PLANKTON AND PRODUCTIVITY IN THE OCEANS

Second Edition

Volume 2—Zooplankton

JOHN E. G. RAYMONT†

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Introduction

The manuscript for this volume of *Plankton and Productivity in the Oceans* dealing with zooplankton and secondary production, was almost complete in August 1979. Had it not been for the help and encouragement of my late husband's colleagues I do not think I would have had the audacity to attempt to finalize the work. To them, and to the many other friends at the Institute of Oceanographic Sciences and elsewhere, I owe a deep debt of gratitude.

In particular I would like to thank Professor Charnock, F.R.S. and Professor Lockwood for allowing me office and library facilities in the Department of Oceanography, Southampton University; Sir Frederick Russell, F.R.S. who read Chapter II; Mrs. Gathergood who completed the typing even during retirement; and the editorial staff of Pergamon Press. Dr. Burton, whose task of reading the text of both volumes was made doubly onerous, has been of invaluable aid, ever ready with helpful criticisms and suggestions.

There has been an inevitable delay between the production of the two volumes; I have endeavoured to check any dubious points, and although I cannot aspire to my husband's standard, I know it would have been his wish that this volume should be completed and I hope I have not failed him.

—To John, who patiently taught me all
the Biological Oceanography I shall ever
know.

August 1982 Brigit Raymont.

Contents

Chapter 1
Introduction

General Considerations and Definitions

The floating and drifting animal population known as the zooplankton cannot be precisely delimited from another great pelagic community in the marine environment—the nekton. However, the plankton is usually regarded as being distinct in that it has little or no power of independent horizontal migration. The zooplankton inhabits all layers of the ocean down to the greatest depth sampled (cf. Banse, 1964; Vinogradov, 1962, 1968, 1972).

It has long been recognized that numerous zooplankton species drawn from many phyletic groups have powers of vertical migration, sometimes performing very extensive vertical movements. Some of the more powerful swimmers in the zooplankton, such as pelagic decapods and the larger euphausiids, may also occur in swarms which appear, at times, to move horizontally, not entirely due to the drift of the water. Although it is doubtful whether this could be called a horizontal migration, the precise difference between the nektonic freely swimming and migrating pelagic community and the plankton is difficult to judge. More recent observations on living plankton in the ocean have suggested that some of the larger medusae and siphonophores are capable of strong swimming movements, and certainly it is not easy to distinguish between such strongly moving plankton and the very small members of the nekton, (mainly small fishes and cephalopods, frequently classed as the micronekton), whose major movements are often essentially vertical migrations resembling those of the zooplankton. Although a very large number of zooplankton animals drawn from a wide variety of taxa (e.g. copepods, ostracods, sagittae, siphonophores, euphausiids, ctenophores, heteropods, pteropods, salps, etc.) remain planktonic throughout their whole existence, a large array of animals occur in the plankton during only a part of their lives. These are known as meroplanktonic animals, in contrast to those holoplanktonic forms which remain permanently in the plankton.

Meroplankton and Holoplankton

The meroplankton includes the various types of trochophore and veliger larvae of benthic worms and molluscs; different kinds of nauplii and zoeas of bottom-living crustaceans; cyphonautes larvae; ascidian and tornaria larvae; the several types of echinoderm larvae; larval squid; the planulae of Cnidaria, as well as medusae of the hydromedusan type. Also included in the meroplankton are the eggs and larval stages of most fishes which when adult are part of the nekton. These meroplanktonic forms are dealt with in more detail in Chapter 2.

As with the phytoplankton (Volume 1), a more or less coastal zooplankton extending from inter-tidal zones to the edge of the continental shelf, and thus very approximately delimited by the 200 m depth contour (the neritic zooplankton), can be distinguished from the oceanic zooplankton, which ranges offshore from beyond the continental slope across the whole extent of the oceans. While neritic and oceanic zooplankton populations are not sharply separated, there are fairly obvious differences. Neritic plankton would tend to have a larger proportion of meroplankton; oceanic meroplankton must be comparatively long-lived (*vide infra*). The meroplankton, particularly in more temperate waters, may also show marked fluctuations in species abundance with seasonal breeding, so that the population is more variable than offshore. Despite the importance of meroplankton in inshore waters, the holoplankton—often represented by a limited number of species—may be extremely plentiful and dominate the population over much of a year.

Harvey, Cooper, Lebour and Russell (1935) showed that certain, mainly neritic, copepods were dominant off Plymouth through most of the year. Of the meroplankton, cirripede nauplii were moderately abundant only over March, and polychaete larvae and rotifers early in the year. Similar investigations in inshore coastal waters have generally confirmed the overwhelming importance of holoplanktonic copepods in the total zooplankton, with meroplanktonic larvae being of minor significance over limited periods of the year (e.g. Wiborg, 1954; Deevey, 1956; Lie, 1967). Details are included in the chapter on seasonal cycles.

In estuarine waters and in certain seas characterized by low salinity (e.g. the Baltic), a considerable variety of meroplankton often can occur in high densities, at times even dominating the plankton population. A very low diversity of holoplankton is typical, but the few species represented may be present in extraordinarily high densities (cf. Jeffries, 1967). For example, Ackefors (1965) found that off Stockholm—where the salinity was about 7‰—copepods, especially *Acartia bifilosa*, dominated the catches; *Eurytemora* was also important. Cladocera (e.g. *Podon polyphemoides*) were plentiful from June to November. Meroplankton included rotifers and bivalve larvae (*Mytilus*, *Macoma*, *Mya arenaria* and *Cardium lamarcki*).

Certain genera and species of copepod are characteristic of estuarine waters. The genus *Acartia* includes a number of species (e.g. *A. bifilosa*, *A. tonsa*, *A. discaudata*) found widely in temperate estuaries while other species are typical of warmer waters. Tranter and Abrahams (1971) found seven species of *Acartia* and the closely related *Acartiella* in brackish Indian waters, in contrast to *A. erythraea*, a euryhaline marine, and *A. negligens*, a stenohaline marine species found outside estuarine waters. Other copepods typical of estuaries are *Eurytemora* spp., *Labidocera wollastoni*, *L. aestiva*, *Tortanus discaudatus*, *Centropages hamatus*, *Pseudocalanus elongatus*, *Paracalanus crassirostris*, *Pseudodiaptomus*, the harpacticoid *Euterpina acutifrons* and certain cyclopoids belonging to the genus *Oithona*, particularly *O. nana* and *O. brevicornis*. Other coastal copepods (*Paracalanus parvus*, *Temora longicornis*, *Isias*) commonly occur in estuaries. Although estuarine holoplankton is often dominated by a single species of copepod (*Eurytemora* or *Acartia*) (cf. Jeffries, 1964, 1967), other taxonomic groups may be significant, for example, chaetognaths (*Sagitta setosa*, *S. crassa*, *S. hispida*, *S. nagae*), the appendicularian *Oikopleura dioica*, ctenophores (*Pleurobrachia*, *Mnemiopsis*, *Bolinopsis*) and, amongst protozoans, a number of tintinnids. In warm waters the decapod *Lucifer faxoni* is a typically neritic estuarine species, as is *Acetes*, though this might be regarded as partly bottom-living—and as are several mysid species which are typical of, and may be very abundant in, estuarine waters. Although not holoplankton, a few hydromedusans (cf. Chapter 2)—*Podon polyphemoides* and *Penilia* among Cladocera, as well as the scyphozoan *Aurelia aurita*—may become enormously plentiful seasonally in estuaries.

In very shallow, particularly estuarine waters, this contribution from animals living partly on the bottom can be significant. The term tychozooplankton is sometimes given to such animals which, whether as young or adults, spend part of the 24-hour day on the bottom, but rise and spend part of their day, often the dark hours, as planktonic organisms. The distinction between tychoplankton and benthos may be difficult, since during storms, especially in shallow estuaries, a number of small bottom organisms may become artificially swept up into the water, but may be able to exist, and indeed to flourish for a time, in the intermediate layers. A genuine tychozooplankton, however, seems to exist, the animals spending more or less regularly a portion of their time every day as planktonic or benthic organisms. Such animals include a number of mysid species, amphipods, harpacticoid copepods, cumaceans, isopods, shrimps, prawns and other crustaceans. Phyla other than the Crustacea may contribute; some protozoans are tychoplanktonic, though these are probably more generally mechanically swept up from bottom deposits. Metamorphosing larvae and post-larvae of a variety of animal groups, as well as some rotifers and occasionally swarming benthic species (e.g. sexually mature polychaetes), may be part of the tychoplankton.

Outside specifically estuarine waters, but in the coastal areas, the zooplankton is much more obviously made up of holoplanktonic species, particularly copepods. Many of the species already listed for estuaries are found, though some very typical estuarine species such as *Eurytemora* hardly exist outside the mouths of rivers. The variety of copepods is considerably increased, however, although diversity is still usually greater in oceanic waters, especially warm oceans. In temperate seas, *Acartia clausi* with *Paracalanus parvus*, *Pseudocalanus elongatus*, *Temora longicornis and Oithona* spp., including *O. similis*, *Corycaeus* and *Oncaea*, become important, with increasing proportions of *Calanus finmarchicus* or *Calanus helgolandicus* in slightly more offshore waters. *Calanus* rapidly becomes an outstandingly dominant species over boreal continental shelf areas.

In warmer neritic waters, there is a greater diversity of copepods, but certain forms are typical of the coastal areas and are not found abundantly in more open oceans. Descriptions of geographical distribution, including distinctions between neritic and oceanic copepods, are included in Chapter 2.

The coastal neritic waters show a greater variety of other holoplankton. A very few euphausiids (*Nyctiphanes simplex*, *N. capensis*, *N. couchi*, *N. australis*, *Pseudeuphausia latifrons*) appear to be limited to coastal waters. Some chaetognaths are more typically inshore (e.g. *Sagitta frederici*) in addition to those listed for estuaries. In warmer waters *Muggiaea kochii* and *M. atlantica* appear to be somewhat coastal, and a few pteropods (e.g. *Creseis acicula*) can flourish over continental shelves. *Limacina retroversa* occurs in colder, mixed coastal waters. For the distribution of these and other taxa, as well as for copepods, the details given in Chapter 2 should be consulted.

A problem in delimiting neritic and oceanic forms arises with some very widely distributed species, because races probably exist which, though physiologically different, are not morphologically distinct (e.g. *Liriope*, *Oithona similis*). Sometimes there is evidence for the existence of two very similar species. Wiborg (1954), for example, believes that *Pseudocalanus* is represented by *P. minutus* living in oceanic regions, whereas *P. elongatus* is an inshore form. However, with some species (e.g. *Acartia clausi*, *Corycaeus anglicus*) long term and wide ranging investigations, such as those carried out by Continuous Plankton Recorder surveys (Glover, 1967), strongly suggest separate oceanic and neritic populations, but morphological separation into distinct species is not possible. Some cladocerans, though strictly meroplanktonic, appear not only to flourish near coasts but to be able to spread out over ocean depths, at least for periods. Some holoplanktonic appendicularians also appear to be able to range very widely over neritic and oceanic provinces. Sharp distinctions between oceanic and neritic species are therefore sometimes not possible and cosmopolitan species (e.g. *Scolecithricella minor*, *Oithona similis*, *Beroe cucumis*, *Tomopteris ligulata*) are well known, but the general distinction between oceanic and neritic zooplankton faunas is well founded.

Although neritic zooplankton is normally dominated by a few holoplanktonic species, there is a considerable variety of meroplanktonic larvae of benthic animals. Meroplanktonic larvae would be expected to be generally more abundant in coastal waters approximately corresponding to the limits of continental shelves, in part because of the greater density of the benthos producing the larvae in shallower seas and in part in relation to the comparatively small distance from the bottom, where the larvae are produced, to the surface waters. Moreover, many deep-sea benthic animals tend to have direct development, so few larvae may be expected throughout the enormous depth of open ocean.

Thorson (1964) suggests a total of 140,000 species of marine bottom fauna. Populations of perhaps 80 % of these species live, at least in part, at depths of less than 200 m, many at much shallower levels. Thorson estimates that 80 % of all the marine shallow water invertebrates studied, which could approximate to 90,000 species altogether, have planktonic larval stages. Not only are planktonic larval stages rare in the life cycles of deep-sea benthic invertebrates, but meroplanktonic larvae are not typical amongst Arctic or Antarctic benthos. The few bottom invertebrates at high latitudes (including larval stages in the life history) breed during the short summer. The vast majority of meroplanktonic larvae inhabit coastal neritic areas in temperate and warm seas. Even in such limited depths the great majority of larvae, according to Thorson, tend to be in the near-surface waters, largely due to their fairly strong positive phototactic responses. Such responses are, however, modified by temperature and salinity, so that the immediate surface is avoided by many species. Older larvae may later become photonegative and be distributed in the near-bottom layers prior to settlement and metamorphosis. Planktonic larvae of inter-tidal benthic species appear to remain photopositive throughout larval life except immediately before settlement. This may be an adaptation to maintaining the stock in inter-tidal areas. A list of meroplanktonic larvae with an indication of their light responses is included in Thorson's (1964) review.

The average period of planktonic life for the larvae of benthic species is believed to be 2–4 weeks. The short period should assist in maintaining a fairly large proportion of the meroplankton in the inshore plankton population despite the enormous mortality, mostly attributable to predation. Data from different authorities emphasize a heavy mortality: *Ostrea edulis* larvae in Dutch waters lose 14 % at each tidal cycle; of 3 million eggs spawned by a pair of *Mya arenaria* only about 0.001 % settle per year; of 13,000 nauplii released by one *Balanus balanoides* over its total life, only 0.2% survive to settlement; one adult crab (*Paralithodes*) gives rise to 200,000 first stage zoeas, but only 7000 on average, survive even to the glaucothoe stage. The success of meroplanktonic life despite this mortality, and the general restriction of the larvae to nearshore waters is evident from the long term stability of the benthos population over continental shelves, in spite of the marked fluctuations known for some species (Stephen, 1931, 1938; Thamdrup, 1935; Jones, 1950, 1956; Smidt, 1951; Sanders, 1956; Thorson, 1957). Such fluctuations in year classes of certain meroplanktonic benthic species are largely due to the relative success or failure of a brood, reflecting environmental factors which existed during the period of larval life.

Only about 5% of Arctic benthos produce planktonic larvae, and the proportion is even smaller in the Antarctic. In temperate latitudes, apart from the very much greater proportion of planktonic larvae, benthos are usually more abundant chiefly in spring and summer, though some larvae occur at all times of the year. Inshore plankton may thus change qualitatively with the changing meroplankton component. Some discussion of periods of meroplankton abundance is included in Chapter 4.

Mileikovskiy (1968) demonstrated that the distribution of a variety of planktonic larvae belonging to such different benthic adults as gastropods, nemertines, bryozoans, decapods, cirripedes, polychaetes, ophiuroids, echinoids, lamellibranchs, holothurians and asterioids, followed closely the shallower areas around the coasts of Norway and Russia. The distribution of larval density was more or less in accordance with the distribution of the breeding adults and was less influenced by currents, at least over areas of maximal larval density. Where more or less circular current systems were present, so that larvae were maintained in relatively shallow waters over extensive areas, as in the South Barents Sea, larvae could be really abundant even 200–300 miles from land. Elsewhere they were restricted to the fairly narrow continental shelves; less than 10% of the larvae were dispersed more than 50 miles offshore.

Scheltema (1975) emphasizes that water circulation, especially the coastal hydrography, and the behaviour patterns of meroplanktonic larvae both contribute to the extent to which larvae spread beyond the edge of the continental shelf where they are spawned. Even with a drift of about 100 miles offshore there is a good chance of return. The length of larval life is another factor in distribution. Scheltema cites the stability of the centre of the xanthid crab population along the Californian coast as evidence of a hydrographic mechanism for retaining the zoeas close to shore. Compensation currents, especially in concavities of the coastline, probably prevent too many larvae from being swept southwards by the current.

Along the Atlantic coast of North America between Florida and Cape Hatteras, zoeas of the crab *Callinectes sapidus* were widely distributed up to 60 miles offshore but were absent beyond the axis of the Gulf Stream. The density of larvae decreased with distance offshore, the early stages being nearer the coastline. Although surface drift disperses the larvae, there is evidence of a shoreward drift of bottom water along the continental shelf of North America, especially in the region off Delaware and Chesapeake Bays, thus providing a good chance for the return of older decapod larvae. Further south, along the Atlantic seaboard, surface and bottom waters both show considerable flow towards shore. Over the whole coastline Scheltema calculated that around 10% of the larvae may be returned shorewards by passive drift. The current pattern shows seasonal changes, however, and the spawning times of several decapod species vary with the area, promoting the maximum retention of the larvae.

Makarov (1969), describing the distribution of decapod larvae on the continental shelf of Kamchatka, agrees with the importance of the spawning area and pattern of nearshore currents in distribution. Larvae were most abundant in shallow waters (35–75 m); samples from stations exceeding 150–200 m rarely contained any decapod larvae. However, the distribution showed an increase in density on proceeding offshore from very shallow depths (*ca.* 30 m) to reach a maximum at 75 m depth, after which the density then declined again. What is described as a "larval belt" was found along the length of the shelf at medium depth.

The direction of offshore currents and the presence of compensatory currents and eddies are listed by Makarov as important factors in retaining meroplanktonic larvae, so that usually only an insignificant proportion passed to the open ocean. The influence of longshore and strong tidal currents was especially important over the central part of the Kamchatka shelf. The larval belt was much narrower in the central area, due largely to the surface current being restricted to a narrow band closely parallel to shore. At the northern and southern ends of the shelf, the surface currents were much wider and more diffuse, and the larvae were more widely distributed. However, they were more abundant in the northern and southern areas, since the strong longshore current in the central part of the coast carried them away from that region.

Although Makarov found that various decapod families followed this overall distribution pattern, there were specific differences. Among the Paguridae and Maiidae, although all the larvae were mainly in the larval belt, they showed depth preferences. The Crangonidae displayed greater differences; while *Crangon septemspinosa* and *C. dalli* larvae were mostly closer to shore (especially the former species) and were not abundant in the larval belt, *Mesocrangon intermedia* and *Crangon communis* larvae were mainly in the middle of the larval belt. Makarov attributed these varied distributions largely to the varying behaviour patterns of the different species. Vertical migration between the water layers, especially in response to light, salinity and pressure, along with tidal changes, could cause the larvae to encounter strata with compensatory or reversed flows and eddies, bringing the species into the particular depth favoured for settlement. Return migration, with shoreward currents, probably operates with many other meroplanktonic crustaceans. For instance, post-larval *Pandalus goriurna* were found to approach shallower and shallower waters, although the young larvae were found in deeper waters. While this might represent an active horizontal migration, in the vast majority of examples distribution results from vertical migration utilizing different current patterns.

A longer larval period may well result in a greater degree of dispersal of larvae offshore, but the use of returning currents may still operate. Johnson (1940) found that the larvae of *Emerita* (the sand crab) from the Californian coast may be swept out by the California Current with its offshore drift to a distance approaching 130 miles from the mainland. This wide dispersal is accompanied by rather a long larval life of up to 4 months. It was presumed that a heavy loss of larvae was inevitable but that the species inhabiting a fairly narrow continental shelf coastline must be adapted to the heavy mortality. Efford (1970) believes, however, that over the 4-month period many of the larvae are returned inshore by the bottom reversed currents.

Another example concerns the distribution of the phyllosoma larvae of *Palinurus interruptus* along the coasts of southern California and Baja California (Johnson, 1960). Although the larvae were widely dispersed over the hatching area and to some distance offshore, they were seldom found far to north or south. Swirls, eddies, including transient ones encountered during the study, and counter-currents retained the larvae for recruitment, avoiding any great loss particularly to the south with the prevailing Californian Current. This strong current might be expected to carry huge numbers of larvae outside their normal area of metamorphosis. In Johnson's words: "It is amazing to note how well the larval population appears to remain within the area throughout the floating larval period."

The seasonal Davidson Current in late autumn and winter may also return older larvae which have drifted south. Thus, despite the long larval life, the population is retained, although Johnson emphasizes that the circulation is not of the semi-enclosed circular pattern. Bigelow (1926) described the larvae of *Sebastes* as being largely retained in the Gulf of Maine, whereas the majority of fish larvae tended to drift out with the near-surface anticyclonic circulation. He attributes the retention of the *Sebastes* larvae to the location of the larval area in the northern part of the Gulf, and to the comparatively deep habitat which they occupy, which protects them from the superficial currents.

Particular behavioural patterns may hold for estuarine zooplankton to enable species, both holo- and meroplankton, to maintain a population against the constant flushing out to sea, or to return a substantial proportion of the population from the more open sea to the estuary. For the cladoceran, *Podon polyphemoides*, Bosch and Taylor (1973) suggest that, as for many other estuarine plankton, a change in level occurs. The cladocerans are mostly in the upper 4-m layer by day and, assuming a typical two-layer estuarine circulation, will be mainly transported seawards. At night they are in the deeper strata, probably due to passive sinking, and thus are returned to some extent by the inwardly-flowing, more saline deep layer. Changes in the level of a typical estuarine copepod, *Acartia tonsa*, in relation to different developmental stages, also appear to be responsible for retaining a proper proportion of the population from being flushed to sea (cf. Chapter 5).

The studies of Grice and Gibson (1975, 1977) have also confirmed the existence of overwintering eggs of some neritic copepods (e.g. *Labidocera aestiva*, *Pontella meadi*) which remain in the bottom deposit in shallow waters and hatch when conditions are favourable, giving rise to a new population. Kasahara, Uye and Onbe (1974) and Kasahara and Uye (1979) cite six calanoid species which produce "resting eggs" found in sediments of the Seto Inland Sea. The eggs of warm temperature species, e.g. *Tortanus forcipatus*, *Acartia erythraea* and *Calanopia thompsoni*, were most abundant in October–November when the animals declined in numbers in the plankton hauls, while the reverse was true for the temperate and winter plankton member *Acartia clausi* for which large numbers ($3.4 \times 10^6/m^2$) of resting eggs occurred in June. Madhupratrap and Haridas (1975) have similarly found resting eggs of copepods in the shallow brackish areas of the Cochin Backwater. If such resting eggs occur generally in estuaries and can accumulate in the bottom mud, they can be an important factor in the renewal of the copepod population of estuaries, especially in those subject to strong seasonal changes. Onbe (1977) has already conclusively demonstrated the presence of large numbers of resting eggs of the cladoceran *Penilia* in shallow waters. Presumably other cladocerans will use overwintering eggs for the re-establishment of populations. Other mechanisms may be employed; for example, some hydromedusans have a resting stage during the monsoon period at Cochin, but rapidly produce generations of medusae when conditions become favourable.

The adults or advanced developmental stages of some estuarine zooplankton species maintain a portion of the population against flushing by sheltering along the sides of the estuary in topographic irregularities, particularly in deeper pockets out of the main stream, so that breeding populations can be re-established (cf. Bakker and de Pauw, 1975). In any event, during the time when extensive populations of zooplankton are present in an estuary, there must be some loss to sea, and a balance is struck between this reduction and the breeding rate (for holoplankton) or spawning intensity (for meroplankton).

Some meroplankton (e.g. oyster larvae) make use of a behaviour pattern which, it is believed, assists retention inside an estuary. The larvae drop to the bottom on the ebb tide and become relatively inactive, so largely maintaining their position. On the flood tide however, they become active, rise in the water, and are carried landwards to some extent in the deeper inflow.

Changes in vertical distribution and swimming activity in some larval species may augment retention. Bousfield (1954a, b) demonstrated an effective pattern for cirripede larvae, mainly *Balanus improvisus*, for returning larvae in an estuary in eastern Canada. The early nauplii (N I and II) were found in great density in the estuary and at the head of the bay near the area of release. The different naupliar stages, however, exhibited a difference in vertical distribution. Young nauplii (I and II) were mostly in the upper 2 m; N III and IV were at 2.5–3.0 m, corresponding to the approximate level of no motion in the two-layered estuarine circulation; older nauplii (V and VI) were deeper (4 m), with some Nauplius VI accompanying the cyprid stage at levels exceeding 5 m.

Although from the exchange ratio in the estuary, about 15% of the 10,000 larvae produced per adult might be expected to be flushed out to sea at each tide—so that after the 18 days of larval life, only about 0.3% would have been retained inside the estuary—a much greater proportion, some 10% of the larval population, remained. Predation losses have not been included in calculating the proportion of larvae retained. The pattern of estuarine circulation as related to the larval behaviour appears to have been responsible for the much greater retention. The early larvae were transported seawards by the residual surface current and were found mainly along the southern side, near the river exit to the bay. Nauplius III and IV stages drifted progressively seawards, though less rapidly, mainly along the southern side, but N V larvae inhabiting the deeper layers were partly returned to near the river exit and were clearly in mid-channel. The N VI centre of distribution was even more landward and was on the northern side. Thus the young nauplii in the surface waters on the south side merge into the plankton of the outer bay at about mid-depth but are then returned to the estuary as older larvae ready for metamorphosis, approximately to the centre of the original population.

Some larvae of benthic invertebrates are swept away from continental shelf areas into the open sea. The great majority of such "strays" die, mostly from predation, but their transport to the ocean has led them away from their effective and viable settlement area. Those with a relatively long larval life may, however, have some chance of survival should they reach a suitable shallower region. Moreover, larvae from a variety of invertebrate benthic taxa can prolong their larval existence to some extent if conditions for metamorphosis are unfavourable. These matters are discussed in Chapter 4.

Neuston

A particular assemblage of zooplankton is now well recognized as being closely associated with the immediate surface film in the ocean. This community, known as the neuston, has its true members which live permanently in this habitat, but numerous other planktonic animals may also be found temporarily at the surface, usually migrating there at night. Some authorities class these temporary members of the neuston as the "facultative" neuston. Larger animals such as fish may also come up to the surface as a transient population. The facultative neuston will not be discussed in any detail.

Nets which have been specially designed to skim the ocean surface may catch animals which, although aquatic, live with their bodies simultaneously in air and water. These animals form the pleuston. Zaitsev (1971) differentiates between the neuston and the pleuston, while admitting that the distinction may be somewhat blurred. Both populations are associated with the surface film. That part of a pleuston animal which projects above the water surface can withstand prolonged desiccation and exposure to direct sunlight. Pleuston organisms tend to be of medium to large size and are usually dispersed by wind. Banse (1975) has reviewed the somewhat confused terminology, and has proposed the term hyponeuston for those organisms beneath, but *attached* to, the surface film. Among the few marine representatives, examples might be quoted from the Craspedophyceae (cf. Volume I). Banse further suggests that animals not attached but living within the uppermost decimeter be termed endopleuston. Zaitsev's broad distinction will, however, be retained in the following general description.

Pleuston animals are usually characterized by some sort of float; familiar examples are *Physalia*, *Velella* and *Porpita*. Apart from these siphonophores, *Ianthina* (a prosobranch mollusc) with its float of bubbles, and the nudibranch, *Glaucus*, which apparently contains bubbles of gas within its body cavity, might almost also be regarded as pleuston animals. David (1965) lists free floating anemones in the pleuston; these are members of the Minyadidae, a tropical family where the pedal disc is modified as a float (cf. Hyman, 1940). Possibly some of the stalked barnacles, which make a bubble float apparently surrounding some sort of foreign fragment, should be included in the pleuston, but precise limitation is obviously difficult.

Some surface organisms may make use of the pleuston as a source of food, or as a substratum. Laursen (1953) found that *Ianthina* would feed on *Velella* and other siphonophores, but stomach contents indicated that the gastropod would also prey on copepods and fairly generally on zooplankton. Bayer (1963) showed that *Velella* and *Porpita* were regularly eaten by *Ianthina*; *Physalia* was also taken. The nudibranch *Fiona* was also observed to feed on *Velella*; Bayer found that *Fiona* characteristically maintained a position on top of the siphonophore. Hyman (1951) quotes all three pelagic nudibranchs (*Fiona*, *Glaucus* and *Phyllirhoe*) as feeding on siphonophores. The diet of the three siphonophores *Velella*, *Porpita* and *Physalia* has also been investigated by Bieri (1966, 1970) (cf. Chapter 6).

According to Zaitsev, true neuston organisms, as distinct from the pleuston, may be aerial forms living on the air side of the surface film (the epineuston) or aquatic organisms inhabiting the water side of the film (the hyponeuston). Neuston organisms are of small to medium size and include organisms of all taxa from algae, bacteria and protozoans to fish fry. The epineuston is extremely limited taxonomically, being represented almost solely by the insect *Halobates*. *Halobates* appears to be very buoyant because of the film of air trapped on the hairs of the body (David, 1965). This insect feeds on the body fluids of animals in the surface film, such as the cnidarians of the pleuston (Cheng, 1973). *Halobates* may be eaten by small fish and, according to Cheng, by certain seabirds.

The assemblage of organisms inhabiting the water side of the surface film—the hyponeuston—is marked by a far greater array of taxa. Apart from representatives of most major zooplankton groups, micro-organisms are present. Autotrophic organisms are apparently less important and abundant than heterotrophic forms, though more recent observations of such algal groups as the Pterospermaceae, which inhabit the surface film (cf. Volume I, Chapter 4), indicate that any algae in the neuston are lost with the usual collecting techniques. A few algae which have been identified, including blue-green forms, flagellates and occasionally dinoflagellates, appear to be associated with foam at the surface. They tend to be nanoplankton forms, presumably remarkably adapted to high surface light intensity. The bacteria present, according to Zaitsev, are especially plentiful in the uppermost 2 cm in the Black Sea. At a depth of only 50 cm, for example, the density is orders of magnitude lower. What is generally termed the "bacterioneuston" is perhaps one hundred times richer than the

Table 1.1. Density of tintinnids (specimens/m^3) of various areas at the surface of the Black Sea (Zaitsev, 1971)

	Species	Tube sampler 0–5 cm layer	Juday net 0–10 m layer
(a)	*Tintinnopsis karajacensis*	82,000	0
	T. beroidea	4,000	0
	T. tubulosa	6,000	0
	Helicostomella subulata	22,000	52
	Stenosemella ventricosa	8,000	17
	Coxliella helix	34,000	65
	C. annulata	0	1
(b)	*Stenosemella ventricosa*	16,000	108
	Coxliella helix	16,000	97
	Helicostomella subulata	4,000	0
	Favella ehrenbergii	2,000	0
	Tintinnopsis campanula	12,000	0
	T. compressa	2,000	0
	T. meunieri	0	1
(c)	*Favella ehrenbergii*	26,000	119
	Stenosemella ventricosa	44,000	50
	Coxliella helix	50,000	32
	Helicostomella subulata	32,000	0
	Stenosemella nucula	10,000	0
	Metacylis mereschkovskii	4,000	0
	M. ehrenbergii	2,000	0