BAUER, 1960, for Copepoda).

The amplitude of the diurnal migrations of most Crustacea may range from 2 to 600 m or even to 1000 m. Mysidae living at about 4000 m are known to feed on surface phytoplankton (BIRSTEIN and CHINDONOVA, quoted from VINOGRADOV, 1959a). The most active migrators belong to the nekton, and much is known about their sustained speed of swimming and range of migrations, from investigations of the Deep Scattering Layer (see section IIIc).

At present, there is no generally accepted theory about the significance of diurnal migrations. A few previous comments have been summarized by BAINBRIDGE (1961).

Diurnal migration is regarded as the normal behavior pattern of pelagic animals. Although BAINBRIDGE (1961) listed a few Copepoda known not to migrate, he regarded these as anomalous in view of the very many species which have been observed to do so. However, BOGOROV (1948, quoted from BEKLEMISHEV, 1957) stated that the plankton of the upper 100 m of the ocean is characterized by the presence of surface species which are small and which do not show pronounced diurnal migrations if any at all. Genera named were *Oithona*, *Paracalanus*, *Centropages*, among the Copepoda; *Evadne* and *Podon* among the Cladocera. It appears that BOGOROV referred to temperate and high latitudes. In regard to warm waters, HEINRICH (1961b) found in an investigation in the Kuroshio that a fairly large number of Copepoda species living in the upper 200 m did not present a clear pattern of diurnal migration (see also, HEINRICH, 1960b). ESTERLY (1912, quoted from RUSSELL, 1927) on the other hand, found definite indications that diurnal vertical migration occurred in sixteen out of nineteen species of Copepoda off southern California. MOORE and O'BERRY (1957) observed, during eleven 24 hr stations in the Florida Current, that out of sixteen common species of Copepoda, seven did not migrate markedly, or showed a reverse migration (deeper during night than during day); five showed moderately extensive migrations; four migrated over far more than 100 m. Absence of diurnal movements is known for many developmental stages of larger species of Copepoda. The greater number of Protozoa, as well as small Metazoa, are not likely to migrate extensively because of their size. For understanding the turnover of organic matter in the ocean, it is necessary to know what fraction of the population is daily leaving and re-entering the surface layers. The bearing of migrations on downward transport of organic matter, and consequently of nutrients, has been referred to earlier (section IIe). KETCHUM and BOWEN (1958) have pointed out that an upward transport of dissolved, adsorbable substances may also occur when the concentration in deep water is high. It will affect mostly the distribution of those elements which rapidly reach equilibrium with the dissolved phase. Elements may be picked up differentially.

BOGOROV (1958) implied that the small, non-migrating species usually contribute little to the biomass of the net plankton, and that possibly three-quarters of the zooplankton mass migrated diurnally. It will be shown here that in the upper layers usually less than half of the plankton retained by nets with mesh apertures of about 0.3 mm does migrate, so that a large part of the grazers are always present in the photic zone. Only very close to the surface can the diurnal change in population density be quite pronounced.

Observations from coastal waters will be discussed in section IIIb which show a marked trend to absence of diurnal migration.

The following data are averages of large sets of observations. In surveys with horizontally towed nets of 0.3 mm mesh aperture in the central Equatorial Pacific, HIDA and KING (1955) found at the surface a night/day ratio of plankton volumes of 1.63, which was statistically highly significant. Hence, the net plankton in the surface did not even double during the night. The ratios for horizontal tows in the discontinuity layer, between 65 and 175 m, and in the water below, between 168 and 200 m, were 0.90 and 0.60. They indicate diminution of plankton during night, but these ratios were statistically not significant. Using a larger material of hauls mostly from 200 m to the surface in the same region, KING and HIDA (1957) found ratios between 1.31 and 1.94 dependent on the locality. In collections at 200, 300 and 500 m near Hawaii, KING and HIDA (1954) found night/day ratios between 1.6 and 1.7; in oblique hauls through the upper 200 m, the night/day ratio was almost 2.0. BOGOROV and VINOGRADOV (1960) found average night/day ratios of 1.3, 1.4, 1.8 and 2.0, in areas farther to the west and south-west (the nets had a mesh aperture of about 0.2 mm only). Other data from the tropical South Pacific (LEGAND, 1958) showed night/day ratios of 2.2 for the surface; for horizontal hauls at about 50, 100, and between 200 and 350 m, the ratios were 1.8, 1.7 and 1.2, respectively. Earlier, LEGAND, had discussed that the ratios are different for various taxonomic groups as might be expected from the different swimming powers.

A mathematical procedure to account for the time of the day was suggested by KING and HIDA (1954), useful for reduction of zooplankton data in regional surveys when samples have to be taken on a station grid regardless of the time of the day. Comments were given by BOGOROV and VINOGRADOV (1960) and ROTSCHI *et al.* (1961).

In the Gulf of Alaska, MCALLISTER (1961) found an average night/day ratio of 8 (range: 0.2 to 37), for 12 series of 24 hr surface observations with a net of 0.33 mm mesh aperture. On six occasions, the average ratios for deeper layers were 17.5 (0 to 50 m; the ratio was only 3.0 when one extremely high value was omitted), 2.1 (0 to 100 m), 2.8 (0 to 150 m), 1.8 (0 to 200 m), 1.6 (0 to 300 m) and 1.2 (0 to 500 m). The last figure indicates that some species migrated to depths greater than 500 m. During one year of observations, WIBORG (1955) found at weathership "M", about latitude 66°N, a night/day ratio of 14.5 for the surface, and of 1.7 for the 0 to 25 m layer. For the 0 to 100 m layer, the ratio was 1.4 (ratios from MCALLISTER, 1961; WIBORG gave monthly means which showed large variability at the surface, and some variability in the lower layers). In Norwegian coastal waters at latitude 67 to 69°N, during the summer, WIBORG (1954) did not find a clear-cut diurnal change of zooplankton biomass in the 5 to 25 m and 30 to 50 m

layers with a net of 0.37 mm mesh aperture. He suggested as an explanation the fairly uniform illumination. BOGOROV (1938, 1946) had already pointed out that the plankton of high latitudes does not migrate diurnally during summer. However, during September, when the diurnal changes of light are pronounced, he observed in the Arctic a night/day ratio of zooplankton biomass of 1.7 at the surface. FOXTON (1958) reported for the Subantarctic and Antarctic regions, that diurnal changes of the vertical distribution of net zooplankton are small and inconsistent in summer, because the three species contributing most of the biomass (two Copepoda and one Chaetognath) do not migrate diurnally.

The following data are individual observations: VINOGRADOV (1954) studied the diurnal migration of zooplankton at a station in the Kurile area. From his figure, the following night/day ratios can be estimated: About 10 (for 0 to 10 m), about 3 (10 to 25 m), slightly above 1 (50 to 125 m and 125 to 200 m), slightly below 1 (200 to 400 m), about 0.5 (400 to 750 m), and about 1 (750 to 1250 m and 1250 to 1500 m). The high ratio in the uppermost, thinly populated layer may have been caused in part by "overspilling" from the heavily populated layer between 10 and 25 m. With nets of a mesh aperture of about 0.33 mm, HURE (1961) made two diurnal migration studies in the Adriatic Sea during summer, with thermal stratification prevailing in the upper 30 m. The night/day ratios of plankton volumes were 3.3 (or possibly 2.2 only) and 2.7 for the 0 to 30 m layer and near 1 for the other 30 m layers down to 200 m (last layer, 150 to 200 m). All ratios were near 1.0 in homothermal waters during spring.

The data of MCALLISTER (1961) as well as the original data of the other studies quoted, indicate how variable the night/day ratios can be at individual stations, depending on the specific composition of the catches. Ratios < 1 are not uncommon, meaning that more plankton was caught during day than during night. This variability has also been emphasized by BIGELOW and SEARS (1939) for the shelf of the temperate western North Atlantic; day and night ratios of catches with the same mesh aperture varied according to depth, area, and season. The effect of season was in part a change in environmental conditions modifying the behavior of a species; in part, a change in species composition, which also can result in a change of behavior.

The reviewed observations show that by no means all larger Metazoa retained by nets of about 0.3 mm mesh aperture leave the surface layers during daytime. One-half, or even more, of the night population usually continues to be in the upper layers during the day. Therefore, it is not quite appropriate to regard diurnal migration as the normal behavior pattern of pelagic animals, though certainly, it is the behavior common to the greatest number of pelagic species. Possibly, the night/day ratios in the open ocean are higher than on the shelf, because the population of large zooplankters living

normally below 200 m during daytime is absent on the shelf. Only few data are at hand. It will be discussed in the following section that haline stratification, which tends to reduce diurnal migrations of smaller species of Copepoda, is more likely to occur on the shelf than in the open sea (although it is quite common in the open tropical and polar oceans). Also for this reason, night/day ratios of net plankton should be small on the shelf and in marginal seas.

In the open ocean and on the shelf, Metazoa <0.3 mm and Protozoa can be expected to show little, if any, diurnal migration, so that the total non-migratory population may be quite large. It is not known which part of the population is more efficient in grazing on the phytoplankton, but it can be assumed that most smaller animals have higher metabolic rates per unit mass than larger ones. Even in the presence of diurnal migration, point sampling with pumps or water bottles has some justification, since a large part of the zooplankton is stationary.

Presence or absence of diurnal migrations can have profound influence on the horizontal distribution of species, as shown by data from the northern part of the mixing zone between the Kuroshio and the Oyashio. During summer, a layer of Kuroshio water, 25 to 40 m thick, spreads on the surface northwestward from the border region between the currents, and carries the plankton with it, finally mixing with Oyashio water. HEINRICH (1958) estimated the range of diurnal migrations of Copepoda in the Kuroshio. Eight of ten species migrating during the night into the upper 25 m had been found by ANRAKU (1954) in the mixing zone north-west of the Kuroshio proper. Only one of seven species staying during night below 25 m in the Kuroshio occurred in the northern part of the mixing zone.

#### b. *Holoplankton in Stratified Water*

In the previous section it was shown that usually one-half or more of the Metazoa retained by nets of about 0.3 mm mesh aperture does not leave the surface layers during daytime. Most of the quoted observations were made in the open ocean. Diurnal migration seems to be even less marked in coastal water when vertical salinity gradients occur. Apparently, stratification is no physical obstacle to swimming but provokes a change in behavior. Experiments by LANCE (1962; with earlier studies) show that gradients of 3.6‰/2 mm, and even multiples of this very sharp gradient, do not constitute a barrier for the vertical movement of small euryhaline species of Copepoda when the gradients are within a range of salinity usually inhabited or endured by the species. Nauplii of Copepoda move through pronounced gradients in the Bay of Kiel. Adult Copepoda also surmount fairly steep salinity gradients during seasonal migrations as reviewed by BANSE (1959).

Yet, far more than half of the students who investigated smaller Copepoda, up to the size of *Calanus finmarchicus*, in areas with haline stratification, did not find diurnal migrations as pointed out by BANSE (1959; also BANSE, 1956a, and Fig. 3). Water was regarded as stratified when the salinity gradient was 0.2 to 0.3‰ or more over a 10 m depth interval. Such gradients occur commonly in the surface layer of all neritic seas. Many of the species involved apparently do not migrate extensively in the open ocean either (p. 94). Temperature seems to be less critical than salinity for suppressing vertical movements. CUSHING (1951) has reported marine and freshwater observations of Copepoda migrating diurnally through thermoclines when temperatures were within the range normally encountered by the species.

Obviously, the limiting salinity gradient suggested was a crude estimate because the hydrographic data had been obtained by point sampling with water bottles. Animals are affected by the gradients prevailing between the top and the bottom of the halocline, and not by the difference between hydrographic observations 10 m apart.

A great number of investigators have not found diurnal migrations of *Calanus finmarchicus* (MARSHALL and ORR, 1955; BANSE, 1959). The reason for failure to observe these migrations has often been sought in differences of the physiological state of the animals. The latter is difficult to investigate in the field, since too many samples have to be taken in order to study the distribution of the animals, and no time is left for experiments. Without any doubt, endogenously controlled physiological factors do influence migrations. Among recent contributors to this subject, MARSHALL and ORR (1960) have shown that the state of the gonads influences the migration of the adult female *Calanus finmarchicus*. A relation between fat content and intensity of vertical migration has been found by SUSHKINA (1961) for this species. In Faeroe-Icelandic Waters during August, animals with high fat content tended to reduce vertical movements and to stay in deeper layers. MARSHALL and ORR have also given other data as to the variability of the phenomenon of diurnal migrations. At present it is not well predictable even in a well-known species.

CLARKE (1934a) had found pronounced migrations of *C. finmarchicus* in the month of July in the Gulf of Maine, but not on the following day on Georges Bank where the vertical movements were restricted to the upper 20 m or so above the discontinuity layer. In the month of August, CONOVER (1960) measured very much higher respiration rates per unit of dry weight in *C. finmarchicus* caught on Georges Bank than in animals caught in the Gulf of Maine, just 100 miles away. In regard to CLARKE's observations, I had pointed out in 1959 that a salinity gradient of 0.2‰ per 10 m occurred at the first station, whereas on the later station it was 0.8‰ S. Although I am no longer so certain that this difference may have been the reason for the different behavior of the animals found by CLARKE, I am still convinced that much would be gained in investigations of diurnal migrations if more attention was paid to measuring the environmental conditions.

More data on migrations in water with salinity gradients may be added in geographical arrangement to those listed by BANSE (1959) which show how variable the diurnal migration pattern is. DIGBY (1961a) studied vertical distribution of members of various phyla in the Isfjord in Spitsbergen during late summer when the incident radiation changed by a maximal factor of 50 (considerably less at other occasions) over 24 hr. Generally, vertical movements related to light were not pronounced. During period one of the observations, *Calanus finmarchicus* showed a population increase in the entire

upper layer at the dates with low incident radiation. The apparent vertical rise of population maxima was far in excess of what can be expected from a light controlled migration and might have been caused by other reasons, possibly advection. Two populations of *Calanus finmarchicus*, copepodid stage V, might have been studied in the tidally mixed Sörgat in period two when there was a marked change of numbers at the surface, apparently related to light. The occurrence of *Sagitta elegans* exhibited the same trend. More observations from these regions are needed.

ROGERS (1940) stated that in the mouth of the St. John River, the concentration of *Sagitta* sp. and Cirripedia nauplii in the ingoing, saline bottom water increased towards the head of the estuary; these forms seemed to be able to orient themselves and to overcome the effect of mixing of bottom water into the surface layers by moving downward. A lack of marine species was observed in the brackish surface layer of the Miramichi estuary by BOUSFIELD (1955). It is not clear whether the animals overcame the effect of mixing, or whether their absence was due to death or low salinities. For the Bay of Kiel, it had been suggested that Copepoda are passively subjected to mixing (BANSE, 1959; limnic observations by SCHRÖDER, 1962, may be consulted). Also *Branchiostoma* larvae did not swim downwards when transported by mixing into water of low salinity (BANSE, 1956b). BARLOW (1955; see also KETCHUM, 1954) stated that the vertical distribution of zooplankton, predominantly the copepod *Acartia tonsa*, in a stratified tidal estuary near Woods Hole, did not seem to be much influenced by diurnal migrations. Large, persistent differences between animal numbers in surface and bottom water were found. The maintenance of the species in the estuary could be mathematically described using the experimentally determined reproductive rate and the flushing and mixing rates, assuming that there were no active vertical movements of the animals. Scattered observations indicate that *A. tonsa* may not migrate diurnally under the thermohaline stratification prevailing in Long Island Sound either, although the species reacts to light in the laboratory (CONOVER, 1956). It must be noted that the species is very euryhaline, and capable of swimming through extremely sharp salinity gradients in the laboratory when stimulated by light (LANCE, 1962, see p. 97).

GILLBRICHT (1954) compared average numbers of six days of observations on the tintinnid *Tintinnopsis beroidea* in an enclosed former harbor basin at about lat. 54°N in March. Samples 2.5 m apart were taken at 0900 and 1800 hr. The salinity gradient varied between zero and 1.2‰ per 10 m. The maximum of vertical distribution occurred at 2.5 m in the morning, and at the surface in the evening. It was concluded that limited diurnal migration was present.

New observations on *Limnocalanus grimaldii*, known previously to migrate vertically in weakly stratified water, demonstrate that the behavior of the

species varies. BITYUKOV (1959) has given three sets of diurnal studies from the eastern Gulf of Finland. Hydrographic conditions may be estimated from BUCH (1945), although positions of the stations are not available to me. Accordingly, the animals stayed in more or less homohaline water when migrating in May, essentially within the upper 20 m. With the body of the population having moved into deep layers in June, the animals showed marked diurnal migrations through salinity gradients of possibly  $0.5\text{‰}$  per 10 m. There was little upward migration during the night in September. On one 24 hr station, LINDQUIST (1961) found in Finnish coastal waters that this species negotiated a salinity gradient of  $2.3\text{‰}$  per 2.5 m. NIKOLAEV (1960), however, had observed that migration was nearly absent in the Gulf of Riga. The temperature conditions were quite similar to those at LINDQUIST's station but the salinity gradient was  $0.2$  to  $0.3\text{‰}$  per 10 m. The bulk of the population remained day and night below the discontinuity layer. These observations on *Limnocalanus grimaldii* support the contention that the tendency of Copepoda species up to the size of *Calanus finmarchicus* to reduce or to suppress diurnal migration in the presence of salinity gradients is due to changes in behavior, and not to insurmountable physical or physiological barriers.

VŪCETIĆ (1961) made observations on diurnal distribution of zooplankton in an inlet of the Adriatic Sea where haline stratification is found during the summer. No marked migration occurred in most species during observations in August. With forms like *Calanus finmarchicus* (rather *C. helgolandicus*?) and *Pseudocalanus elongatus*, this may have been due to the high temperature of the surface water, though the explanation does not hold for *Sagitta setosa* known to migrate elsewhere in the region. Much of the population of *Paracalanus parvus*, however, appeared to have migrated in August through a salinity gradient of about  $1\text{‰}$  per 10 m, but great variability of the catches cautions against a firm conclusion. A similar vertical distribution pattern as in August had been found for this species in July. PETIPA *et al.* (1960) stated that in the Black Sea, a salinity gradient of "...  $>0.04$  to  $0.05\text{‰}$  per 1 m is an almost impenetrable barrier for the majority of small zooplankton". The investigation showed that large zooplankton like *Calanus* migrated through gradients of this kind. Diurnal migrations of Copepoda and other zooplankton under a probably strong stratification of an estuary was also reported by YAMAZI (1957). It appears from his data that the dependence of the animal numbers on the state of the tide was very marked, but a "residual" migration was present.

Diurnal migrations of larger animals such as Mysidae through thermaline discontinuity layers have been observed by JOHANSEN (1925), HESSE and VALLIN (1934), and NIKOLAEV (1960), among others. The annual distribution of *Neomysis americana* in an estuary has been studied by HULBURT

(1957). The interaction of reproduction rate, light influence, and water circulation, including "trapping" of the animals in the deeper, more saline layers, leads to a much greater accumulation of *Neomysis* there than in the surface water or in the waters outside the estuary (see also p. 99, ROGERS). New observations on Euphausiidae in stratified water have been made by LACROIX (1961).

Deep Scattering Layers have occasionally been observed to be impeded in their diurnal movements by the presence of thermoclines. Because the scatterers are not known, it cannot be stated whether this was due to steepness of the gradients encountered, or because the thermocline happened to include the isotherm normally limiting the spreading of the organisms.

The following conclusions are drawn from this discussion: Salinity gradients of 0.2 to 0.3‰ per 10 m which had earlier been found to reduce or suppress diurnal vertical movements of smaller Copepoda, are commonly observed in all marginal seas that are not tidally well mixed. In these areas, during periods without seasonal migrations, Copepoda, as the main consumers of plant matter in the sea, tend to feed, digest, and grow in a single water layer. In consequence, the budget of organic matter might be easier to investigate in a neritic environment than in the open ocean, since active downward transport of organic matter and nutrient elements by the zooplankton is not present. In this respect, a neritic water mass might be a model case of the ocean, more easily studied than a segment of the open sea.

Observations on vertical distribution patterns of zooplankton in stratified water that are not related to light distribution may be added here. GILLBRICHT (1954, 1955) studied phytoplankton and *Tintinnopsis beroidea* during three years in an 18 m deep, enclosed former harbor basin and found accumulations of the tintinnids in the discontinuity layer. Being aware of sedimentation effects and reaction of the animals to light, he concluded that the tintinnids were actively seeking discontinuity layers, depending on the size of the vertical gradient. They swam ahead of the diatoms settling on the discontinuity layer. *Peridinium triquetrum* of the Dinoflagellata was sometimes distributed like the tintinnids. Copepoda in the Bay of Kiel tend to accumulate in discontinuity layers but no explanation can be offered (BANSE, 1959). In the Black Sea, PETIPA *et al.* (1960) observed a maximum of plankton around the depth of the summer thermocline where the distribution range of the warm-water plankton and that of the plankton living below the thermocline, overlap.

A large amount of particulate matter can accumulate in discontinuity layers in the open sea. *In situ* beam transmission measurements (JOSEPH, 1957; hydrographic observations in DIETRICH, 1954) have shown a tenfold increase of extinction coefficients for red light at several stations that represents a turbidity screen a few meters thick extending over large

parts of the North Sea. Observations on the same cruise by HAGMEIER (1960) have shown that the intermediate maximum of turbidity is caused by an accumulation of inorganic material, phytoplankton and non-plant matter that contains protein (zooplankton). The summer thermocline in the North Sea can be followed on echo sounders as a distinct band of sound-scattering (JOSEPH, 1957; see also p. 103).

COOPER (1961) has also suggested that the stratification of the deep-sea (p. 56) may be accompanied by accumulation of detritus on discontinuities where filter feeders might gather.

Preliminary experiments by HARDER (1952, 1954) indicate that the cause of accumulation of zooplankton in discontinuity layers may be the change in density of the water although physical impediment of swimming is not involved (see also LANCE, 1962). Dr. E. R. BAYLOR (personal communication) is engaged in experimental studies on the influence of density gradients on zooplankton behavior, with particular reference to their effect on "color dances" (BAYLOR and SMITH, 1957; DINGLE, 1962). Color dances appear to represent a behavior pattern leading the animals to food. Also, according to BAYLOR, density gradients in water without food influence the behavior in such a way that the animals accumulate in discontinuity layers.

In view of these observations, it seems useful to pay attention to stratification, particularly of salinity, when investigating the vertical distribution of zooplankton. Because more and more evidence indicates that sudden vertical changes of salinity and temperature are quite common, even in the so-called wind-mixed layer, recording instruments should be employed for the study of the vertical distribution of these parameters, rather than water bottles. The depths of zooplankton sampling should be adjusted accordingly. Because advection or internal waves can change the details of stratification quite rapidly, it is not sufficient to make hydrographic observations only at the beginning of a 24 hr plankton study. Rather, they must be repeated prior to each series of plankton samples.

It may be noted how misleading the use of standard depths in studies of diurnal migrations can be when divided hauls are being taken. Suppose that a discontinuity layer is found at 20 m depth at the beginning of the observations, and it is decided to make hauls from 50 to 20 m and from 20 to 0 m. If internal waves, common in stratified water, occur, animals from the lower layer may be caught in the upper hauls and vice versa, since Copepoda have been observed not to compensate for vertical displacement of water layers (p. 67). The investigator would thus find "vertical migrations".

It may also be pointed out here that very few investigators of diurnal migrations did show that their conclusions, presence or absence of diurnal movements, were statistically well founded. Almost all studies demonstrate influence of patchiness by irregularities of distribution patterns even if there is no apparent horizontal advection. Some duplicate samples can improve the value of an investigation markedly (see also p. 74).

*c. The Deep Scattering Layer*

The Deep Scattering Layer (DSL) is discussed separately, because the fast swimming animals constituting the vertically moving layers can be regarded as nekton. The midwater reverberation of sound at shallow depth associated with discontinuity layers will not be treated (see BEKLEMISHEV, 1956; WESTON, 1958; SCHRÖDER, 1962).

Normally, the DSL is found during the daytime at 300 to 800 m. It may occur at depths of 200 to 350 m below surface water of reduced transparency, and is more frequently found deeper in the tropics than in higher latitudes. It is not clear whether the DSL represents an incidental accumulation of animals with similar light preference or whether the daytime depth offers other advantageous conditions for many species with a resulting concentration of animals. The first alternative is more likely to be correct, in view of the relation of daytime depth of the animals to light.

The main constituents of the DSL seem to be Euphausiidae in its upper portion (see, however, HERSEY and BACKUS, 1962) and fishes in the lower. Shrimps and squids can also be of importance. More often than not, the layer moves up and down diurnally, corresponding to the fluctuations of light whereby it often splits. Temperature may modify the pattern, particularly near the upper or lower range of migration. The migration is more regular under the warm seas than in higher latitudes. A summary of the earlier literature can be found in TCHERNIA (1953). Recent reviews have been given by BEKLEMISHEV (1959), BODEN (1962), and HERSEY and BACKUS (1962). Additional biological information can be found in the studies by UDA and co-workers (see UDA, 1956), MOORE (1958), and VINOGRADOV (1959b). MOORE has pointed out that at the depths where the DSL normally is encountered, the illumination cycle "... cannot be considered as just a diluted version of that of the upper waters". New measurements on irradiance and spectral composition of daylight at depths of several hundred meters can be found in KAMPA (1961), and data on twilight irradiance, with particular reference to the DSL, have been given by BODEN (1961; both articles with additional references).

According to CLARKE and HUBBARD (1959; also CLARKE and DENTON, 1962), the greatest depths at which a perception of day-night changes of illumination is possible to organisms, are from 700 to 1000 m. However, KOCZY (1954) has observed layers at 4500 m rising at about the time of sunset. Because of incomplete data, a diurnal periodicity of the animals at these great depths can be assumed only, but Mysidae known to live at about 4000 m and to feed at the surface on phytoplankton show that very deep reaching diurnal movements occur (section IIIa). Because at those depths the beginning of the upward migration cannot be controlled by light, it could be

suggested that an internal clock is involved. However, the problem would only be shifted to the question as to how the clock is checked (re-set) because drifting of the timing mechanisms must be prevented.

At the level of the DSL, there can be considerable animal luminescence, affecting the reading of submarine photometers (KAMPA and BODEN, 1957). CLARKE and HUBBARD (1959), however, did not note coincidence of maximal bioluminescence and sound scattering. The disagreement does not seem surprising, because abilities to emit light and to scatter sound are independent. The two pairs of observers might have studied aggregations of different species (see also CLARKE and DENTON, 1962).

Some authors found more net plankton within the DSL than above and below it. Others did not, presumably because the physical properties related to sound reflection differ in plankton. Only a part of the population registers on the echo-sounders. In the North Atlantic, there is no decrease of transparency in the DSL (JOSEPH, 1959, 1962), contrary to the situation in scattering layers at shallow depths. The shallow sound scattering layers are mostly associated with discontinuity layers which effectively retain particles; the DSL usually is not. Echo-sounders lowered to the DSL have shown that the organisms in the layer are distributed in patches (KANWISHER and VOLKMANN, 1955; JOHNSON *et al.*, 1956).

Quantitative estimates of the constituents of the DSL present more gear problems than do other fields of plankton research, since the animals live deep and are good swimmers. Very little is known, therefore, about number and biomass of the scattering animals in the DSL (BEKLEMISHEV, 1959); both may be quite low (HERSEY and BACKUS, 1962). It is not known whether the bulk of the scatterers has been collected by the nets used in the investigations on vertical distribution of biomass (see section IIe) or not. Euphausiidae, though, should have been sampled fairly reliably, particularly in darkness. Table I of VINOGRADOV (1961a) contains a few records of large pelagic prawns which were very rarely caught but should scatter sound markedly. They were omitted from the presentation in Fig. 4. The ratio of fishes to other animals in the DSL is unknown.

In midwater trawl studies in the upper layers of the North Pacific during summer (ARON, 1962), the fishes in night catches made up one-third, or somewhat less, of the nekton biomass (which is mostly Euphausiidae and Decapoda). The nekton in turn, seems to be a small part of the net plankton during summer in this area (BANSE, 1962). However, unpublished winter data from the same region indicate that sometimes Euphausiidae in the euphotic layer represent more biomass than the net plankton. Thus, it may be that allowance for the large nekton will have to be made in the curves of Fig. 4, at intermediate depths.

In 1959, CUSHING suggested that in the deep ocean the DSL may ecologically replace the benthic animals of the continental shelves. Comparison of Fig. 4 with the data given by ZENKEVICH *et al.* (1960) shows that, even with

large nekton not collected, the biomass of net zooplankton in the open ocean is several times larger than that of benthic animals retained by screens of about 0.5 mm aperture.

#### IV. VERTICAL DISTRIBUTION OF MEROPELAGIC LARVAE

##### a. *Vertical Distribution and Phototaxis*

There were many earlier investigations of the pelagic larvae of bottom animals, particularly of economically important species, but larval ecology as a distinct study was brought to general attention in 1946 by THORSON. In his monograph, he also reviewed phototactic behavior. Almost all young larvae are found to swim towards the light when kept in dishes in the laboratory, whereas old larvae tend to be photonegative, except those of species which live as adults near the surface.\* In the field, collections for life history studies were often made with surface tow-nets. Although simultaneous hauls at depth were not done, it was often concluded from the rich catches that the positive response of young larvae to light made them rise to the surface (also THORSON, 1946). Following RUSSELL (1927), it can be argued that the photopositive response of larvae to the weak light prevailing in a laboratory might be reversed under the influence of strong light in the field, and that diurnal migrations would occur. Thus, during daytime there might be more larvae at depth than at the surface.

In the investigations at hand, which in part were of very limited scope, there appear to be very few common features in the behavior and distribution of bottom animal larvae. Treating the larvae as pelagic organisms (as it is submitted here) rather than as stages in the life history of benthic organisms serves as much to emphasize diversity as uniformity. The absence of pronounced diurnal migrations, however, seems to be common to very many species; obviously, all have to reach the bottom at some time in their development.

First, field investigations on vertical distribution without emphasis on diurnally changing features may be mentioned (other references in THORSON, 1946). A uniform trend of behavior does not appear. Larvae have been found to be distributed fairly evenly in the water, or with a changing pattern on subsequent dates, by FLATTELY (1923, Polychaeta), BANSE (1955, 1956b, Polychaeta and Echinodermata and unpublished observations on unidentified

\* Dr. G. THORSON told me that he found in the literature much more data on the subject which were presented at the 10th Pacific Science Congress, in Hawaii, 1961. I gratefully acknowledge the benefit I received from discussions with Dr. THORSON at Friday Harbor in the summer of 1961

larvae of Lamellibranchia and Gastropoda in the Bay of Kiel in 1953), KORRINGA (1941, European oysters), MANNING and WHALEY (1954, American oysters), and COLE and KNIGHT-JONES (1949, European oysters in tanks). Larvae have been found to swim at depth by DEW and WOOD (1955, Polychaeta and Lamellibranchia), KAMSHILOV (1958, nauplii of Cirripedia), BANSE (unpublished observations on nauplii of Cirripedia in the Bay of Kiel in 1953), JORGENSEN (1923, Decapoda), RUSSELL (1925, 1926, 1928a, mostly Decapoda), SAVAGE (1926, Decapoda Macrura and Anomura), and MEEK (1923, Echinodermata). The account by BOURDILLON-CASANOVA (1960) from the western Mediterranean shows that the behavior of different species of larvae of Decapoda can be quite variable, both in respect to the general vertical distribution in the upper 30 m and to diurnal migrations. RUSSELL also noted variations in vertical distribution (see also below). T. C. NELSON and PERKINS (quoted from KORRINGA, 1941) found that oyster and other larvae accumulated in, or just above, very pronounced haloclines. THORSON (1946) observed on five occasions in the Øresund that larvae of species of many phyla, apparently brought in from the Kattegat, showed maxima of distribution just below the discontinuity layer separating the low salinity effluent of the Baltic from the Kattegat water, which has higher salinity and lower temperature. There were, however, secondary maxima of occurrence of the same species at greater depths.

In some observations, the age of larvae was mentioned. CARRIKER (1959) stated that in an estuary, young and medium-old larvae of American oysters generally occurred most abundantly at the surface. Older larvae tended to be closer to the bottom (CARRIKER, 1951; see also below). KUNKLE (1958) found in another estuary the same stages fairly uniformly distributed in the water column. TURNER and GEORGE (1955) stated from observations in culture flasks that very young larvae of *Mercenaria mercenaria* swim actively up to the surface although they apparently do not react to light. They are able to swim through vertical salinity differences of 5‰ (gradient not given). Whereas medium-old larvae are evenly distributed in culture jars, old larvae tend to gather near the surface. The quoted tables by JORGENSEN contain many examples where young larvae of Decapoda were collected only in deeper water. LEBOUR (1928) noted that the first zoea of the brachyuran *Ebalia tuberosa* occurred near the sea bed. The first zoea of the pea crab, *Pinnotheres osterum*, though photopositive, was only occasionally found at the surface, but was frequently caught in the bottom water (CHRISTENSEN and MCDERMOTT, 1958). Conversely, GURNEY (1942) stated that late larvae of bottom-living Decapoda were quite commonly found in the surface plankton. The quoted data of KORRINGA, COLE and KNIGHT-JONES, and BANSE did not substantiate the importance of age on the vertical distribution of larvae.

Because of the bearing of haline stratification on vertical distribution as discussed in section IIIb, it may be mentioned that the quoted observations of LEBOUR and RUSSELL were made in an area with little, if any, haline stratification. A slight salinity gradient can be associated with the summer thermocline in the areas where the material of FLATTELY, JORGENSEN, MEEK, and SAVAGE was collected. BANSE and THORSON worked in the Transition Area (between the Baltic and North Seas), where there is always pronounced stratification in the deeper layers. The investigators of oyster larvae, and CHRISTENSEN and McDERMOTT, worked in tidally influenced estuaries for which general statements can not be made. PERKINS studied an area of exceptionally strong salinity gradients.

Many of the studies on the vertical distribution of larvae were made during the daytime. Some occurrences of larvae in deeper layers, therefore, may represent daytime depths, but there is only scattered evidence. During a solar eclipse, PETIPA (1955) observed vertical movements of larvae of Lamellibranchia, Gastropoda, Cirripedia and Decapoda. The observations of QUAYLE (1952) also suggest that there was a diurnal migration of the larvae of the lamellibranch *Venerupis pullastra*, the larvae being at depth during the daytime; a tidal influence was superimposed on the changes in vertical distribution (REES, 1953). On the other hand, European oyster larvae, though photo-positive, did not migrate diurnally in the strongly vertically mixed and turbid Oosterschelde (KORRINGA, 1941). PETERSEN (as quoted by KORRINGA) did not find a difference in oyster larvae distribution between bright and cloudy days in the Limfjord. COLE and KNIGHT-JONES (1949) found similar numbers of European oyster larvae of all sizes in surface and near-bottom hauls during cloudy days, but smaller numbers near the surface during bright days. T. C. NELSON (quoted from MEDCOF, 1955) and MEDCOF found more upward swimming during daytime than during night for advanced American oyster larvae. During the night, the larvae stayed close to the bottom. *Mercenaria mercenaria*, in observations by CARRIKER (quoted from CARRIKER, 1959), "... showed a slight tendency to assume a higher position in the column at night". From more detailed data (CARRIKER, 1961), it appears that young and medium-old larvae tend to accumulate in the upper layers during daytime, and are more evenly distributed during night. The same author had shown earlier (1951) that the younger stages of *Crassostrea virginica* tend to be near or on the bottom during ebb tide, and to rise to shallower depths on the flood (see also CARRIKER, 1959). The latter results were corroborated by KUNKLE (1958). It is not quite clear whether the greater number of larvae of *Mercenaria mercenaria* found in the water with higher tidal turbulence (CARRIKER, 1961) was caused by a physical effect (whirling-up) or was due to behavior of the larvae. BOUSFIELD (1955) studied the distribution of larvae of Cirripedia in a strongly stratified estuary, and argued that there must be diurnal migration to retain the larvae in the estuary. Further, he found that the older stages tended to occur during daytime at slightly greater depths than did the younger stages; no night observations were available. Neither larvae of Cirripedia, nor of other classes of Crustacea, or of other phyla,

were observed to migrate diurnally (BANSE, 1955). Also KAMSHILOV (1958) did not find a great difference in numbers of barnacle larvae at the surface between sunny and cloudy days. RUSSELL (1926) found larvae of Decapoda higher in the water on a foggy day than on two clear days and reported diurnal migrations (RUSSELL, 1925, 1928a, and 1931). SAVAGE (1926) noted only a slight change in vertical distribution of Decapoda larvae between day and night.

Most of the quoted observations were done either on expedition-type itineraries where the same population is usually not encountered twice, or in estuaries which are difficult to study because of the strong horizontal and vertical gradients of environment, and the high rate of change. When the distribution of larvae of Polychaeta and Echinodermata was investigated in Kiel Bay with emphasis on concurrent hydrographic observations (BANSE, 1955, 1956b), it turned out that populations had been revisited. It was suggested that the larvae are bound during their entire pelagic life to certain water strata. They are essentially captured in the water in which they began their pelagic existence. Diurnal migrations were absent in all larvae studied. It was argued that the results may hold for the entire Transition Area between the Baltic and the North Seas. With the idea of larvae bound to water layers, and the varying results of studies on vertical distribution in mind, it was submitted in 1955 that the notion of crowding of young larvae at the surface of the sea may have originated from incomplete observations, that is, surface tow-netting. Apart from the doubtful exception of *Phoronis muelleri*, the species records from the North Sea and the Baltic listed by THORSON (1946) can be explained by adults living and spawning in surface water. The larvae are bound to occur at the surface, and upward migration does not have to be postulated. The contention that larvae in Kiel Bay were bound to the water in which they began their pelagic life is in line with the thesis presented in section IIc, i.e. the main features of vertical distribution of non-migratory holopelagic organisms may not represent a reaction of the animals toward the surrounding conditions present at the time of collection, but are largely determined by advection. By and large, the animals seem to just counteract the effect of gravity. The accumulation of larvae observed by THORSON (1946) below the discontinuity layer between the Baltic and the Kattegat water may have been caused by intrusions of water containing many specimens at this depth, rather than by phototactic rise of larvae to the discontinuity layer. The vertical distribution of some species showing deeper secondary maxima as found by THORSON, would be difficult to explain by a general phototactic rise of larvae blocked by the discontinuity layer.

It would be interesting to learn whether or not the passive vertical transport of larvae, not migrating diurnally, is as important in other regions as it is in Kiel Bay. The parallel to the situation of the holoplankton is suggestive

(p. 72). Because animal behavior is involved, care should be taken in making generalizations, and the observations by PRITCHARD (1953) may serve as a memento. While studying oyster larvae in relation to hydrography in an estuary, he found that the distribution of the animals could not be treated mathematically in the same way as the distribution of dissolved material.

#### b. *Settling and Metamorphosis*

Bottom invertebrates with pelagic larvae usually produce large numbers of eggs. THORSON (1946) has brought forward much evidence that the greatest single source of loss of offspring is due to predation on the larvae during their pelagic state. Earlier it had been thought that many larvae may be lost because they "rain" in a haphazard manner onto unsuitable substrates. Meanwhile, it has been shown experimentally that larvae can be very capable in selecting the proper place for settling. In the absence of a suitable substrate, they can continue pelagic life for some time, and currents may carry them over vast areas so that the probability of successful settling is greatly increased. WILSON (1958) has reviewed some problems of settling and metamorphosis so that only one field of interest need be discussed.

Some species check the grain size or the roughness of the rock before settling in order to evaluate the site. In some cases, it has been shown that settling and metamorphosis are promoted by chemical substances emanating from the substrate or from established settlements of the species. Two new investigations may be mentioned. HANNERZ (1956) has studied the polychaete *Spio martinensis* (*Type I larva*). He states that those larvae which are ready to metamorphose, react to water that has been in contact with the proper sandy sediment, by sinking "... more or less as if a narcotic has been added". On the bottom, the substratum is checked, and only later does the rapid metamorphosis set in. Young larvae do not react to water or substratum in the manner of the advanced larvae. SCHELTEMA (1961) has also reported that larvae of the gastropod *Nassarius obsoletus* are not attracted by physical characters but by biochemical properties of the sediment. The adults inhabit intertidal coarse sand. The properties of the sediment are probably water-soluble and can be transferred to water in contact with the sediment.

In consequence, settling must be difficult if larvae are bound to the water in which they began their pelagic life as indicated earlier, and if this water happens to be separated by a discontinuity layer from the sea-bed. The discontinuity layer will prevent the vertical spreading of dissolved substances so that the larvae will not receive the stimulus to turn to bottom life. A prolongation of pelagic life, and, possibly, after some time, mid-water metamorphosis, result. Observations of metamorphosed animals caught in mid-water, which were not likely to be upwelled bottom stages, have been listed

by THORSON (1946), WILSON (1952), MARUMO and KITOU (1956), and BANSE (1956b). In the latter's paper, it was shown that the "overdue" larvae of the polychaete *Prionospio malmgreni* continued to be bound to a physically defined water mass; they did not sink into the underlying water. As metamorphosis and growth must result in loss of swimming ability, the mid-water life cannot be extended indefinitely. Therefore, in stratified water, the "rain of larvae to the sea-bed" suggested by the early workers may occur. This was demonstrated in the Bay of Kiel by a comparison of the horizontal and vertical distribution of metamorphosed specimens of the brittle-star *Ophiura albida* with that of water masses (BANSE, 1956b). The observed vertical distribution of the animals was caused by slow sinking out of the water in which they had been transported into the Bay of Kiel (see also MARUMO *et al.*, 1958). It is suggested that a similar fate will befall all larvae which have been carried by physical mixing above the lowermost discontinuity layer and which do not migrate downwards for settling. The quoted occurrence of fairly well developed juvenile Echinodermata, and "overdue" larvae of other groups in the plankton beyond the shelf, testifies to this suggestion. In most cases, these individuals will be doomed, but as shown by MILEIKOVSKY (1961) for the continental slope of the Arctic region, they may establish an expatriated population of benthic animals.

#### V. SUMMARY

Some aspects of vertical distribution of marine zooplankton are reviewed.

It is not known whether or not the vertical distribution of the majority of species living below the epipelagic zone can be described by environmental factors like temperature or depth or food. Some species have been shown to be bound to the water masses defined by physical oceanography. If this proves to be the rule, the gross features of horizontal and vertical distribution could be described in the same terms.

The understanding of the ecology of the deep-living zooplankton suffers from the ecologically ambiguous collection of data. There is little reason to assume that deep-sea plankton is evenly distributed over wide vertical ranges at a station. Divided hauls between standard depths far apart do not seem useful for ecological studies of plankton. It is suggested that sampling depths be selected according to hydrographic data. Even better would be to sample horizontally over short distances in core layers and hydrographically midway between them. Thereby, most of the water column is neglected in order to obtain a manageable number of samples together with reliable information on the environment. Collecting should be distributed evenly over day and night. Also, sampling should aim at seasonal coverage of selected places.

Even though certain species cannot stand low oxygen concentrations, it is only in very few regions that the aeration of the water is so poor that the biomass becomes abnormally low.

Pressure sensitivity of pelagic animals has been shown repeatedly in experiments, but very few field data are available showing that pressure controls vertical distribution to a large extent.

An homology between the vertical distribution of plankton and dissolved radioactive fallout is suggested for the surface layer of the open temperate and cold oceans above the main discontinuity layer. It is proposed for the plankton not migrating diurnally that its vertical distribution may be largely determined by convection and advection and not by active movements of the animals. The vertical arrangement at a station, then, may not reflect the behavioral reaction of animals to actual conditions of life, but would be due to former conditions at other places. A plea is made for abandoning nets, in favor of pumps or water bottles, for collecting Copepoda and smaller zooplankton. To keep collections small, sampling depth should be selected according to hydrographic data from recording instruments.

Little is known about plankton near the sea-bed both as to its vertical distribution and as to the relation of holoplankton to the benthic community.

Seasonal vertical movements are briefly discussed, and it is shown that in autumn they result in a twofold to fourfold increase of net plankton biomass at about 1000 m depth in subpolar and polar waters. The bearing of this phenomenon on the annual distribution of phytoplankton standing stock at the surface of temperate and higher latitudes is also pointed out.

Sufficient data are now available for generalizations about the vertical distribution of biomass of zooplankton caught by medium-fine nets. The biomass of net plankton at great depths depends on the surface production. It is not yet known what the amount of total zooplankton at depth is, but there are indications that the amount of nanoplankton is smaller than that of the net plankton.

The transport of organic matter by vertical migrations seems to be of greater importance for the nutrition of deep-sea animals than sinking of dead organisms, or *in situ* heterotrophic production from dissolved organic matter.

Recent schemes of vertical divisions of the pelagic domain are discussed. Biological evidence comparable to that on which the provinces of animal zoogeography are based is not yet compiled, and changes of the reviewed systems may be expected. In particular, the line between the mesopelagic and bathypelagic zones cannot yet be drawn convincingly.

In the open ocean, only about half of the zooplankton mass retained by nets of about 0.3 mm mesh aperture leaves the upper layers during daytime, the very surface layer excepted. The smaller organisms not retained by this mesh size cannot be expected to migrate, but little is known about their mass.

Their contribution to the turnover of organic matter is not known either. It is concluded that the effective fraction of the grazers staying in the photic layer all the time is large. In the presence of small salinity gradients as they occur in all marginal seas, diurnal migration of smaller Copepoda tends to be suppressed.

In regard to the Deep Scattering Layer, it is emphasized that almost nothing is known about the number of scatterers per unit volume, or the biomass represented by them.

Diurnal migration is weakly pronounced if present at all among pelagic larvae of bottom invertebrates. It is doubted that the positive phototaxis of young larvae makes them generally rise to the surface. It is submitted that larvae often may leave the water layer, in which they began their pelagic existence, only for settling. Stratification of water can result in a rain of old larvae onto the sea-bed, when animals above the discontinuity layer are prevented from coming into contact with the bottom at the appropriate time.

#### NOTE ADDED IN PROOF

To my regret, it was not possible to obtain a copy of the monograph on *Euphausia superba* by MARR (1962) in time to incorporate the many observations on this species in the present review. The discussion of the moderate diurnal migrations, of ontogenetic movements, near-surface swarming, and maintenance of the species in the Antarctic region are particularly pertinent to the present paper.

In section IIal, observations by COOPER were reviewed which indicate layering of water even at great depth. SIEDLER (1963) has published an actual recording for the upper 1600 m of the western Mediterranean Sea, near Toulon, where BERNARD had worked. Sharp discontinuities amounting to 0.1°C were common down to 400 m, possibly representing layers of the type described by COOPER. The temperature gradients changed often also in deeper layers. The repetition of the station from the drifting ship half an hour later indicated that details of the temperature distribution may be of quite local significance. Dr. KRAUSE, Kiel, has shown me unpublished continuous temperature records from the Irminger Sea for early summer, with marked layering to the end of the registration at 1400 m.

The correlation of plankton occurrence with water masses, as defined by the *T-S*-relation, made on a large scale by BARY (1963) for the surface waters of the eastern North Atlantic is mentioned here, although at present the analysis is concerned with horizontal and not three-dimensional distribution. This work is similar to the attempts discussed on p. 59 for deep water where the use of the *T-S*-relation is much easier than at the surface.

Concerning marine snow (p. 77) and organic detritus (section IIe, p. 84 and 88), RILEY (1963) has published the results of a two-year study of organic aggregates in Long Island Sound and has made some remarks on oceanic conditions. The size of the aggregates in the sea varies between 5  $\mu$  and several mm, and their amount is always large. They can be generated experimentally from dissolved organic matter by bubbling air through particle-free sea water, as also shown by BAYLOR and SUTCLIFFE (1963, and p. 73). They increase in size when standing in the laboratory, a process presumably of importance below the surface of the sea. Nauplii of *Artemia* can be raised with experimentally produced particles (BAYLOR and SUTCLIFFE, 1963), and the detritus thus may be a source of nourishment for filter feeders particularly in water of low nanoplankton content.

A new attempt to explain the adaptive value of vertical migration (p. 94) has been presented by McLAREN (1963), using a temperature-growth model. If sufficient food can be obtained in the upper layers, which are usually warmer than the deeper layers, during part of the day, metabolic energy is saved by spending the other time in deep cool water, and more organic matter can be utilized for growth. Diurnal and seasonal migrations have been considered.

In regard to data on Deep Scattering Layers (p. 103), it can be seen from BARHAM (1963) that Siphonophora may be major contributors to the phenomenon. ENRIGHT (1963), in continuing his studies of pressure sensitivity of Crustacea (p. 67) has shown that the specific compressibility of an intertidal amphipod and of *Euphausia pacifica* is 15 to 40 per cent lower than that of sea water which is of interest also in respect to sound reflection.

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