MARINE PLEUSTON—ANIMALS AT THE SEA–AIR INTERFACE

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INTRODUCTION

The word pleuston (from the Greek πλεω, meaning to float) has been used, especially by Soviet scientists, to describe organisms that are associated with the water surface or the uppermost water layer and possess special adaptations enabling them to float there passively (Savilov, 1968). Most western scientists, however, include such marine organisms more commonly in the neuston (from νεω, meaning to swim). The term pleuston was originally used in freshwater biology for describing microscopic plants and animals associated with the surface film and supported by the surface tension of the water, but it is now also used by marine biologists to describe organisms found in the upper 100 m of the ocean. Since this review will be confined to animals which live exclusively at the sea–air interface, the term pleuston will be used for that community, but since pleuston animals are often collected together with the neuston, a brief consideration of some marine neuston animals will also be included. (Much more detailed discussions of the terminologies used in describing organisms occupying the surface waters of the ocean have been presented by Zaitsev, 1970, and Hempel and Weikert, 1972; a summary of the various terms and their meanings can be found in a brief note by David, 1967.)

The layer of water immediately under the sea–air interface has certain unique chemical and physical characteristics. Animals living in this layer have to deal not only with changes in atmospheric conditions, such as temperature and wind, but also with sudden reductions in salinity after heavy rains. These animals may also be exposed to relatively high concentrations of surface-active organic matter, including pesticide residues and, by adsorbing or incorporating them, may serve to pass them along the food chain. Although some of these organisms may be "potentially of great economic and ecological importance" (David, 1965a), we still know very little about even the taxonomic status of many of them.

REVIEW OF GENERAL LITERATURE

NEUSTON AND PLEUSTON

The most significant recent contribution to the study of marine neuston was made by Zaitsev (1970). He not only discussed the physical, chemical, and

biological properties of the surface layers of the ocean but also dealt with methods of sampling different kinds of organisms, and with their systematics, biology, and distribution. There is a very extensive Soviet literature on neuston which tends to be neglected by western scientists, due largely to the language barrier, although, much of the western literature has been reviewed by Zaitsev. An equally monumental work was compiled by Hartmann (1970), who dealt exclusively with the distribution and food of fishes in the uppermost layer of the ocean, which he termed "ichthyoneuston", in the subtropical northeastern Atlantic Ocean. A study of the invertebrates of the same area was published by Weikert (1972) and the ecology of invertebrates, fish eggs, and larvae was reviewed by Hempel and Weikert (1972). From these studies it is often difficult to determine whether certain organisms live exclusively in the uppermost (top 5 cm) layer of the ocean, whether they are there only during certain periods of the day, whether they spend only part of their life cycle there, or are present only occasionally in this layer. Studies of neuston will inevitably involve some organisms from each of these categories. Moreover, studies of pleuston should not exclude considerations of neustonic animals merely for reasons of convenience, especially since some of them serve as the main food source of pleuston.

The most important recent contribution to the study of pleuston was made by Savilov in 1968, using data collected between 1955 and 1961 on various cruises of R.V. VITYAZ in the Pacific Ocean. He discussed the taxonomic status of some of the better known genera, and compiled data on the distribution of *Velella velella*, *Physalia utriculus*, *Porpita pacifica*, *Ianthina* spp., and *Halobates* spp. He made a detailed analysis of the dimorphic forms of *Velella* and *Physalia*, and formulated a hypothesis to explain how the distribution of the different forms of these two species could be affected by wind. He also attempted to delimit the geographical ranges of various pleustonic species, and presented a rather lengthy but critical review of the literature on pleuston, providing a solid background for future research on the floating communities of the ocean.

According to Savilov (1968), pleustonic animals are quite distinct from those occupying other strata of the ocean and should be considered as "individuals of a unified faunal complex" occupying "a special life zone of the ocean with typical living conditions". He divided organisms occupying this special sea–air interface into three major ecological groups:

(1) Typical pleuston forms, animals spending much of their life cycle at the ocean surface, such as *Physalia*, *Velella* and *Porpita* (Coelenterata), *Ianthina* and *Glaucus* (Gastropoda), and *Halobates* (Insecta).

(2) Forms constantly associated with the pleuston, including commensals and symbionts, such as certain turbellarian worms, *Planes* (Decapoda), *Idothea* (Isopoda), *Fiona* (Nudibranchiata), *Lepas* (Cirripedia), young penaeid shrimps, some fish, and symbiotic algae known as zooxanthellae.

(3) Temporary components, comprising mainly larvae of benthic animals such as molluscs, fish eggs and larvae, and polychaetes.

Literature on these various groups will be discussed in subsequent sections.

SURFACE BACTERIA

Apparently little attention was paid to the bacterial populations of the surface of the seas before the 1970s. Tsyban (1971), who reviewed the earlier literature on surface neuston, found very few references to research on the bacterial life of surface waters or "bacterioneuston" prior to his own work, carried out during a nine-year period on two distinct microlayers at the water surface (respectively 150 μm and 1–2 cm deep) in the Black Sea. He found that, in general, the bacterial population in the uppermost 150 μm layer was five to ten times as dense as in the 1–2 cm microlayer, and ten to twenty times as dense as in the rest of the water column. The dominant genera, according to Tsyban, were *Pseudomonas* and *Bacterium* (though the taxonomic status of this name is questionable). A higher proportion of the bacteria isolated from the surface film was found to break down fats, carbohydrates, and starch, whereas more of those from the water column were found preferentially to break down proteins.

The bacterial complex was found to be relatively stable even during storms or when disturbed by air bubbles. How surface bacteria avoid lethal damage by solar radiation is not known. Pigmented bacteria are known to be more resistant to UV rays than are colourless microbes, and most of the 600 strains of bacteria isolated from the Black Sea and the Pacific Ocean were found to be brightly coloured (yellow, orange, brown or red) (Tsyban, 1971). A close correlation was also found between the densities of bacteria and microzooneuston in the Black Sea samples.

PHYTOPLANKTON AND ALGAE

Studies on the algal composition of the surface film have not received much attention. A recent study carried out by Maynard (1968) revealed that large numbers of diatoms, dinoflagellates, green and blue-green algae may be found in surface foam. She found the majority of these algae to be of benthic or periphytic origin, suggesting that they may be carried to the surface by air bubbles. Whether these algal species remained viable in the surface foam was not determined, since her samples had been preserved in formalin. She also found an increase in the proportion of planktonic algal species in foams collected further away from shore. Many algae, notably the blue-green *Trichodesmium* and the diatom *Rhizosolenia*, have been found in high concentrations near the surface during certain times of the year in the north Pacific Ocean, but whether any of these algae are truly pleustonic is doubtful. There seem to be no marine equivalents to the freshwater genus *Nautococcus*, a specialized algal component of what might be called the limnopleuston (Javornicky, 1963).

The macro-algae are represented in the pleuston by two Atlantic species of *Sargassum*, *S. natans*, and *S. fluitans*, well known in the Sargasso, Caribbean, and Cayman Seas, and in the Gulf of Mexico. Many species of animals are associated with the floating forests of these brown seaweeds. Studies on the Sargasso weed and its community have been carried out and published by Prat (1935), Parr (1939), Woodcock (1959), Weiss (1968), Fine (1970), and Ryland (1974).

PERMANENT COMPONENTS OF MARINE PLEUSTON

Animals that, as adults, live permanently at the sea–air interface are specially adapted to this environment, and are not normally found anywhere else. One of their most striking adaptations is a reduction in their specific gravity achieved by forming a float. Another device which aids flotation is an increase in the area of contact with the water surface. Some of these animals may spend their entire life cycle at the surface, but the majority have planktonic larvae and only assume surface existence when their floats are formed.

SIPHONOPHORA

This order is represented in the pleuston by the family Physaliidae, with only one genus, *Physalia*. The taxonomy of the genus is still debatable. This is the earliest known and best-known siphonophore in the literature, and many 'species' have been described in widely scattered publications. Haeckel (1888),
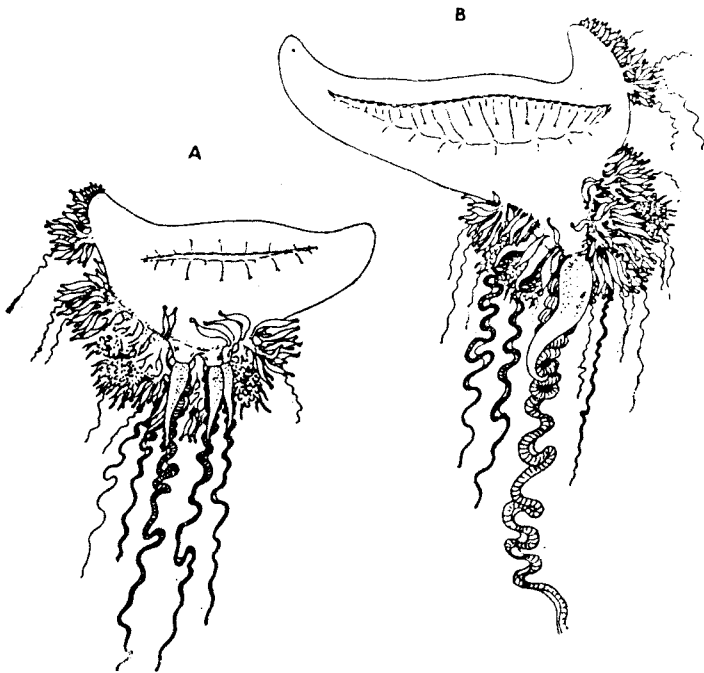

Fig. 1.—Two forms of *Physalia* with (A) several or (B) one main dactylo-zooid(s) (from Savilov, 1968).

who reviewed the early literature, included four species in the genus but later Chun (1897) and Bigelow (1911) recognized only two—the Atlantic *P. physalis* (L.) and the Indo-Pacific *P. utriculus* (La Mart.)—distinguished mainly by the presence of several or only one large dactylozooid(s), re-spectively (Fig. 1). As both these forms have since been recorded from the

Atlantic as well as the Pacific, all the *Physalia* in all oceans have been assigned to one species, *P. physalis*, with several different forms (Moser, 1925; Totton, 1960; Daniel and Daniel, 1963): however, Savilov (1968) considered all the specimens collected in the Pacific Ocean during the Vityaz expedition to be *P. utriculus*, but he admitted that several of the larger ones appeared to be more like the typical form of *P. physalis*. Until age and form variations of these animals are more critically studied it is probably not possible to resolve such taxonomic problems.

The word *Physalia* is somehow derived from the Greek word, physaleion (φγσαλειον) meaning full of wind. In English the animal is commonly known as the 'Portuguese man-of-war', probably because of a fanciful resemblance to one of the formidable galleons of the time when Portugal was a great naval power (Lane, 1960). Its most conspicuous structure is the large blue float or pneumatophore, 1–2 mm to over 300 mm in length, filled with gas with a composition rather similar to that of the atmosphere, with an addition of carbon monoxide (Wittenberg, 1958; Totton, 1960): nitrogen (over 75%), oxygen (20%), carbon dioxide (0·5%) and carbon monoxide (trace to 8%). It is essentially a membranous bag, strengthened with muscular bands capable of changing its shape by contraction and perhaps thereby enabling it at least partially to submerge. Wilson (1947) considered this to be a "wetting" or "dipping" action, especially necessary to prevent desiccation on calm days in tropical waters. Mackie (1960) considered this dipping behaviour as simply a consequence of the asymmetry of the animal which becomes unstable in the absence of wind. Woodcock (1971) postulated that changes in the osmotic pressure may trigger "dipping". His experiments suggested that a higher salinity on the exposed windward side of the float, where the rate of evaporation is higher, may stimulate local muscular contractions which thereby alter the stability of the float and cause it to dip to one side. On contact with water the salinity decreases, the muscles relax, and the float rights itself again.

The structure of *Physalia* is extremely complicated: interested readers can find a detailed description of it in Totton's paper (1960). For our present purposes only the float and the three main kinds of 'polyps' will be mentioned. The blue float contains gas secreted by a special gland and bears a crest or sail, also blue but with pinkish edges. The size and structure of the gas gland have been investigated by Totton (1960), who observed that there is a direct correlation between its diameter and the capacity of the float. The dactylozooids, which are the longest of the polyps—they have been reported to reach 50 m when fully extended—are thin tentacles bearing stinging cells or nematocysts, whose main functions are presumably for defence and to capture prey. The gastrozooids, or feeding polyps, are shorter and each has an expandable mouth opening at its distal end. A resting gastrozooid may have a diameter of only 2 mm, but its mouth can be expanded to 20 mm or more while feeding (Lane, 1960). Polyps of the third kind, the gonophores, are responsible for reproduction (Fig. 2).

The mode of asexual reproduction by budding and the development of larval stages have been studied and illustrated by Totton (1960); evidence of sexual reproduction is still lacking. Totton also reviewed the literature on *Physalia*, including records of its distribution in Atlantic and Australian waters, and gave an account of its general biology. He suggested that *Physalia* probably developed by neoteny from an actinulan hydroid larva. The general
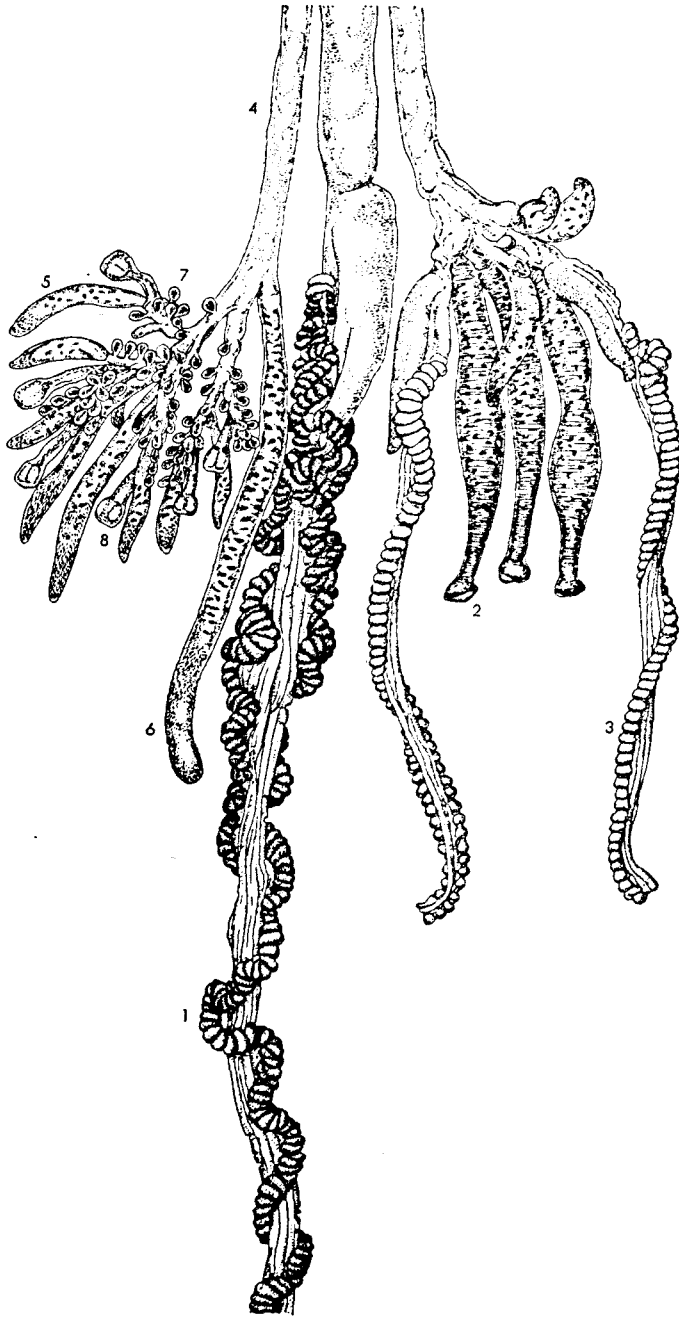
Fig. 2.—Portion of mature colony of *Physalia* showing (1 and 3) dactylo-
zooids, (2) gastrozooids, and (7) male and (8) female reproductive forms
on (4) gonadendron, together with associated structures (5 and 6) of
unknown function (from Lane, 1960).

behaviour of *Physalia*, and the histology of various organs, have been studied in detail by Mackie (1960).

Physalia feeds mainly on fish. The capture of prey by a healthy *Physalia* which had been stranded and transferred to the laboratory was observed and described by Wilson (1947), who illustrated his account with photographs. The fish was captured by dactylozooids, presumably being stung by nematocysts and thus anaesthetized. In a short time some 50–60 gastrozooids had applied their mouths to its surface and were evidently feeding on it. The rhythmic muscular contractions of the dactylozooids make them apparently very efficient organs for capturing and strangling prey. A fully extended nine-metre dactylozooid can contract to 1/70th of its length within a minute (Parker, 1932). The action of the nematocysts and the nature of their toxin have been investigated by Lane and Dodge (1958), who found that the toxic agent is a heat-labile protein complex, denatured at 60 °C; glutamic acid is its chief constituent, followed by glycine, alanine, and proline. It causes a general paralysis of fish, affecting particularly the respiratory centres; the small fish *Nomeus gronovii*, often found in association with *Physalia*, is, however, apparently immune to its sting. The discharge action of the nematocysts is described and illustrated by Lane (1960); 95 % ethanol is reported as a useful de-activating agent for undischarged nematocysts.

Although *Physalia* is generally found in tropical and subtropical zones of the oceans, sometimes in large numbers in patches, it has also often been found stranded on beaches in various parts of the world. Strandings have been recorded for the coasts of the British Isles and parts of western Europe by Wilson (1947), for Florida by Lane (1960) and for Hawaii by Bonnet (1946). Such strandings are apparently more closely related to wind conditions than to water currents (Wilson, 1947). Beached *Physalia* may serve as food for beach crabs, e.g., *Emerita pacifica* (Bonnet, 1946).

The sail of *Physalia* is set obliquely to the long horizontal axis of the float in such a way that the animal tends to sail at an angle of about 45° to the wind. The animals occur in two forms (right-sailing and left-sailing, respectively) which may be described as 'stereoisomers', being mirror images of one another. This peculiar dimorphism in *Physalia* has been the subject of much discussion in the literature (Woodcock, 1944, 1956; Totton and Mackie, 1956; Bieri, 1959; Totton, 1960, etc.). Woodcock (1944, 1956) suggested that under moderate wind conditions the movement of *Physalia* would be influenced by Langmuir circulation patterns, and correlated this with the predominance of left-sailing forms in the northern hemisphere and right-sailing forms in the southern hemisphere. Totton (1960), however, disagreed with this hypothesis since he found that both left- and right-sailing forms drifted to the same beach on the same day. A detailed discussion of this subject, with special reference to the distributions and movements of the two forms relative to the wind, may be found in Savilov (1961, 1968). The known distribution of the left- and right-sailing forms of *Physalia* is given in Figure 3.

CHONDROPHORA

This order of coelenterates is represented in the pleuston by two families, the Velellidae and the Porpitidae.

The Velellidae include one of the earliest known and most familiar pleuston genera, *Velella*. Haeckel, who reviewed the family in 1888, included three genera, which were later found by Chun (1897) merely to represent different stages in the development of the same animal. Haeckel (1888) listed five species for the genus *Velella*, and several other species were added later, but Bigelow (1911), who presented a very good discussion on the systematic
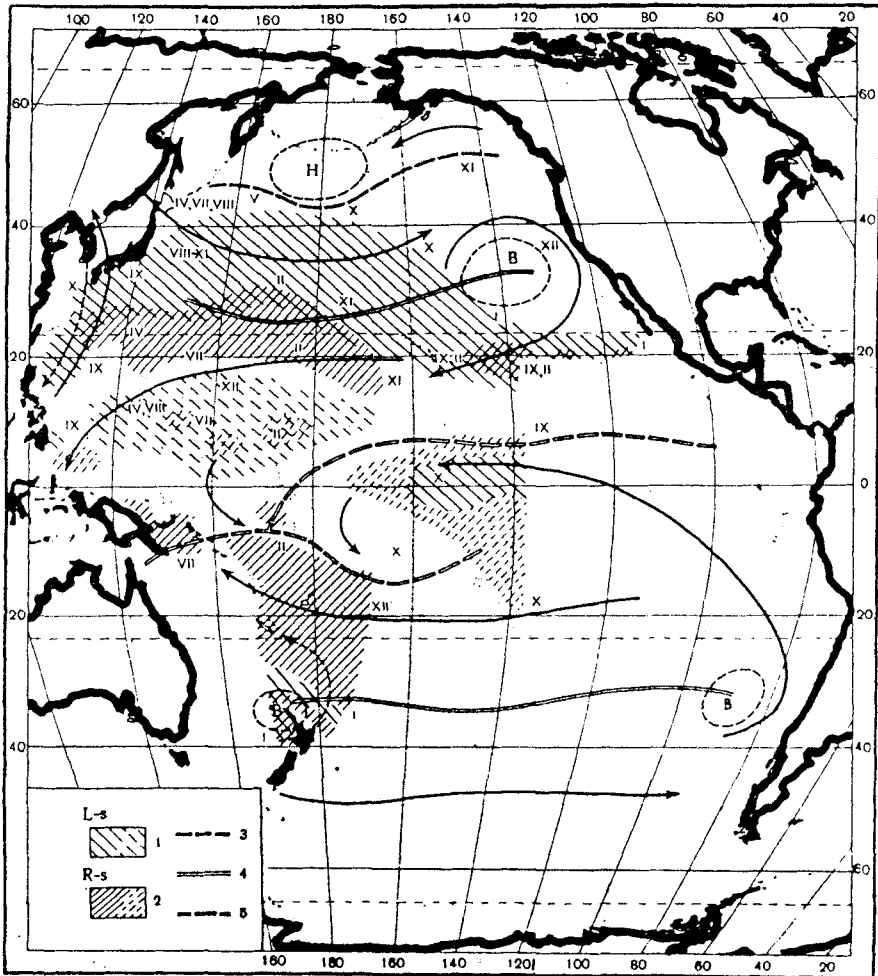

Fig. 3.—Distribution of two forms of *Physalia* in the Pacific Ocean: (1) left-sailing, (2) right-sailing, (3) Arctic front of atmosphere, (4) subtropical belts of high pressure, (5) tropical convergence: arrows denote the direction of prevailing winds: Roman numerals show the months when observations were made: H, low pressure cell; B, high pressure cell (from Savilov, 1968).

problems of the genus, came to the conclusion that the Atlantic specimens can all be assigned to a single "good" species, *V. velella* (L.), and all the Pacific forms to *V. lata* Chamisso et Eysenhardt. (He was not too certain about the specific status of the Indian Ocean forms, since only limited

material was available to him for study.) The former species is characterized by a narrower lamella with a width-to-length ratio of 1 : 3 and a triangular velum, whilst in the latter species the corresponding ratio is 1 : 2 and the velum is more rounded. Many recent authors consider that throughout the world there is only one 'good' species, *V. velella* (L.), with several varieties (Bigelow and Sears, 1937; Totton, 1954; Daniel and Daniel, 1963).
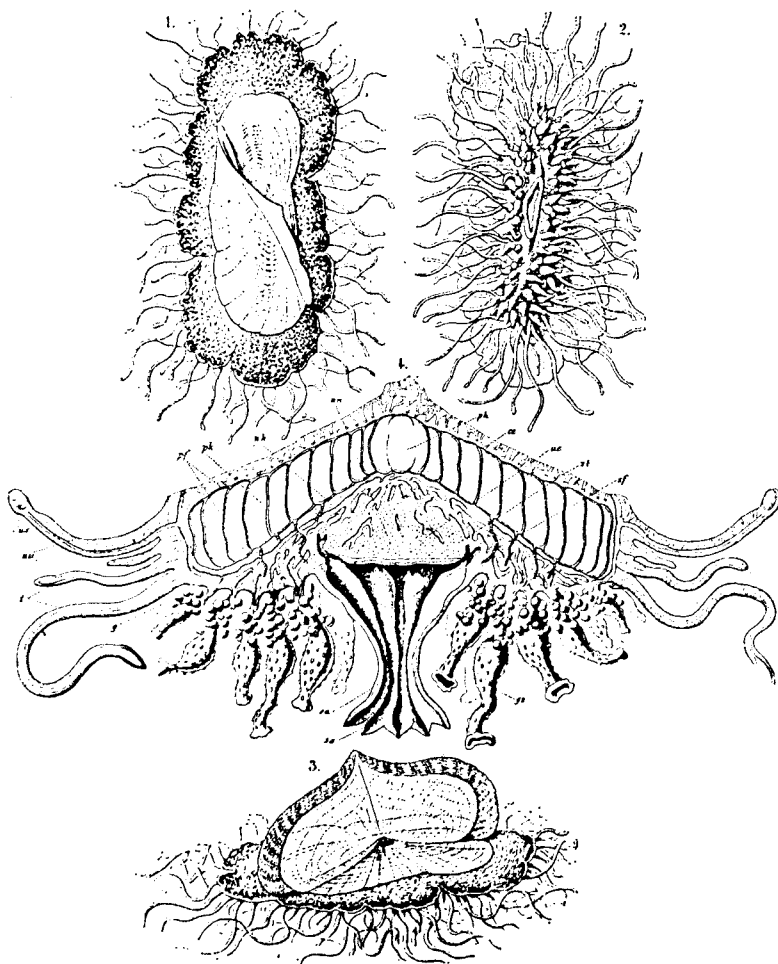

Fig. 4.—(1) Dorsal, (2) ventral, (3) lateral views of *Velella*, and (4) sagittal section showing multi-chambered float, central feeding siphon, gonophores and peripheral tentacles (from Haeckel, 1888).

The name *Velella* is a diminutive of the Latin word velum, meaning a sail. This little blue animal is commonly known in English as the 'by-the-wind sailor'. The body consists of an elliptical or nearly quadrangular raft portion, housing a many-chambered pneumatocyst formed in concentric rings, and bears an oblique, vertical sail. As in *Physalia*, two forms may be distinguished,

depending on the angle of the sail with reference to the long axis. Underneath the raft, which may measure up to 50 mm long, there is a central siphon with a distal mouth opening, numerous smaller peripheral siphons also with mouth openings, and gonophores. In addition, the raft section is fringed with short submarginal tentacles bearing numerous nematocysts (Fig. 4). Since the early studies on the biology and development of *Velella* (see Garstang, 1946; Totton, 1954; Brinkmann, 1964), apparently little information has been added, although this is one of the most important animals in the pleuston, providing not only food but also a physical substratum for many other organisms in the community. Bieri (1961) found that the diet of *V. lata* consists largely of
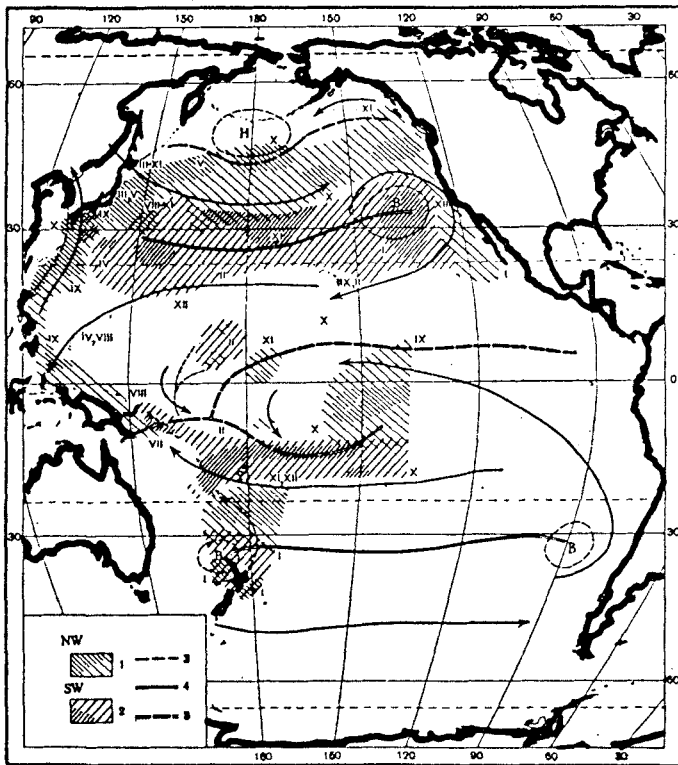

Fig. 6.—Distribution of two forms of *Velella* in the Pacific Ocean: (1) left-sailing, (2) right-sailing, (3) Arctic front of atmosphere, (4) subtropical belts of high pressure, (5) tropical convergence: arrows denote the direction of prevailing wind: Roman numerals show the months when observations were made: H, low pressure cell; B, high pressure cell (from Savilov, 1968).

copepods, fish eggs, euphausiid eggs, and larval crustaceans. Some interesting determinations of trace elements in the same species were made by Bieri and Krinsley (1958). Some recent studies by Fields and Mackie (1971) have shown that *Velella* behaves more like a large individual hydroid than a colony made up of different polyps and is thus more closely related to *Porpita* than to *Physalia*. Ultrastructural studies of the symbiotic zooxanthellae of *Velella* may be found in Taylor (1971).
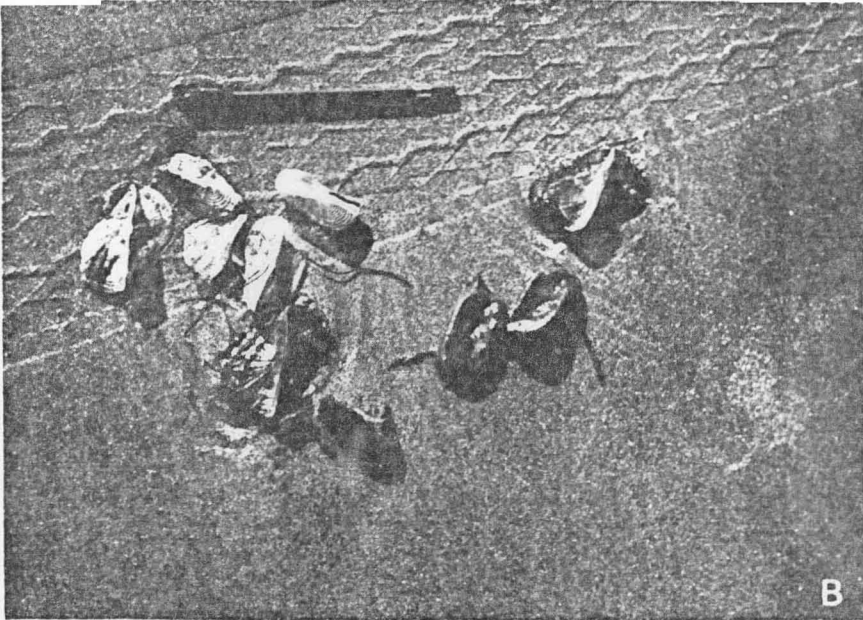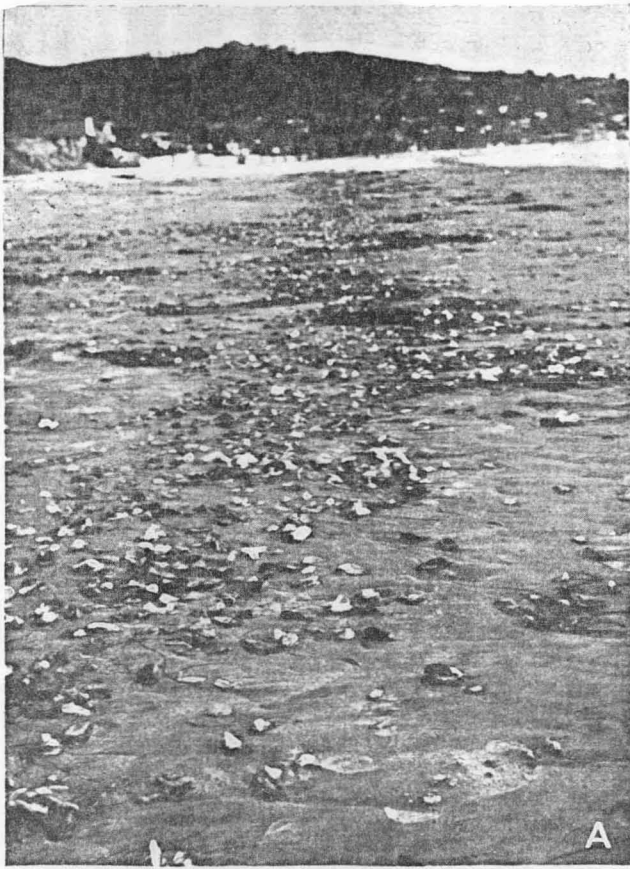
Fig. 5.—Wind-rows of *Velella* stranded on (A) Scripps beach and (B) showing
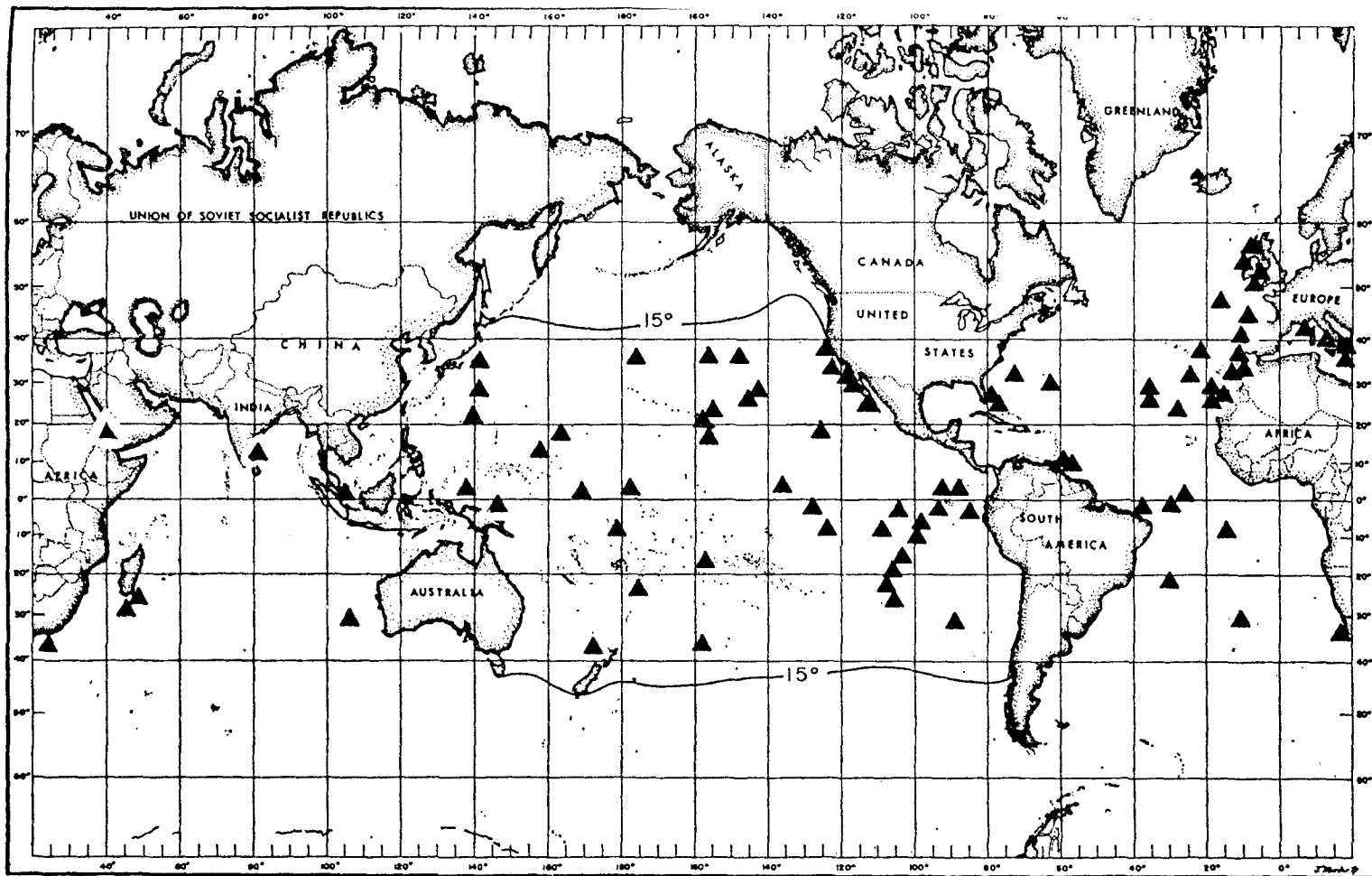crests of all left-sailing form.

Fig. 7.—Some locality records of *Velella velella* from the literature (15 °C summer surface isotherm shown for the Pacific).

Velella is widely distributed in the warm waters of the oceans, and many records of swarms, stretching for miles in the ocean or cast up in wind-rows on beaches, may be found in the literature (see Wilson, 1947; Savilov, 1968). Large numbers of *Velella* (several dozen/m) were found beached in front of the Scripps Institution of Oceanography in May, 1967 (R. A. Lewin, pers. comm.) and again in April, 1972 (see Fig. 5A and B). All of the individuals examined were of the left-sailing form. The pattern of distribution of *Velella*, especially in relation to the two forms, has also been a subject of much discussion (Mednikov, 1957; Bieri, 1959; Savilov, 1961; Edwards, 1966; etc.). Some of the other factors affecting its distribution have been studied in detail by Mackie (1962) and Savilov (1968). The geographical ranges of the two forms in the Pacific Ocean are shown in Figure 6. Some locality records of this species from the literature are given in Figure 7.
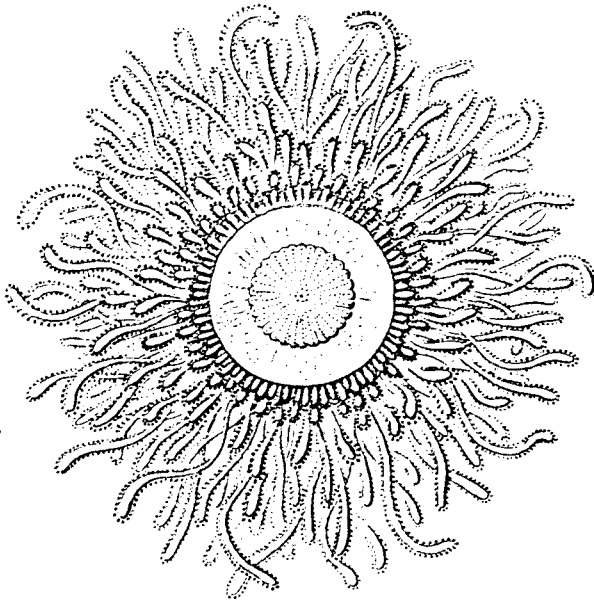

Fig. 8.—Dorsal view of *Porpema* showing numerous tentacles surrounding the central float (from Haeckel, 1888).

The family Porpitidae is represented in the pleuston by two genera, *Porpita* and *Porpema*, characterized by having a circular umbrella bearing a central feeding polyp surrounded by numerous tentacles and a multi-chambered float (Figs 8 and 9). Though lacking a sail, their general structure is in other respects very similar to that of *Velella*.

The taxonomic status to *Porpita* is still unresolved. Chun (1897) and Bigelow (1911) referred all Pacific specimens to *P. pacifica* Lesson, and all Atlantic specimens to *P. umbella* Müller; they were undecided about the Indian Ocean species. Moser (1925), after studying both Pacific and Indian Ocean forms, concluded that there were no clear-cut specific distinctions between them and identified them all as one species, *Porpita porpita* (L.), attributing their variations to age differences. Bigelow (1926), who agreed in

general with her view, found that all the larger specimens (over 12 mm) that he examined had a tuberculate disc whereas all the smaller ones had a smooth disc, and consequently he later considered that there may be two species after all (Bigelow and Sears, 1937). Savilov (1968) found that in his collection all the specimens under 15 mm in diameter possessed characteristics described for *P. umbella* and all those larger than 15 mm were typical of *P. pacifica*. Since there is much variation even among individuals of the same size, more detailed studies on size and age variations will undoubtedly be needed before the species status in *Porpita* can be resolved. Most recent workers, however, tend to agree that there is only one species (Totton, 1954).
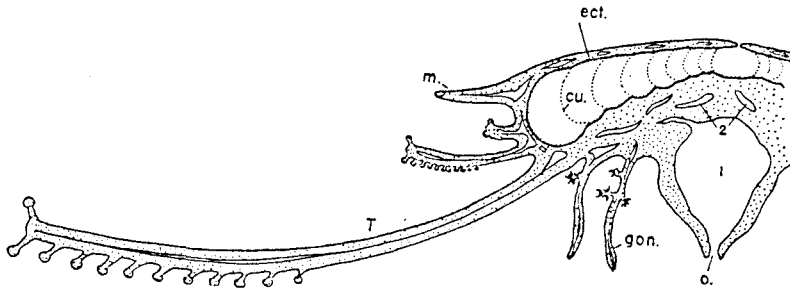

Fig. 9.—Section of *Porpita* showing (cu.) float chambers, (o.) mouth, (gon.) gonophore, tentacles (T), mantle flap (m.), ectoderm (ect.), oral chamber (1) and aboral chambers (2) (from Mackie, 1959).

Not much is known about the developmental biology of *Porpita*, although some stages in the development of young larvae were described by Delsman (1923). Certain aspects of the behaviour of *Porpita* were studied by Mackie (1959). The animals are evidently unable to expel air from their float and sink, and so, lacking locomotive organs, they are obliged to drift passively on the sea surface. When turned upside-down, however, they can somehow quickly right themselves. Mackie observed that in their behaviour these animals are very similar to the sessile hydroid *Corymorpha*, and considered this evidence for a tubulariid affinity of the Chondrophora. The tentacles, used primarily for food collecting, move synchronously. Bieri (1970), who analysed the food organisms caught or ingested by several *Porpita*, found that, in contrast to *Velella* whose food consisted mainly of eggs of fish and crustaceans, over 90% of their diet consists of copepods or other actively swimming crustaceans. Some notes on the symbiotic algae of *Porpita* are given by Taylor (1973).

The distribution of *Porpita* was discussed by Savilov (1968), who reported large concentrations in the western Pacific (Fig. 10), especially in the tropical belt where *Velella* occurs only sporadically.

The related pleuston genus *Porpema* is even less well known. Bigelow (1911), who studied the morphology of these animals in some detail, considered the Pacific species to be *P. prunella* (Haeckel) and the Atlantic species to be *P. globosa* Esch., but later workers assigned them all to one species (Moser, 1925). Since there is no clear-cut generic distinction between *Porpema* and *Porpita*, Totton (1954) suggested that the single genus *Porpita* is sufficient to include all the different species. Thus the systematic status of the genus
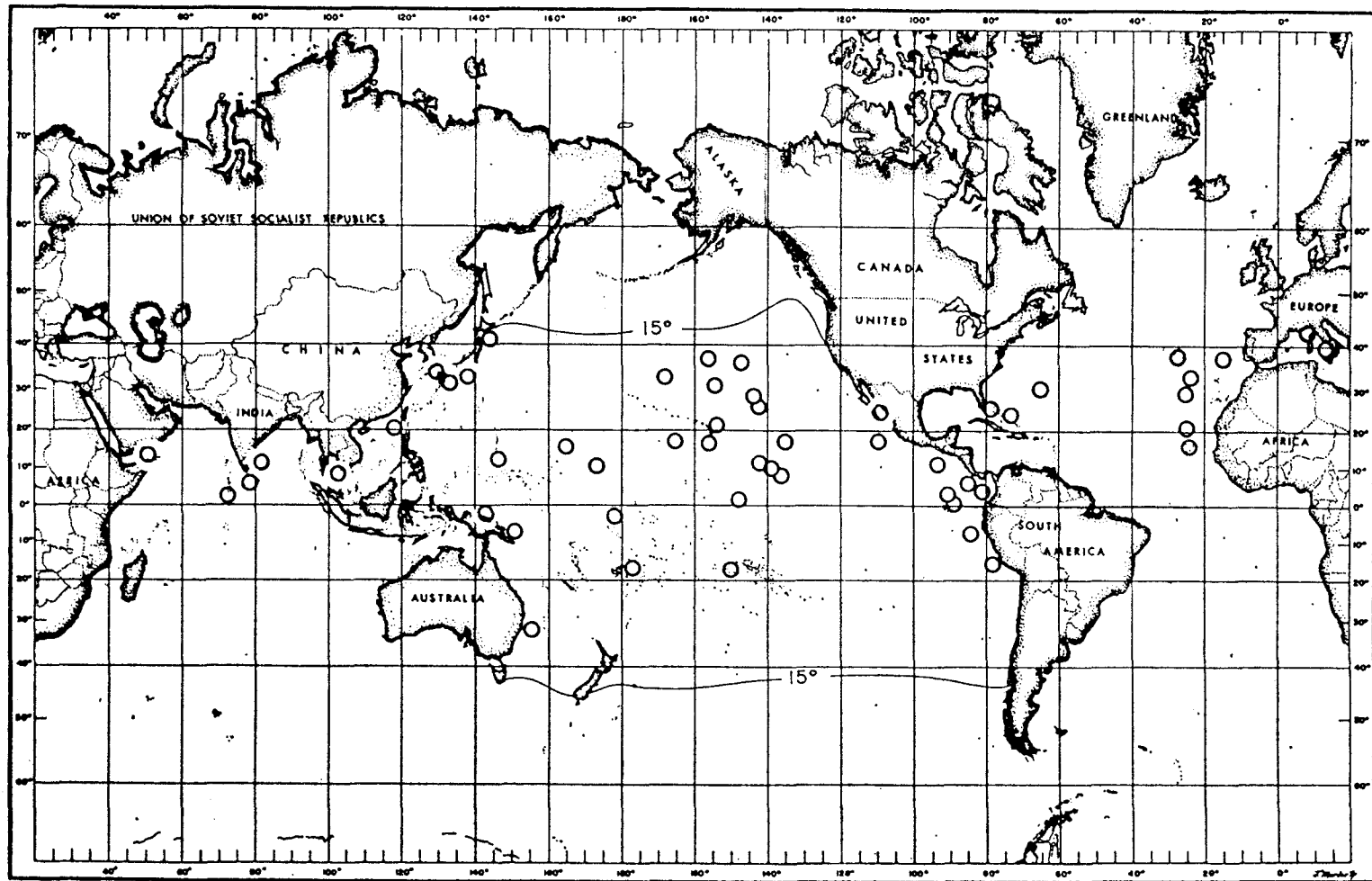
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Fig. 10.—Some locality records of *Porpita porpita* from the literature (15 °C summer surface isotherm shown for the Pacific).

Porpema is still in doubt. Savilov (1968) found some specimens which he identified as *P. prunella* in the Pacific Ocean. The largest recorded specimen was only 7 mm in diameter (Savilov, 1968). Virtually nothing is known about its biology.

ACTINIARIA

The sea anemones are represented in the pleuston by members of the family Minyadidae, with only one genus *Minyas* and five described species (Carlgren, 1949). The pedal discs of these animals are modified to form a float (Hyman, 1940). Apparently very little is known about this family except that its representatives are found in tropical waters of all the three oceans. During the Vityaz expedition in the Pacific, limited numbers of *Minyas* were collected in areas both north and south of the equator. Since they were mainly young animals, the species were not determined.

David (1965a) stated that some members of the Abylidae, too, are found free-floating in tropical waters, although they can also assume a sedentary existence. They occur in the Indo-Pacific, but are not known from the Atlantic. The animals, which are blue or dull green in colour, are buoyed up by a small float consisting of a cluster of air bubbles in the middle of the foot.

Of their food and reproduction, it seems, nothing has been recorded.

GASTROPODA: PROSOBRANCHIATA AND NUDIBRANCHIATA

The pleustonic Prosobranchiata are represented by two genera in the Ianthinidae, *Ianthina* and *Recluzia*. The latter comes to the surface only occasionally, but the former is found only at the surface, where it floats on a raft of air bubbles (Fig. 11).

The systematics of *Ianthina* are complicated by a considerable variation in the form of the shell. Laursen (1953), who reviewed the genus, reduced some 60 described species to five: *Ianthina janthina* (L.), *I. exigua* Lamarck, *I. umbilicata* d'Orbigny, *I. prolongata* Blainville, and *I. pallida* Thompson. *I. janthina* and *I. umbilicata* are the commonest and most widely distributed species in the Pacific Ocean.

The pretty purple shell of *Ianthina* is very thin and light, and may sometimes be found washed ashore on beaches. According to Wilson and Wilson (1956), who recorded strandings for England and Wales, large numbers were found on the northern coasts of Devon and Cornwall in 1954 after violent storms and persistent westerly winds from the Atlantic. The height to width ratio of the shells varied considerably, supporting the conclusion of Laursen (1953) that this character is of questionable taxonomic value. The Wilsons collected some of the more healthy animals and kept them alive in the laboratory for some days. They observed that a mobile appendage of the foot, the propodium, is responsible for capturing the air bubbles for the float. Each new bubble is cemented to the existing bubbles of the float with a rapidly hardening mucus secreted by special glands. If an animal becomes detached and sinks, it is unable to re-float unless the propodium can break the water surface. One animal was observed to expel pellets each containing 20 or so veliger larvae with brownish-purple shells 100–230 μm wide. Another was observed to discharge spermatozoa, also contained in packets. Since these

animals cannot swim freely, the sexes presumably meet only by chance. Evidently *I. janthina* is viviparous, at least under some circumstances; but other species in the genus are known to lay encapsuled eggs, attaching them to the under surface of the float.

Purple snails are known to feed on several pelagic animals (Laursen, 1953) but the main item of their diet is probably *Velella*, on which they have been observed to feed in the laboratory (Wilson and Wilson, 1956), Young animals have also been found on *Velella* taken in nature. In laboratory experiments *Ianthina prolongata* seemed to prefer *Velella* and *Porpita* to *Physalia*, and a 20-mm wide *Ianthina* consumed a 10-mm *Porpita* in 15 min (Bieri, 1966). Noble (1973) states that *Ianthina globosa* may be used as an intermediate host by the parasitic copepod, *Cardiodectes medusaeus.*

Savilov (1968) reported that *Ianthina* is occasionally extremely abundant in some parts of the Pacific Ocean, and that he was sometimes able to collect more than 1,000 specimens in 20 min. He discussed the distributions of all five Pacific species, indicating that temperature is likely to be a factor limiting their distribution as suggested by Bieri (1966), but we still have no critical data on the limits of distribution for each of the species. The distribution of *I. janthina*, in the Pacific Ocean, is given in Figure 12.

Isolated individuals of another snail, *Recluzia* (*R. montrouzieri* Brazier?), have sometimes been found associated with *Ianthina* (Savilov, 1968). The shell of this rare animal is similar in shape to *Ianthina* but pale creamy-yellow instead of purple in colour.

The Nudibranchiata are represented in the pleuston by the family Glaucidae, comprising two genera, *Glaucus* and *Glaucilla*. A critical review of the published literature on the Glaucidae was given by Thompson and McFarlane (1967). They revised the earlier taxonomic studies by Bergh (1868, 1884, 1899), added detailed accounts of the morphology, anatomy, and histology of the alimentary, nervous, and reproductive systems of these unusual molluscs and concluded that all the described 'species' of *Glaucus* should be referred to a single circum-tropical species, *G. atlanticus* Forster.

Glaucus (Fig. 13) is usually found at the water surface with its ventral surface uppermost, floating with the aid of an air bubble in its stomach. The bubble is presumably of swallowed air, since the animal does not appear to be able to secrete gas (Thompson and McFarlane, 1967). Feeding of these molluscs has been described by Bennett (1836) and Bieri (1966). In nature their main food appears to be *Velella* and *Porpita*, but in the laboratory they were found to prefer *Physalia*, taking as much as several hours to eat the gastrozooids of their prey (Bieri, 1966). Adults, which are dark-blue like almost all other pleuston animals, may reach over 30 mm in body length. They are hermaphroditic; mating takes place on the surface of the sea. The eggs, held together in strings of 12 to 15, may be shed into the sea or first attached to prey (Bennett, 1836). Details of the development of the egg and larva are not known.

Thompson and McFarlane (1967) recognized two other valid species in this family, both belonging to the genus *Glaucilla*, namely, *G. briareus* Bergh and *G. marginata* Bergh. They are apparently both quite rare, and are distinguished from *Glaucus* by the arrangement of the cerata in more than one series and by the absence of a hooked spine on the penis (Thompson and McFarlane, 1967).
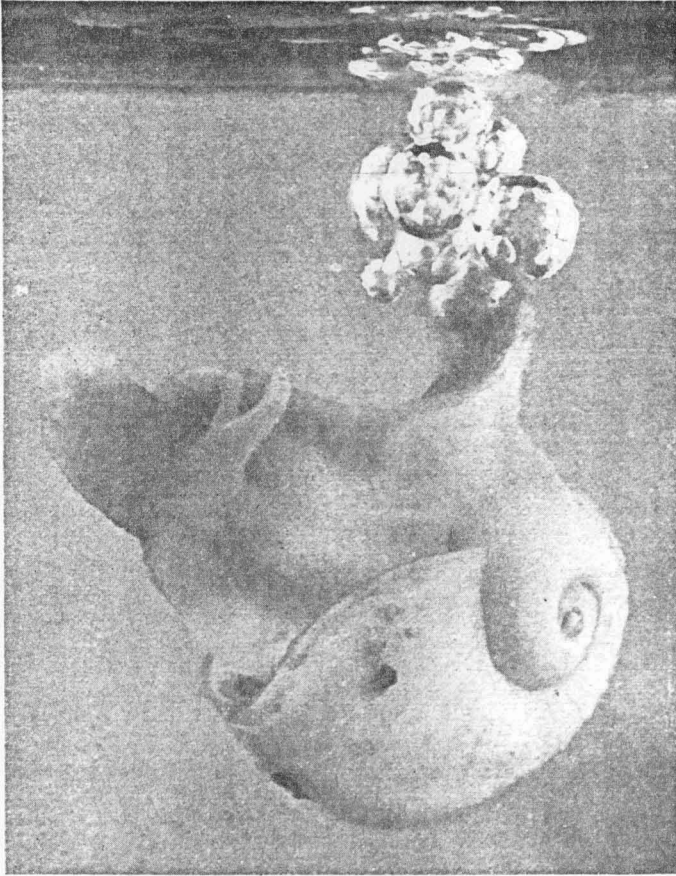
Fig. 11.—*Ianthina* with half-built float of air bubbles;
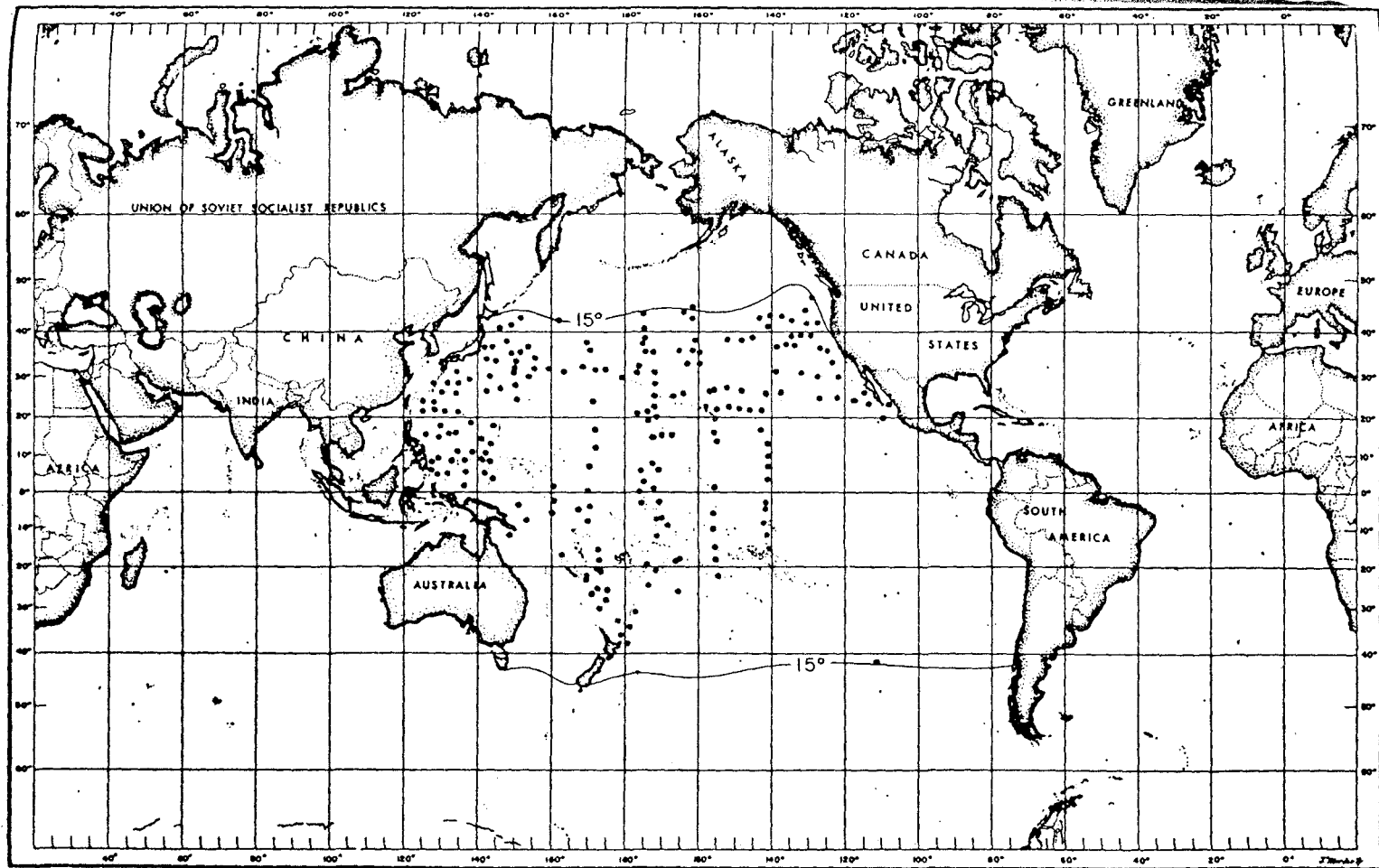shell width ≈ 20 mm.

Fig. 12.—Some locality records of *Ianthina* spp. in the Pacific Ocean: records not available for the other two oceans (15 °C summer surface isotherm shown for the Pacific).
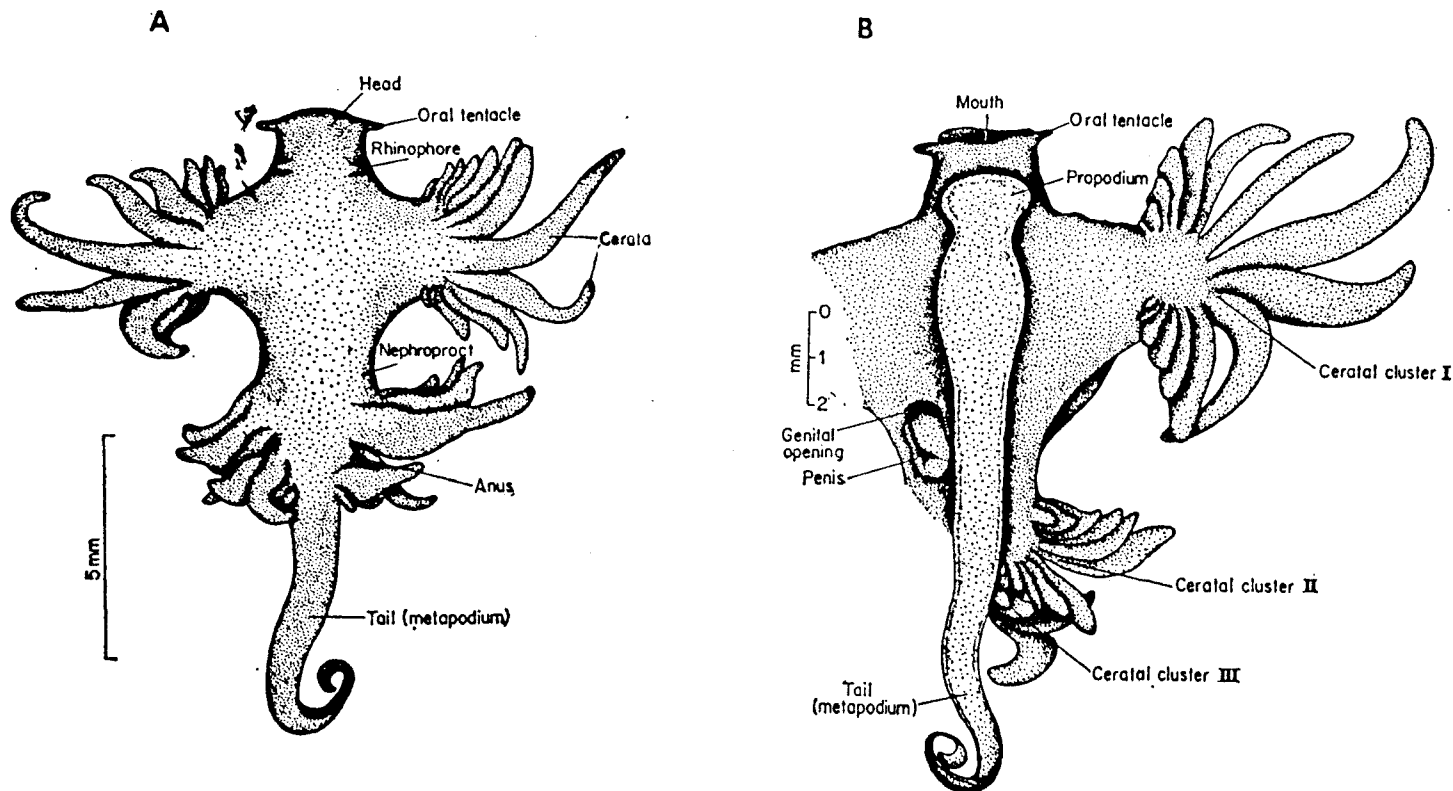
Fig. 13.—(A) Dorsal and (B) ventral views of *Glaucus* showing various structures (from Thompson and McFarlane, 1967).

CEPHALOPODA

Many kinds of cephalopods may occasionally be caught at the sea surface, but the only true pleuston representatives are members of the family Argonautidae, with its only genus *Argonauta*. These animals have light, almost paper-thin shells, and further increase their buoyancy by retaining air in the inner chambers of the shell, as in the pearly *Nautilus* (Denton and Gilpin-Brown, 1966).

The systematic status of the genus *Argonauta* has not been elucidated. On the basis of rather small samples, Robson (1932) described six species. Until age and other sources of variations of the shell have been further studied it would be difficult to determine how many of these species are valid.

Savilov (1968) collected specimens from some 40 stations in the Pacific Ocean and assigned them to two different species, *Argonauta hians* Solander and *A. böttgeri* Maltzen (the latter possibly a variety of *A. hians*). The adults ranged in size from 20 to 40 mm; individuals under 20 mm, mostly juveniles, were not identified to species. Many of the shells contained eggs. Females with heavy egg masses are reported to attach themselves to floating objects to help them keep afloat (Savilov, 1968).

CRUSTACEA

Although many different groups of crustaceans may be found associated with surface animals or occur in surface waters, some being especially attracted by lights at night, the only species that can be considered as a typical permanent member of the pleuston is the cirripede *Lepas fascicularis* Ellis and Solander (Fig. 14).

Members of the genus *Lepas* all attach to floating objects at the cyprid stage. *Lepas anatifera*, *L. pectinata*, and *L. (Dosima) fascicularis* are occasionally found growing on *Velella* skeletons or other floating debris, but only the last species has adapted itself to pleuston life by reducing the weight of its skeleton and by developing the ability to secrete a float. Initially the larvae are free-swimming members of the plankton, but they need to settle, generally on a feather or some other small and light object in the flotsam, for a very short period of time before the float is formed. According to Savilov (1956) who observed these animals at sea, the adult can swim slowly, by moving its stalk, at the water surface where, instead of straining plankton from the sea like most other barnacles, it is adapted to capturing and preying on other animals such as *Velella*.

Lepas fascicularis is cosmopolitan in distribution and in some areas may be found in large numbers. In addition to individuals, Savilov (1968) also found groups of as many as 20–25, aggregated by sharing a common float. Such floats may reach 15 cm or more in diameter. Evidently their inability to swim freely under these circumstances does not seriously impair their ability to survive.

It is worth mentioning here that for some unaccountable reason many normally planktonic crustaceans have water-repellent exocuticles, and tend to be trapped at the sea surface if they chance to break the water–air interface. In this condition they more readily fall prey to pleuston predators, especially to *Halobates* (see next section).

INSECTA

The insects are represented in the surface water by members of the Hemiptera, two families of which have marine forms: the Veliidae and the Gerridae. Several genera of veliids, notably *Halovelia* and *Trochopus*, are known from nearshore marine habitats. Members of the Gerridae, among the commonest inhabitants of the surface film, include several genera with nearshore marine forms, e.g., *Rheumatobates* (Cheng and Lewin, 1971) and *Hermatobates* (Cheng, 1966), and the only known genus of exclusively oceanic insects, *Halobates*. Since the last genus was reviewed in an earlier volume of this series (Cheng, 1973a) several more recent studies on their behaviour, biology, and biochemistry have been added to the literature (Cheng, 1973b, 1974; Cheng and Enright, 1973; Lee and Cheng, 1974), and a new species has been described from the Red Sea (Schmidt and Müller, 1973).

OTHER ANIMALS ASSOCIATED WITH MARINE PLEUSTON

Many other animals are closely associated with typical pleuston organisms, using them as either substrata or as food. Some of the commonest associates of pleuston are pelagic crabs and young shrimps, isopods, the nudibranch *Fiona*, *Lepas*, and pelagic polychaetes.

The existence of oceanic crabs was first documented by Columbus and his crew when they sailed across the Atlantic in 1492 and, seeing crabs on floating seaweed, thought they were close to land. Various other records of oceanic crabs may be found scattered in the early literature, and a dozen names were given to specimens collected from widely separated geographic locations between 1775 and 1858. Although *Pachygrapsus marinus* (Rathbun) is occasionally found associated with pleuston organisms in nearshore habitats, the commonest truly pelagic crabs associated with floating seaweeds and other flotsam are species of *Planes*. A review of the genus, giving the early literature on these oceanic crabs, was given by Chace (1951), who examined all the available material and came to the conclusion that there are only two 'good' species, *Planes minutus* (L.) in the Atlantic and Indian Oceans, and *P. cyaneus* Dana in the Pacific Ocean. Since, however, these crabs are extremely variable, the specific distinctions seem rather arbitrary, the main difference being the smaller size (3·7–19 mm in carapace length) and the much longer walking legs of *P. minutus* compared to those of *P. cyaneus* (5–25 mm). Some earlier workers considered, perhaps rightly, that all such pelagic crabs belong to a single species (Boone, 1926).

Planes is commonly found on floats of *Ianthina* and *Lepas*, skeletons of *Velella*, pieces of wood, floating *Sargassum* and other algae, and also on tar lumps and plastic chips. The colouration of these crabs depends somewhat on that of their substratum, being generally yellowish with paler patches when associated with *Sargassum*, yellowish on turtles and pale plastic chips, dark-reddish-brown on driftwood, lilac blue on *Ianthina*, and dark-blue to black on tar (Crane, 1937; Chace, 1951; Savilov, 1968; Cheng, personal observations). The colouration and colour changes of *Planes minutus* have been studied
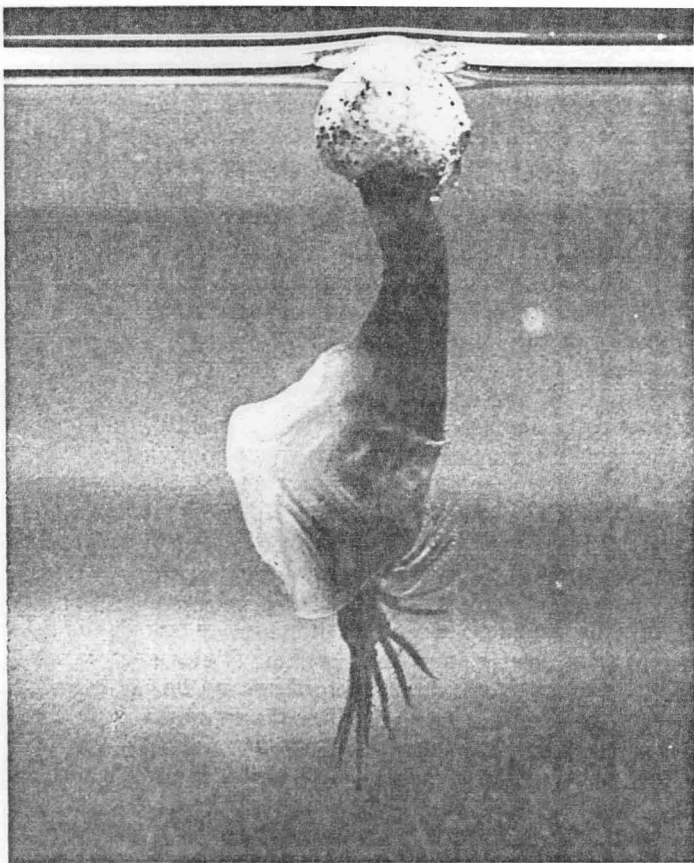
Fig. 14.—Lateral view of *Lepas Dosima fascicularis* showing float
and translucent, lightly calcified shell; capitulum ≈ 20 mm.

by Hitchcock (1941), who found their chromatophores responsive to white, black, red, blue, yellow, and green backgrounds.

The food of *Planes* is not known. One individual, found on the tail of a green turtle, was found to contain partly digested animal matter in its gut and was thought to have been feeding on the excrement of the turtle (Chace, 1951).

The distribution of *Planes* depends largely on the abundance of flotsam or pleuston organisms. The known distributions of the two species have been given by Chace (1951).

The idopod *Idothea* is often found clinging to pleuston organisms as well as to other floating objects such as lumps of tar and pieces of plastic. In this animal, too, there may be considerable colour variation depending on the substratum, its colour ranging from greyish-brown to reddish-brown or blue-black. Many of the animals found on tar exactly match the colour of the oil aggregates (Herring, 1969; Cheng, pers. observ.). The pigmentation of *I. metallica* Bosc., the commonest species, has been discussed in some detail by Herring (1969). This isopod feeds on algae and on smaller crustaceans such as pontellid copepods (Dow and Menzies, 1957; Herring, 1969); the diet and feeding mechanism have been studied by Naylor (1955).

The nudibranch *Fiona pinnata* (Esch.) may sometimes be found on the skeletons of *Velella* and *Porpita*, floating fragments of algae, wood, and other objects. Specimens found on the chondrophores have blue papillae, whereas others generally have brown papillae (Savilov, 1968). Their diet is, so far, a complete mystery.

Although many species of polychaetes are known to swarm at the surface, only one, *Hipponoe gaudichaudi* Audoin et Edwards (Amphinomidae), is known to be specifically associated with a pleuston animal (Savilov, 1968). These worms are found in the mantle cavities of *Lepas fascicularis*, where they may reach 20 mm in length. Savilov (1968) found that in the central Pacific Ocean south of the Equatorial Countercurrent some 30–40% of the *Lepas* were infected, each having one or two worms, whereas in more northern regions none of the *Lepas* examined was infected. Possible reasons for this differential infection were not discussed.

In addition to the typically pleustonic *L. fascicularis*, several other species of *Lepas* can sometimes be found on skeletons of *Velella* and *Porpita*, shells of *Ianthina* and other floating objects. Unlike *Lepas fascicularis* they do not make bubble floats and depend entirely on their substratum to remain afloat. Other animals often found on similar substrata include bryozoans, hydroids, turbellarians, and even young penaeid shrimps.

One of the most important symbiotic relationships among pleuston organisms is that between *Velella* or *Porpita* and its intracellular algae or zooxanthellae (Droop, 1963). Although the importance of zooxanthellae in the nutrition of their coral hosts has been demonstrated by Goreau and · Goreau (1960), Yonge (1963), Muscatine and Cernichiari (1969), and others, it seems probable that no similar work has yet been carried out on the chondrophores.

The little fish *Nomeus gronovii* is often found among pleuston animals, especially among the tentacles of *Physalia*. It appears to be immune to the toxin of this coelenterate (Lane, 1960), as is the clown fish *Amphiprion* to the stinging cells of certain host anemones: they may even feed on the tentacles of their 'hosts'.

It seems probable that the unequal upper and lower mandibles of fishes such as 'half-beaks' (*Hemirhamphus*) and birds such as 'skimmers' (*Rhynchops*) are specific adaptations to feeding on prey at the sea surface.

TEMPORARY COMPONENTS OF MARINE PLEUSTON

Samples of marine pleuston often contain many species found only temporarily or occasionally on the water surface. They include eggs and larvae of fish, copepods, euphausiids, amphipods, pteropods, salps, certain siphonophores, cephalopods, polychaetes, the larvae of various other benthic animals, and even terrestrial insects blown out to sea. Some of these, notably eggs and larvae of the mullet and anchovy, adult myctophids and pontellid copepods (*Pontella, Labidocera, Pontellopsis*, etc.), are potentially important since they serve as food for many of the pleuston organisms described above.

The literature on surface eggs and larvae of fishes has been extensively reviewed by Hartmann (1970) and Zaitsev (1970). References to studies on the biology and behaviour of some species, especially with regard to vertical migration, may be found in articles by Zaitsev (1959, 1961, 1964), Hartmann (1971), Hartmann and Weikert (1969), Hartmann and Schnack (1969) and John (1973). Some of the literature on other temporarily pleustonic animals has been reviewed by Zaitsev (1970), Weikert (1972), Hartmann (1972) (invertebrates); Heinrich (1971), Weikert (1973) (copepods); Clarke (1966), Hartmann (1969) (cephalopods); and Tebble (1960, 1962) (polychaetes).

DEBRIS IN THE FLOTSAM

A note must be added on the presence of lumps of tar and plastics in the ocean, which in recent years have attracted increasing attention from oceanographers sampling the organisms of the sea surface. Lumps of tar collected from the Mediterranean Sea and the north Atlantic have been discussed by Horn, Teal and Backus (1970) and from the north west Atlantic by Morris (1971); data on pelagic tar from Bermuda and the Sargasso Sea have recently been compiled by Morris and Butler (1973); those from the Pacific Ocean by Wong, Green and Cretney (1974). It has been estimated that in some areas of the ocean surface the amount of tar may be as high as 0.5 mg/m^2 (Horn et al., 1970) in the Atlantic, or 14 mg/m^2 (with an average of 3.8 mg/m^2) in the Pacific, in the same order of magnitude as the weight of neuston organisms caught (Wong et al., 1974). Animals commonly associated with surface tar include the isopod *Idothea*, the barnacle *Lepas*, megalopa larvae of crabs (*Planes*?), and *Halobates* eggs (Horn et al., 1970; Wong et al., 1974; Cheng, unpubl. data).

Pieces of plastics of various sizes, colours, shapes, and compositions have been observed on the ocean surface (Carpenter and Smith, 1972; Venrick, Backman, Bartram, Platt, Thornhill and Yates, 1973; Wong et al., 1974; Cheng, unpubl. data), and some quantitative measurements have been made. On the whole, their 'standing crop' (so far!) is low compared to that of lumps of tar, averaging one plastic fragment/280 m^2 in the Sargasso Sea (Carpenter and Smith, 1972) or 0.3 mg/m^2 in the Pacific (Wong et al., 1974). Since most

of the plastic particles encountered were of rather small size (in the 1–10 mm range) the most common organisms associated with them are small: diatoms, hydroids, bryozoans, and *Halobates* eggs (Carpenter and Smith, 1972; Cheng, unpubl. data). The distribution of tar in the Pacific was found to correlate well with tanker routes; high concentrations of tar and plastic were also correlated with prevailing wind and, presumably, movements of surface water (Wong et al., 1974).

SPECIAL PROBLEMS AT THE SEA–AIR INTERFACE

SURFACE TENSION

A unique feature of the sea surface is the surface tension created by the cohesive forces of the water molecules. Some animals living at the sea–air interface can utilize the surface tension to support them, as does *Halobates*; others must be able to break the surface membrane in order to surface or submerge.

CHEMISTRY

Being immediately in contact with the atmosphere, the surface layer of the ocean contains more dissolved oxygen than the underlying water mass, except when the latter has been supersaturated by the photosynthetic activities of phytoplankton. Baylor, Sutcliffe and Herschfeld (1962) have shown that a much higher concentration of organic phosphate, too, may be found at the sea surface, providing an augmented source of this nutrient for neustonic microorganisms. In addition, various hydrophobic substances and materials lighter than water tend to accumulate at the surface film, as also do proteins (Dietz and LaFond, 1950; Ewing, 1950) and other dissolved organic carbon compounds, nitrates, and nitrites (Cooper, 1948; Goering and Menzel, 1965; Goering and Wallen, 1967), and surface-active materials in general. The water-insoluble components of the surface film consist largely of lipids and hydrocarbons (Garrett, 1965). Recent studies have shown that surface water, in the top 100–150 μm, has a much higher concentration of heavy-metal ions such as lead, iron, nickel, and copper, as well as fatty acids, hydrocarbons, and chlorinated hydrocarbons (Williams, 1967; Duce, Quinn, Olney, Piotrowicz, Ray and Wade, 1972), from various sources: atmospheric transport and coastal run-off are probably the major contributors. Air bubbles migrating through the water column may also carry adsorbed organic substances to the sea–air interface (Baylor and Sutcliffe, 1963; Sutcliffe, Baylor and Menzel, 1963; Carlucci and Williams, 1965, etc.) where they may form aggregates (Riley, 1963). Special chemical and physico-chemical properties of the top millimetre of the ocean have recently been reviewed by MacIntyre (1974).

SOLAR RADIATION

An important ecological factor in the marine environment is solar radiation which provides energy for photosynthesis by phytoplankton but which may also have deleterious effects on living systems. Most marine organisms are

screened from such effects, since in clear ocean waters at least half of the total incident radiant energy (virtually all the light in the infra-red range above 700 nm) and at least 15% of the ultraviolet radiation (below 300 nm) are absorbed by each metre of water (John Tyler, pers. comm.; Holmes, 1957). Pleuston organisms, lacking such a protective screen, presumably need other means to protect themselves, in particular from UV and infra-red radiation. Several special features of surface animals, e.g., the almost universal presence of blue carotenoproteins or a whitish sheen on the dorsal surface, have been suggested as serving this function (Herring, 1967), but the mechanism by which these animals avoid or avert UV damage has not been quantitatively evaluated.

TEMPERATURE

A direct effect of the absorption of solar energy is an increase in water temperature at the surface layer; conversely, heat loss through evaporation and infrared radiation from the surface tend to reduce it. Ewing and McAlister (1960) found that the temperature of the top 0·1 mm of the ocean may be 0·6 °C cooler than that of the water just below. Zaitsev (1970) stated that, even in the absence of wind-induced mixing, there were no detectable temperature differences in the top 5-cm layer of water in the Black Sea; however, my experiments with a thermistor have indicated that in an aquarium the surface water (the top 1 mm) may be warmed to a temperature at least 3 °C above that of the underlying layers (25 °C at a depth of 3–5 cm) by surface irradiation from a 200-watt lamp. It is possible, therefore, that on calm days the surface water may be appreciably warmer than the water mass beneath it. This problem is complicated by the general lack of adequate instrumentation for measuring temperatures precisely at the water surface. There is a practical need for more detailed studies in this field, since the temperature at the water surface must affect the rates of development of certain forms of economic importance, notably fish eggs and larvae.

SALINITY

After heavy rains, the salinity of surface water is reduced to a value below that of the underlying layers. The effects of such temporary decreases in salinity on the life of surface animals are not known.

WIND

Wind plays a key rôle in surface mixing, but its effects on pleuston organisms are not adequately known. Most pleuston organisms are passive drifters; only *Halobates* is capable of effectively controlling its movements over the ocean surface. Yet, even for these active insects, the main factors determining their distribution are the relative actions of wind and ocean surface currents. Since their bodies are mostly above the water, winds probably play a much more important rôle than currents in this respect, so that after heavy storms large numbers of pleuston animals may be found stranded on beaches far from their normal ranges (see pp. 187, 192, 195 on *Physalia*, *Velella*, and *Ianthina*).

SAMPLING PROBLEMS

The sampling of the surface film, especially for chemical analysis, presents special problems (see MacIntyre, 1974; Hatcher and Parker, 1974); it will not be discussed here.

Various sampling devices for collecting neustonic or near-surface bacteria, phytoplankton, invertebrates, fish eggs, and fish larvae have been described by Zaitsev (1970), who was one of the first to devise nets specifically designed to catch animals at the water surface (Zaitsev, 1962). For sampling the fauna of the uppermost 10 cm of the sea, David (1965b) devised a neuston net which has since been modified and used by various other workers. A comparison of all neuston samplers described prior to 1970, including the Booby II (Bieri and Newbury, 1966) and the Otter Surface Sampler (Sameoto and Jaroszynski, 1969), was published by Hartmann (1970). The most important feature of all these nets, as opposed to conventional plankton nets, is the presence of some kind of float to keep the mouth of the net at the water surface. Unfortunately, with such nets quantitative data can be obtained only when the sea is extremely calm, a rather rare phenonemon in nature. Miller (1973) therefore devised a 'push-net', for continuous quantitative sampling of surface organisms, so designed and operated that even in less than totally calm sea conditions the mouth opening tends to remain at the water surface, permitting more reliable quantitative samples to be obtained. He found it especially satisfactory for sampling fish larvae. Miller's push-net is, however, designed for operating from a catamaran or other twin-hulled small boat, and is not suitable for work on the open ocean. On research vessels of the Scripps Institution of Oceanography the device currently in use for collecting surface organisms, including pleuston, consists of a net hanging behind a rectangular metal-framed opening 1 m wide and about 30 cm high, maintained at the surface by a pair of styrofoam floats. This device has been found quite easy to handle and is generally satisfactory under calm sea conditions. By suitably adjusting the angle of the tow line one can sample the water surface for 95–100% of the time even at a towing speed of 4 kt in moderate swells of 1–2 m. This net is not, however, reliable for providing quantitative data. An ideal pleuston net, usable under various sea conditions, capable of maintaining its position during the entire sampling period, easy to handle, and preferably towed off the side or pushed in front of the ship away from disturbances caused by the ship's movement, remains to be devised.

FOOD CHAIN RELATIONSHIPS

The unique feature of the pleuston community is the apparent absence of free-living primary producers and hence of herbivores; only carnivores of the first, second, and higher levels are present. The commonest and most abundant animals in the pleuston are the 'lift predators' *Physalia*, *Velella* and *Porpita*, which appear to form the bases of this surface-living community by drawing up from below such food as eggs and larvae of fish, copepods, and euphausiids. *Velella* has been reported in the stomachs of coho salmon collected off the coasts of British Columbia by Pritchard and Tester (1944).
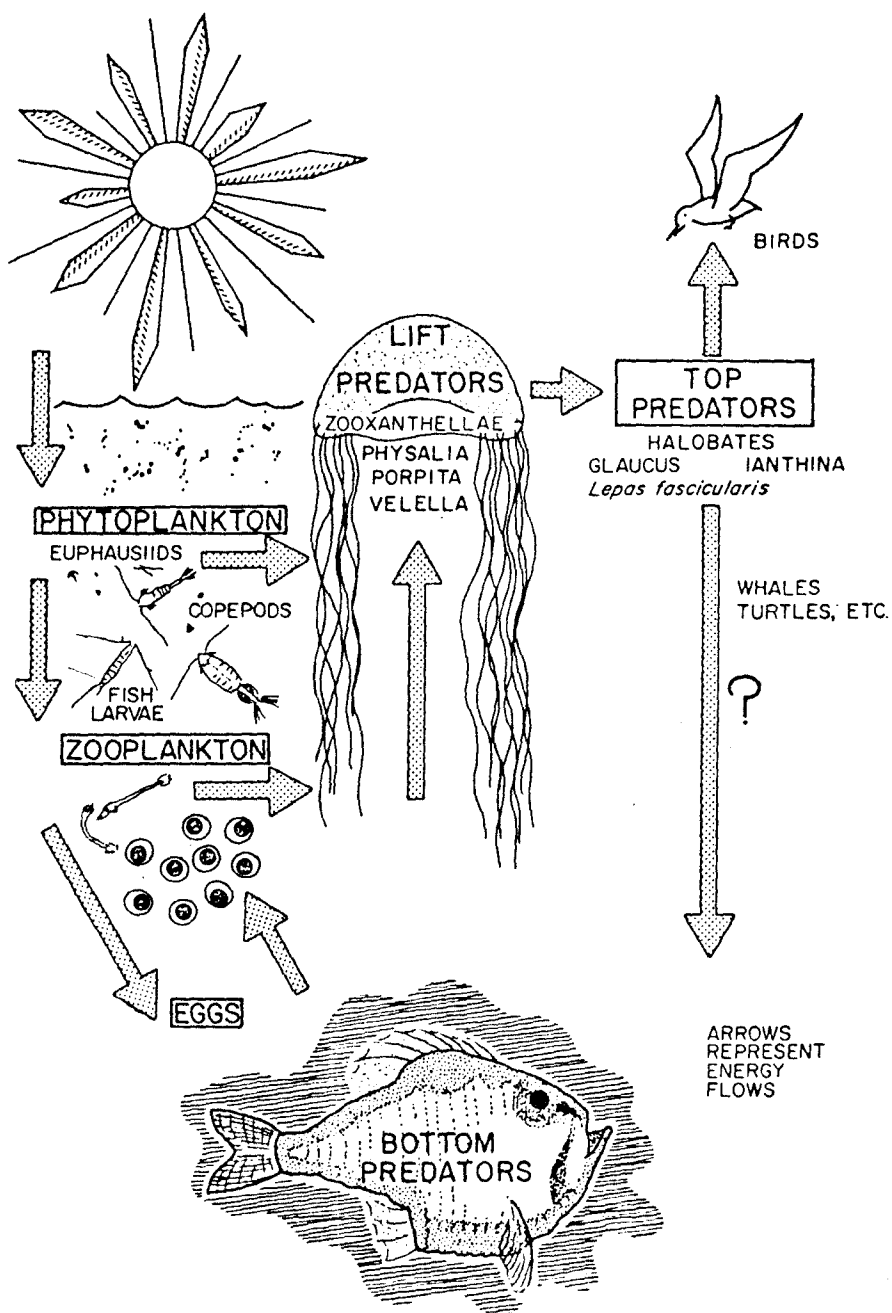
Fig. 15.—Food-chain relationships of pleuston in the marine environment.

Certain of these lift predators presumably also obtain some nutrient from their symbiotic zooxanthellae. Little is known about which animals prey on the 'top predators' (*Halobates, Glaucus, Ianthina*) of this community in their natural environment. *Halobates* has been occasionally found among the stomach contents of some sea birds (Ashmole and Ashmole, 1967; Cheng, 1974) and may also be taken by surface-feeding fishes (Cheng, 1974). There are, however, no known predators of *Ianthina* and *Glaucus*, neither in their juvenile nor in their adult stages (Bieri, 1966).

The nutrient relationships among different organisms in the pleuston community have been summarized by Savilov (1968) in his "food-chain scheme". A simpler food web, including only some of the better-known animals, has been presented by Bieri (1966). A diagram partly based on these two models is given in Figure 15, to show possible food and energy pathways between pleustonic and other animals in the ocean.

ECOLOGICAL CONSIDERATIONS

SPECIAL ADAPTATIONS

One of the prerequisites of a pleustonic existence, as has been mentioned before, is the possession of some kind of flotation device. This is achieved by different animals in different ways. Thus, *Physalia* has a single-chambered float secreted by special gas glands, *Velella* and *Porpita* have similar floats but with many chambers, *Glaucus* swallows air into the gut, *Minyas* has a float in the foot, *Ianthina* and *Lepas* build floats of air bubbles cemented together by mucus, while *Halobates* supports itself by the surface tension of the water. Unfortunately, apart from the anatomical and morphological structures involved, details of the mechanisms of most of these flotation devices are still unknown. For instance, there has been apparently no adequate consideration of the extent to which an animal like *Physalia* can control its own sailing. It has, as it were, a retractable keel, rather like the centre-board of a sailing vessel. When its tentacles are fully contracted close under the float it is clearly subject to displacement by every gentle breeze, but if it extends the tentacles into the relatively still layers of the underlying water, the animal is effectively 'rooted' to the spot—unless or until the wind-shear is so great that it tears the float loose from its anchorage. How often this might happen in fact is quite unknown.

COLOURATION

The next most striking feature shared by almost all pleustonic organisms is perhaps their brilliant blue coloration which contrasts with the red or orange colour of most pigmented zooplankton found in deeper waters. The taxonomic distribution of these blue animals, and the location of the pigments in their various organs and tissues, have been reviewed by Herring (1967). He found that the pigments extracted from several unrelated neuston animals all have an absorption maximum in the range of 630–660 nm. This is not readily understandable since, as Herring pointed out, light of this wavelength (red) is not considered to be particularly harmful to living organisms, and so the

blue pigments are not likely to have any direct protective function, as was suggested by Heinrich (1960). Fox and Haxo (1959) considered that the blue pigment in *Velella* might protect its symbiotic algae against radiation damage, but this requires further investigation. Certainly the blue colour of these animals matches, at least on fine days, that of the clear ocean water on which they occur, and may thus serve to camouflage them and to conceal them from possible predators. Several other possible functions of the pigments have been suggested by Herring (1967), but none of them provides a satisfactory explanation for all of the animals concerned.

GENERAL DISTRIBUTION

Marine pleustonic animals are more or less confined to a two-dimensional environment at the sea–air interface. They are generally found only in tropical and subtropical regions between latitudes 40° N and 40° S, where the surface temperature rarely falls below 10 °C (Savilov, 1968). Though the exact boundaries of their distribution probably vary with seasonal wind and surface current conditions, some pleuston animals may be found as far north as the British Isles (56° N) (Russell and Kemp, 1932; Wilson and Wilson, 1956), Vancouver Island (50–52° N) (Doe, 1955) and even in the Gulf of Alaska (54° N) (Savilov, 1968). Until seasonal and quantitative data for each species are available, their distribution limits cannot be drawn accurately.

PRODUCTIVITY AND BIOMASS

The seasonal productivity of the pleuston cannot be estimated since we do not know the generation times of any of the organisms (except for some guesses for *Halobates*). We can, however, make some rough estimates of standing crops. The biomass of the oceanic pleuston has been calculated by Savilov (1968) to be in the range of 1 g/m², or 1 tonne/km². (Note that since the animals occupy only a two-dimensional environment, pleuston figures are given for km² and not km³.) This figure, presumably based on wet weight, seems to me unrealistically high. Estimates calculated from personal experience with pleuston densities (after subtracting non-pleustonic organisms) in the central north Pacific Ocean (28–30° N: 155° W) in the winter months hardly exceeded 200 g (dry weight)/km² or 2 kg (wet weight)/km². (These figures are still two orders of magnitude higher than that for the biomass of terrestrial insects found on the surface of the Black Sea (42–46° N) in the summer, and calculated by Zaitsev (1970) to be about 2·5 g (dry weight)/km². On the north Pacific the weight-ratio of terrestrial insects to total pleuston is roughly 1 : 1000.) Though the biomass figure for the summer season may be slightly higher, say by one order of magnitude, it is still extremely low compared with estimates of total neuston biomass, namely, 2 to 4 tonne/km³ for subsurface waters in the Gulf of Mexico and 3 to 6 tonne/km³ for the Black Sea (Zaitsev, 1970). It is perhaps for this reason that the animal community of this particular layer of the ocean has not hitherto received much attention by marine biologists. This is a pity, because in some ways a two-dimensional system is much easier to study than that of plankton.

POPULATION STABILITY

An essential feature of any stable population is the ability of at least some of the progeny, sooner or later, to return to the breeding area of their parents. In the case of pleustonic organisms—which are passive drifters, subject to the movements of winds and waves—a stable population can only be maintained on a surface system which is still, reciprocating or circulating. The elucidation of details of such systems is one of the primary objectives of zoogeographic studies: for pleustonic animals, whose distributions are not complicated by vertical movements of the water, the problems are greatly simplified.

CONCLUDING REMARKS

The literature on pleuston animals, dating back to the 1750s, is widely scattered and is at present largely limited to considerations of taxonomy, some anatomical, morphological and general biological information, together with distribution records for certain species or taxonomic groups. Savilov (1968) estimated that in the world's oceans there are only about 100 species of pleustonic animals, mostly belonging to the following orders: Siphonophora, Chondrophora, Actiniaria, Turbellaria, Gastropoda, Cephalopoda, Polychaeta, Isopoda, Decapoda, Cirripedia, Copepoda, Insecta, and Pisces. On the whole, comprehensive and up-to-date studies on most of these animals are still lacking and our present knowledge of any of them is at best only fragmentary. Many more systematic collections, natural observations, and laboratory studies have to be made before we can claim to have adequate information on their diets and life cycles, and before we can begin to analyse the associations, the patterns of their geographical distributions, and the effects of various chemical and physical factors on these fascinating animals.

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