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Marine neustonology

by Yu. P. Zaitsev

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MARINE NEUSTONOLOGY

by

Y.P. Zaitsev

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This monograph summarizes for the first time data on the biology of the sea-air interface, which form the subject matter of a new field of hydrobiology - neustonology. An examination is made of the methodology of investigating the structure, composition, numbers, ecology, dynamics and distribution of neuston. The important role played by neuston in the propagation of marine organisms and in the cycle of substances in nature is discussed. An assessment is given of the importance of neustonological research in increasing the effectiveness of practical measures aimed at the protection, regeneration and rational utilization of the biological resources of the ocean.

This monograph is written for oceanographers, hydrobiologists, ichthyologists, radiobiologists, fisheries experts and nature conservationists.

EDITOR-IN-CHIEF

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INTRODUCTION

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Half a century has passed since the renowned Swedish hydrobiologist E. Naumann (1917), counselled by his colleague O. Holmberg, proposed the term "neuston" (das Neuston) to denote the bacteria, Euglena, chlamydomonads, amoebas and other minute plants and animals populating the surface film of small ponds and pools. The established term "plankton", which was introduced by Hensen (1887) to embrace organisms suspended in the body of the water and the term "pleuston" proposed by Schröter and Kirchner (Schröter u. Kirchner, 1896) to denote half-submerged plants like duckweed, did not fit what Naumann defined as the "community of the surface film". This particular life form was best described by the word "neuston" (from the Ancient Greek neo- to float, swim, whereas "pleo", from which the word "pleuston" is derived, denotes swimming or floating in a half-submerged state). Naumann did not insist on his term, but he defined what he meant exactly - microorganisms in the surface film of a water body, as distinct from "plankton" and "pleuston".

Soon however, it became evident that a far greater number of animal and plant species than envisaged by the discoverer of neuston are intimately associated with the surface tension film of water. Observations in nature and in the laboratory

*The numbers in the right-hand margin indicate the page numbers in the original text - Translator's note.

showed that unicellular organisms (bacteria, flagellates, protozoans, etc.) cannot be studied in isolation from such mollusks as Limnaea, Physa, Planorbis, from certain planarians and crustaceans such as Scapholeberis, from the larvae and pupae of culicids (Anopheles, Culex, Dixa and others), or from the larvae of a number of fishes and other organisms, which spend if not their entire life at least a considerable part of it on the underside of the surface tension film - crawling over it or hanging from it, or else swimming just below the surface of the water - and feed on the neustonic microorganisms.

On the other - aerial - side of the film various adult insects dwell and their eggs develop. On the surface of water bodies are spent the lives of the imaginal stages of such widely distributed insects as Collembula (Podura aquatica), Hydrometridae (Hydrometra stagnorum), Gerridae (Gerris lacustris and Heterobates dohrandti), Veliidae (Velia currens) and others. These insects are intimately connected with the aquatic components of neuston through their larvae or food, and they all (hydrobionts and aerobionts) possess a whole set of special devices enabling them to exist within the area of the surface tension film. Hence there is every reason to assign them to the neuston. /6/

Since the complete neuston embraces two large groups of organisms populating both sides of the water-air interface, the necessity arose for distinguishing between them.

The first attempt was made by P.S. Welch (1935). He proposed using the name "infraneuston" to describe the planarians,

cladocerans, larvae and pupae of culicids, mollusks and other organisms living below the surface tension film, and "supraneuston" to denote gerrids, veliids and some spiders living on the surface tension film of fresh waters.

Later L. Geitler (1942) proposed two terms that are etymologically more correct to describe these neuston groups-- i.e. "hyponeuston" (das Hyponeuston) and "epineuston" (das Epineuston).

These were subsequently adopted in the limnological literature (Ruttner, 1952; Kiselev 1956; Liebmann, 1958; Rapoport a. Sanchez, 1963, and others).

As regards the minutest organisms, such as bacteria, which are technically difficult to divide into hypo- and epi- groups, though it is clear that they dwell both under water and on top of it (in foam), the term "neuston" is normally used, as in "bacterioneuston".

The specificity of the neuston assemblage of organisms emerged so clearly that S.A. Zernov (1934) considered it necessary to make it a separate class of communities on an equal footing with plankton (including, according to Zernov, pleuston and nekton) and benthos.

For a long time neuston and pleuston were regarded as specifically freshwater biological structures, though no proofs of basic differences between the surface of continental and marine water bodies as habitats were adduced in support of this position. The first important argument in favour of the

community of these biotopes was the description of marine pleuston given by S.A. Zernov (1934). To this peculiar ecological group of hydrobionts leading a half-aquatic, half-aerial mode of life, which at first included only freshwater plants such as Lemna, Utricularia and Victoria regia, Zernov assigned the sea-dwelling siphonophorans, most of whose float projects above the surface of the water, whereas the lower part of the colony extends to a considerable depth. Recently A.I. Savilov (1956a,b, 1958, 1965) described communities of pleuston siphonophorans from the genera Physalia and Velella for the warm-water part of the Pacific.

Thus only neuston remained as an exclusively freshwater near-surface assemblage of organisms, and there is an explanation for this. As typical representatives of neuston (hyponeuston) attention was very frequently devoted to the larvae and pupae of blood-sucking mosquitoes, control of which forms part of the extensive anti-malarial campaign. The fact that these characteristic components of hyponeuston develop solely in small stagnant or sluggish water basins, where they can quietly cling to the surface tension film, breathe atmospheric air and feed on neuston microorganisms, strengthened the belief that the neuston assemblage of organisms could develop only in ponds and pools sheltered from the wind and were incapable of surviving in the exposed areas of lakes or reservoirs, let alone in seas and oceans. This point of view was widespread and held back development of hydrobiological research on the water-air interface, so that most

of the research was done in the field of medical entomology. Even examples long known to science of obvious analogy to freshwater neuston in the sea (the existence of oceanic gerrids, mollusks crawling over the underside of the surface film of water, crustaceans clinging to it or leaping out of the water, and so on) failed to shake the conviction that it was impossible for an assemblage of organisms such as neuston to populate the surface of seas and oceans. Therefore, none of the diverse types^{of}/gear and procedures for sampling water, bacteria, phytoplankton, zooplankton and ichthyoplankton from the so-called "zero layer" of the pelagic zone of the sea were designed for special investigation of the upper 2-3 cm of the water column. This layer was either ignored, or, at best, removed together with water from the underlying layers. When using the commonest methods of obtaining "surface" biological samples from the sea, bacteriologists and phytoplanktonologists, working with reversing water bottles, actually have zero layer samples within their grasp, but pass them by. Zooplanktonologists use "Juday" nets and obtain "surface" samples by the method of total vertical fishing of the 10-0 m. layer, while ichthyoplanktonologists practise vertical fishing of the same layer or horizontal fishing of the 0.8-0 m. or 1.13-0 m. layer.

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As a result, the least studied biotope of all the productive layers of the sea proved to be the region of the surface tension film, and it should come as no surprise that special research in this biotope yielded from the very beginning a veritable flood of new scientific information.

In one case these investigations were prompted by a study being made of the habitat of highly buoyant pelagic fish eggs (Zaitsev, 1958), in another, by a study of the food items utilized by sea birds (David, 1963), in yet another, by a collection of pelagic Foraminifera (Willis, 1963). These investigations, differing in purpose, scale and comprehensiveness, were conducted in widely separated regions of the ocean and revealed that in the sea, as in fresh water, a rich and varied assemblage of neustonic organisms exists alongside pleuston. However, the main point was not that a uniformly based neuston had been proved to exist in all water bodies of the hydrosphere (as was to be expected), but the role which the neuston turned out to play in the life of the seas and oceans. Because of the extensiveness and depth of marine basins the proportion of pelagic forms in them is much higher than in continental basins. This is graphically illustrated by the example of marine neuston.

As special investigations in the near-surface microlayer of the sea developed, the biological processes taking place in it acquired ever greater importance. The fact that the first link in the chain of investigation was a study of the habitat of the early developmental stages of fish was of positive methodological significance in the sense that this inevitably pointed the way to the solution of a wider range of problems.

The initially determined fact that there was a high concentration of eggs and larvae under the surface tension film on the one hand led to this biotope being named the most import-

ant "incubator" in the pelagic zone, and on the other pointed to the necessity of explaining the reasons for this important circumstance. Later, using special methods, a hitherto unknown aggregation of comparatively large invertebrates was discovered in the biotope - invertebrates which were found extremely rarely in normal samples of "surface" plankton. Subsequently the search for the causes of the abundance of life in the upper /9/ layer of sea measuring less than 5 cm led to the discovery in this layer of an even larger aggregation of small metazoans, followed by protozoans and saprophytic bacteria. This first link in the food chain of neustonic organisms - bacterioneuston - was 2-3 times as dense as the bacterioplankton further down.

The search for the causes of the abundance of saprophytic bacteria near the surface of the sea disclosed phenomena of equal importance. Thus, biological confirmation was obtained of the results of the latest research in the field of marine chemistry, showing that inert organic matter was concentrated at the surface; the phenomenon "antirain" of dead bodies was discovered, as the result of which a considerable number of dead organisms accumulates on the surface of the water and in foam; and the biologically active properties of sea foam were revealed, the foam being able to accelerate substantially the development and growth of animals and plants.

In the light of the new facts marine neuston could be depicted as an extremely important element in the biological structure, of crucial significance in the life of the sea. It

became evident that research in this direction would have to be developed on a global scale. Accordingly, the Presidium of the Ukrainian Academy of Sciences decided to establish the first hyponeuston division in 1966, around the nucleus of the hyponeuston laboratory in the Odessa branch of the Institute of South Seas* Biology. The correctness and timeliness of this organizational measure was confirmed by the results produced by the new division.

Similar research is now being conducted in biological, oceanographic, medico-oceanographic, radioecological and other scientific centres in many countries.

No more than 10 years have passed since the first special studies of marine neuston were made. Yet the volume, significance and applicability of the scientific data accumulated during this period is so considerable that we can speak of the birth of neustonology - a new and extremely promising branch of hydrobiology (Zaitsev, 1967a).

The present book is the first attempt to systematize and summarize the factual material forming the subject of marine neustonology - a field which, though younger than freshwater neustonology is already more deeply researched.

This book is not without defects of course, and the author will be grateful for any critical comments.

During his ten years of research the author has constantly

*This appears to mean the southern seas of the USSR - Translator's note.

received much assistance from specialists and moral support from many colleagues, to whom he expresses his deep gratitude.

In particular he would like to thank all those who played a direct part in the birth of the new book: his highly enthusiastic colleagues in the hyponeuston division, whose results form the basis of the factual contents of this monograph; the head of the Odessa branch of the Institute of South Seas Biology, Professor K.A. Vinogradov, who supported the author's researches throughout; Professor A.A. Strelkov, who did much to ensure its publication; and G.G. Polikarpov, associate-member of the Ukrainian Academy of Sciences, whose many years of creative collaborative effort bore fruit in the development of the fundamentals of neustonology.

PART I

THE UNIQUE NATURE OF THE ECOLOGICAL CONDITIONS IN THE
TOPMOST LAYER OF WATER IN THE SEAS AND OCEANS

Until recently hardly any effort was made to study the ecological factors operating in the top 2-3 cm of the water column. The abundant material characterizing the present abiotic and biotic conditions near the sea-surface, i.e. temperature, salinity, gas regime, illumination, spectral composition of light, content of organic substances etc., actually relates to layers situated 5-10 cm and more from the surface. The bathometers, thermometers and other oceanographic equipment widely used are not suitable for studying the water closer to the surface, which in any case was of no interest to specialists until recently. That is why, in the early stages of its development, neustonology faced great difficulties when confronted with the necessity of describing the physical and chemical nature of the near-surface biotope, the distinctive life of which had been revealed in some depth by biological methods of investigation.

On the basis of certain data discovered in the oceanographic literature and of results obtained by the hyponeuston division of the Odessa branch of the Institute of South Seas Biology a description will now be given of the environment which produced neuston and determined its role in the life of the sea.

Chapter 1. Illumination, temperature and salinity of the water

The part played by sunlight in the life of the plants and animals inhabiting the sea is well known, and a great deal of research has been devoted to the question of its penetration into the water. However, because of the circumstances already mentioned, a fairly copious literature contains very few papers devoting attention to the upper layers of the pelagic zone.

According to the data of V.A. Rutkovskaya (Table 1), total solar radiation is absorbed most intensely by the first 10 cm of water, which accounts for more than half of all the radiation. The values for the penetration of solar radiation recorded at various depths of the water column reveal the same pattern. For instance, in the Gelendzhik region (according to the same author), 46% of the total quantity of solar radiation reaches a depth of 10 cm, 25% reaches 1.5 metres, and only 7.1% penetrates to 10 m. /12/

Thus, measurements showed that the upper 10 cm of the pelagic zone of the sea "intercept" nearly half the entire quantity of sunlight entering the sea. However, this information is insufficient for studying the neuston habitat. It is important to find out how the solar radiation is distributed within the layer. According to the findings of S.G. Beguslavskii (1956), the topmost 1 cm layer of the Black Sea off the south coast of the Crimea absorbs 20% of the total radiation, the 5 cm layer - 40%, and the 10 cm layer - 50% of

all the sun's rays entering the water. The data of S.G. Boguslavskii and V.A. Rutkovskaya on the absorption of solar radiation by the 0-10 cm layer are similar, but the former author states that the first centimetre has a special place in this layer (Fig. 1).

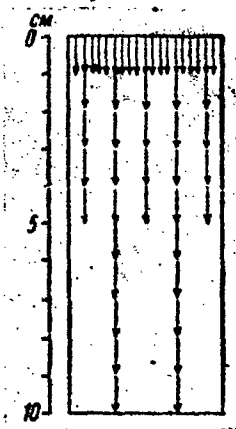


Fig. 1 - Absorption of total solar radiation in near-surface microlayer (depth in cm) of pelagic zone in Black Sea. Each arrow corresponds to 1% radiation absorbed (orig., based on data of Boguslavskii, 1950).

It is evident that further detail will reveal inhomogeneity of illumination in the upper 1 cm layer also. However, the already established characteristics of the vertical microdistribution of solar radiation characterize this layer fairly convincingly as the region of most intense penetration and absorption (hence transformation of the electromagnetic field energy of the light waves into other forms) of sunlight. Bearing in mind the part played by light in the lives of hydrobionts, the biological significance of this fact is difficult to overestimate.

Table 1

Absorption of solar radiation (in % of radiation falling on surface of water body) by layers of water of different thickness, in conditions of cloudlessness and some cloud (Rutovskaya, 1965)

Толщина слоя, м 1	Крымское побережье 2	Геленджик 3	Толщина слоя, м 1	Крымское побережье 2	Геленджик 3
0,1	—	54	7	—	90,0
0,5	60	69	8	—	91,0
1,5	66	75	10	91,0	92,9
2,0	74	80	15	94,4	95,1
3,0	77	83	20	97,0	96,9
4,0	—	86	25	—	97,8
5,0	84	88	30	—	98,6
6,0	—	89	33	—	99,0

Key: 1. Thickness of layer; 2. Crimean littoral; 3. Gelendzhik.

At the same time we know that the rays of different parts of the solar spectrum have different effects on this or that organism or process, and therefore, following on discovery of the fact that the near-surface microlayer of the pelagic zone is strongly illuminated, the question naturally arises as to what the qualitative composition of the penetrant solar rays is. The literature on the subject is extremely poor, but certain general propositions relevant to the question in hand have been established with a fair degree of certainty.

From the data of V.A. Rutkovskaya (1965) it follows that the proportion of longwave ($\lambda = 710$ millimicrons) and shortwave ($\lambda = 420$ millimicrons) radiation diminishes sharply with depth. S.G. Boguslavskii considers that there is hardly any penetration of longwave radiation beyond a depth of 10 cm from the surface of the sea. V.S. Bol'shakov (1963) discovered that this layer absorbs

all rays with a wavelength greater than 1200 millimicrons and cited the data of J. Strong showing that even highly distilled water still absorbs all the rays with a wavelength equal to or greater than the following:

Thickness of layer with complete absorption	Length of light rays, in millimicrons
1	2400
10	1500
100	1000

We know that shortwave radiation (medium and long ultra-violet rays) is absorbed by water just as readily as infra-red radiation. Increase of absorption is particularly steep in the 300-200 millimicron range (Tsukamoto, 1927; Armstrong, Boalch, 1961, et alia).

K.E. Zobell (1946) cites material confirming this and providing an idea of the quantitative aspect of ultra-violet absorption near the sea surface (Fig. 2). The diagram shows that the upper 10 cm-layer of sea water absorbs over 75% of rays with a wavelength of 254 millimicrons^{and} some 60% of rays with a wavelength of 266 millimicrons. Therefore, as Zobell notes in "Marine Microbiology", the intensity of the most harmful bactericidal radiation is reduced by half after passing through the entire 10 cm layer of water. From the viewpoint of neustonology this statement should be rephrased: the upper 10 cm layer of water contains the greatest quantity of biologically active long and medium ultra-violet rays. /14/

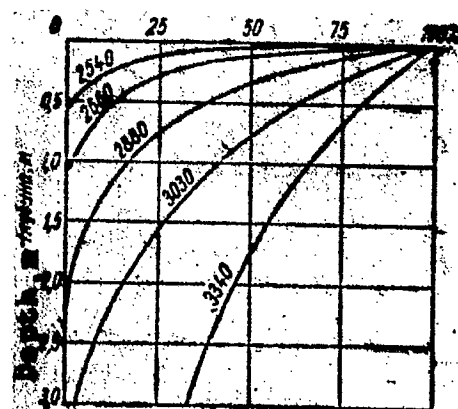


Fig. 2 - Absorption (in %) of shortwave solar radiation (wavelength in Å) by various thicknesses (in metres) of pure sea water (Zobell, 1946, after Hulburt).

And so, in spite of the limited amount of work done on the optical properties of the topmost part of the pelagic zone of the sea, the results of the research which has been undertaken reveal that the near-surface layer, with a thickness of several centimetres, occupies a special position in relation to this ecological factor, as is evident from the intense illumination and concentration here of most of the infra-red and ultra-violet rays of the solar spectrum. Quantitatively and qualitatively the optical characteristics of the upper 5-10 cm of the pelagic zone, and especially the top centimetre, differ sharply from those of the rest of the water column, including the layer situated no more than 10-15 cm from the surface.

Illumination is closely linked to water temperature, since solar radiation is the chief source of warmth in the seas and oceans. However, owing to the fact that mixing (particularly turbulent mixing) processes are constantly occurring in the pelagic zone, the temperature regime of the near-surface layer may

not be marked by the same specificity and stability as the light regime. V.S. Bol'shakov (1963) measured the water temperature in the Black Sea at depths of 5, 10, 20, 50 and 100 cm from the surface, using a Zhukov resistance thermometer with an accuracy of 0.1 C. The investigations, which were conducted during five cruises in fine weather with small waves, failed to reveal any difference in temperature between the depths explored which exceeded the limits of accuracy of the measurements. /15/ These results evidently reflect the consequences of mixing, leading to vertical equalization of temperatures. Nevertheless, in the topmost layer, where most of the thermal infra-red radiation is absorbed, an elevated water temperature was often observed. Thus, in the open part of the Caspian in July 1962, M.S. Rozengurt (oral communication) recorded a temperature of 27.6 C at a depth of 10 cm, and 26 C at 30 cm. Unfortunately, sea water temperature measurements with standard oceanographic equipment do not provide for special study of the upper 5-10 cm layer, which is considerably warmer in calm weather than the 15-20 cm layer. This condition does not last long, but in terms of the lifespan of many hydrobionts it merits attention. Several hours of elevated water temperature is several generations of bacteria, 1-2 cell divisions of microphytes, several stages of development of pelagic fish eggs, and so on.

According to the data of M.V. Tovbin (1949), the water temperature of the surface film of small freshwater ponds on sunny days with no wind is also somewhat higher than in the midwater, but in cloudy weather the picture may be different. In those conditions evaporation leads to a drop in water temperature of

0.3-0.4 °C in the upper microlayer of 4-5 mm. In theory the same thing should happen in the same conditions at sea, but so far there are no data to show this.

Thus, in the light of present knowledge of the subject it looks as though the temperature regime of the near-surface microlayer of the pelagic zone is generally little different from that of the upper 2-3 metres of the water column, but in individual cases where the mixing processes are retarded for some reason or other it develops its own microregime, which is undoubtedly of biological significance, particularly for forms with a short life cycle. This applies to cases where the water temperature is above zero.

At present we do not know the characteristics of the vertical microdistribution of water temperature at the surface of the sea in the presence of ice, but as various initial forms of floating ice (ice needles, ice sludge, shuga*, snezhura**, sklyanka,***, pancake ice, etc.) are typical of the upper 4-5cm of the pelagic zone (Zhukovskii, 1953; Egorov, 1966), we can conclude that with regard to low temperatures the near-surface microlayer of the seas and oceans in the respective latitudes and seasons of the year differs from the underlying layers. /16/

* shuga - small fragments of ice appearing before the freeze-up and in spring when the ice breaks up. - Translator.

** snezhura - a viscous mass formed when snow falls on chilled water.- Translator.

*** sklyanka - meaning could not be ascertained, but probably thin sheets of transparent ice.- Translator.

This fact is also bound to have biological consequences.

The salinity distribution in the Black Sea at depths of 5, 10, 20, 50 and 100 cm was studied by V.S. Bol'shakov (1963). He selected water samples from the first three microlayers with the aid of a special hose-water sampler, the design of which was based on an idea by S.O. Makarov (1894). At depths of 50 and 100 cm an Alekseev water bottle, type "Severnnyi Polyus", with a capacity of 350 cc, was used.

The observations revealed no substantial differences in salinity as between various microlayers. Only in one or two cases was a discrepancy noted in the 50-100 cm layer which exceeded the limits of accuracy of measurement, but was close to them. It is probable that the mixing described above also affected the salinity. Without it the concentration and composition of the salts in the topmost microlayer of ^{the} pelagic zone might be substantially different than in the midwater, as the result of evaporation, accumulation of atmospheric aerosols by the sea surface (Popov, 1965), flotation and other phenomena.

A comparative study of the trace element composition of the Black Sea at depths of 0-10 cm and 10 m (Vinogradova and Kogan, 1966; Kogan, 1967b) showed that in most cases the concentration of trace elements (Fe, Cu, Mn, V, Co, Ni, Ti, Al, Mo, Sn, Pb, Ag) in the surface layer is higher than at a depth of 10 m. This is evidently one of the manifestations of the specificity of chemical and trace element composition of the water of the near-surface microlayer of the sea. Further

research in this direction will provide information important for neustonology, particularly on the "facteur rapide" revealed by the researches of A.E. Pora (1966).

Together with this the near-surface microlayer of the pelagic zone may experience not only an increase in the concentration of salts, but also a drop, as the result of the deposition of atmospheric precipitation. This is especially characteristic of those cases where a large quantity of rainwater falls on a calm sea in regions with normal and elevated salinities. In the summer of 1965 the author happened to observe such a phenomenon in the Florida Strait, close to the Cuban coast. Sometimes even 20 hours after a downpour the surface layer of water some 10 cm thick was turbid due to an abundance of suspended matter of terrigenous origin, and freshened, as could be determined even by tasting. Usually the amount of rainfall on the surface of the sea is greater near the coast, where direct atmospheric precipitation is combined with storm water run-off from the land. However, in open waters too, especially in the tropics, this ecological factor may be important in the lives of the denizens of the sea-air interface, particularly as it is not only an inflow of fresh water that is involved here. According to M.V. Fedosov (1965), every year some 412,000 km³ of precipitation is deposited on the surface of the World Ocean, containing up to 100 mcg/l of nitrogen compounds which accumulated in the water while it was still in the form of drops and vapour in the atmosphere. /17/

Chapter II. Non-living organic matter

Along with live organisms the water of the seas and oceans

also contains dead, inert organic matter, which exceeds by far the biomass of living creatures. Beneath 1 m^2 of ocean surface there is an average of 2.4 kg of dissolved (Duursma, 1960) and 500 g of suspended organic matter, of which considerably less than 1/10 consists of live organisms (Parsons and Strickland, 1962). Hence, the total quantity of non-living organic matter is approximately 50 times greater than the total of living organic matter (Sutcliffe, Baylor, Menzel, 1963). In one of his recent papers V.G. Bogorov (1967) cites an even more imposing figure: 500 times more dead organic matter than living. According to Z.Z. Finenko (1965), the composition of the seston in the different regions of the World Ocean is: 0.4-3.5% phytoplankton and bacteria, 3-10% zooplankton, and 85-90% detritus and zooplankton not counted by the net method. These figures are not definitive. The ratio of live to dead organic matter varies markedly in space and time, but it is a firmly established fact that the latter clearly predominates over the former.

The study of dead organic matter in natural water basins was begun only in recent years, and its role in the life of the hydrosphere is still not completely clear. Most researchers consider, however, that it is a most important ecological factor, playing a large part in the nutrition, growth and development of hydrobionts, the exchange of substances between organisms, and regulation of the ecological processes taking place in water basins.

The natural sources of inert organic matter in sea water

vary: on the one hand we have the plants and animals which themselves inhabit the sea, their metabolic products and especially the post-mortem secretions, and on the other, rivers discharging into the sea, precipitation and aeolian deposits. These materials are in a suspended, colloidal or dissolved state and can be traced from the surface to the bottom of the sea.

Let us see, to the extent that the available material permits, how this highly important ecological factor affects the near-surface layer of the pelagic zone. /18/

As far as the largest particles of dead organic matter in sea water are concerned, we must begin with insects. The fate of land insects borne away to sea by the wind for a long time failed to excite the interest of researchers. This may have been due to the fact that this problem lay outside the usual sphere of interest of entomologists and oceanologists, or perhaps it was merely another reflection of that inattention to the study of the near-surface layer of the pelagic zone. Whatever the case, the neustonologist finally became aware of the need to tackle the subject, since land insects proved to be not only a common and large component of neuston hauls, but also an ecological factor with which the component organisms of the neuston come into direct collision.

It is known that winds have a substantial influence on the migrations of land insects, not only the flying varieties but also many wingless forms with a sufficient wind-catching area. For example, gipsy moth caterpillars of the first stage are borne by the wind for distances of up to 20 km. At the

same time even such insects as the locust Schistocerca gregaria, which are very strong fliers, are blown off course by winds exceeding 2 m/sec. As regards insects lifted by ascending currents of air to heights of several thousand metres, they are carried for hundreds of kilometres (Bei-Bienko, 1966). Analysing the current body of knowledge on insect flight, Y.M. Zalesskii (1955) observes that insects have been caught in special traps at altitudes of up to 4500 metres. At all altitudes, including the highest, were found representatives of the orders Jugatae, Hymenoptera and Diptera. Among the Hymenoptera (representatives of 250 genera have been found in the air) predominate flying ants, and among the Diptera, representatives of the families Chloropidae, Chironomidae, Culicidae. At heights up to 3355m. are found as many as 4420 species of Coleoptera, belonging to 191 different genera. Lepidoptera occur at altitudes up to 1525 m.

All these data show that many insects may find themselves at the mercy of air currents and be carried far from their take-off points. In the same way they can be swept out to sea for tens or hundreds of kilometres.

After being deposited on the surface of the sea the insects soon die as a rule, but they do not sink. Their bodies, which contain tracheae and often air sacs as well, are highly buoyant, so that the insects may remain on the surface for days and even /19/ weeks. Only after becoming waterlogged do they sink to the bottom, by which time the body is generally disintegrating. Thus, land insects deposited in the sea are a source of dead organic matter concentrated in the near-surface layer of water.

Some idea of the number and distribution of insects in the sea can be gained from the results of research conducted by workers in the hyponeuston division. In net hauls of hyponeuston obtained in September 1961, from the eastern half of the Black Sea (as determined by V.D. Sevast'yanov), were discovered whole organisms or fragments of the following land insects: Homoptera (Megamelus sp., Deltoccephalus sp., Jassidae g.sp., Cicadella sp., Aphidodea); Heteroptera (Nabis fesus, Pirates hybridus, Camptotus lateralis, Ceraleptus optus, Pyrrhocoris apterus, Strictopleurus sp., Aelia sp.); Coleoptera (Harpalus sp., Taphoxemus sp., Agomum sp., Phytonomus sp., Sitona sp., Apion sp., Staphilinidae g. sp. sp., Phyllotreta nemorum, Phyllotreta sp., Adomia variegata, Coccinella undecimpunctata, C. quinquepunctata, Adalia bipunctata, Aphodius melanosticus); Hymenoptera (Solenopsis sp., Tetramorium sp., Apanteles sp., Braconidae g.sp., Ichneumonidae g.sp.); Diptera (Sepsidae g.sp., Gaenia sp., Syrphus corollae, S. ochrostoma, Syrphus sp., Drymeia sp., Fucellia sp., Fungivoridae g.sp., Dolichopodidae g.sp., Cordiluridae g.sp.).

Less identifiable remains belonged to representatives of Lepidoptera, Neuroptera, Orthoptera and spiders.

Of particular interest (to the quarantine service too) is the Colorado beetle (Leptinotarsa decimlineata), which was first discovered in Black Sea hauls of hyponeuston taken in 1964 near the mouth of the Danube. The Colorado beetle can survive in sea water for several days, during which time it is carried a long way by currents from the point where it entered the water. Cases are known where a live Colorado beetle crossed the English

Channel (Thomas, Dunn, 1951) and where one was washed up on the coast of Kaliningrad region after being carried away from the Baltic (Zhuravlev, 1904). Between the 29th and 31st of July 1966, the waves, heaped up by the wind, cast a large number of Colorado beetles up on the beaches of the Odessa region (according to estimates made by V.P. Zakutskii, the average figure was 18 specimens per linear metre of beach). Many of them were alive and even had to be sprayed from the air before they died. From the 22nd-24th of April 1904, on "Golden Beach" near Feodosiya, insects cast up by the waves formed an unbroken line several kilometres long. They were mainly stink bugs (10 species), curculios, ground beetles, maybeetles, culicids (11 species), and others.

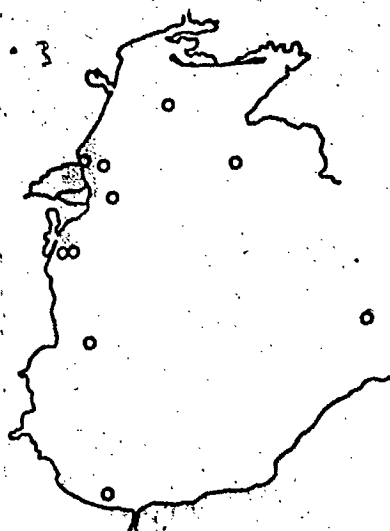


Fig. 3 - Places where insects of fam. Dytiscidae and Hydrophilidae found on surface of western half of Black Sea in July-August 1961 (Zaitsev, 1904a).

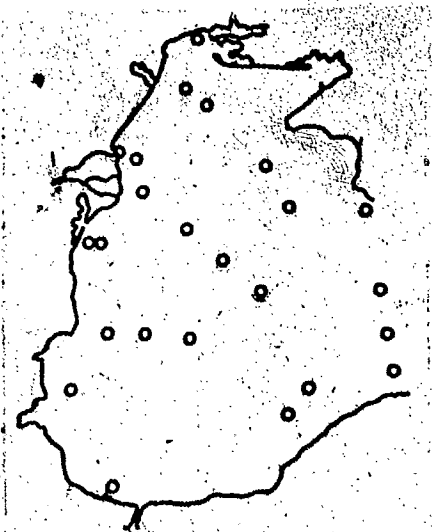


Fig. 4 - Places where insects of fam. Carabidae and Chrysomellidae found on surface of western half Black Sea in July-August 1961 (Zaitsev, 1964a).



Fig. 5 - Distribution and numbers of land insects in western half of Black Sea in July-August 1961 (Zaitsev, 1964a).

The examples given show that there are a large number of land insects on the surface of the sea which, when the wind and currents are right, are tossed up on the shore by waves. More often, however, they are found all over the sea, where in

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most cases they perish. The distribution patterns of representatives of various groups of land insects on the surface of the Black Sea indicate the paths by which they entered this - for them - alien element.

If we plot on one of the maps of the western half of the Black Sea the places of discovery of species of Dytiscidae and Hydrophilidae, which dwell in fresh water or close to it (Fig. 3), and on another map species of Carabidae and Chrysomelidae, which are not directly associated with fresh water (Fig. 4). it is easy to see the difference between the points. While water scavengers and diving beetles occur mainly close to the Danube delta and where the waters of the Danube penetrate, ground beetles and leaf beetles are distributed with comparative uniformity over the entire water area. This indicates that representatives of the first two families are brought into the Black Sea chiefly by rivers, and those of the latter two families by air currents.

The total number of insects on the surface of the western half of the Black Sea during this period (from July 18th to August 5th 1961) is shown in Fig. 5. The highest density of insects corresponds to the areas of hydrologic fronts and zones of current convergence. By a rough estimate the total number of land insects present simultaneously on the surface of the entire Black Sea is 10^9 specimens in summer, and the total weight some 10 tonnes. These figures are very approximate since it must be borne in mind that new "showers" of insects are

continually being deposited in the sea and immediately devoured. Nevertheless the figures give an idea of the order of magnitude and show that the source of organic matter retained on the surface of the sea merits attention.

After studying the biochemical composition of insects from samples of hyponeuston from the north-west part of the Black Sea, E.F. Kostylev (1968c) came to the conclusion that they contain a large number of organic substances used by fish and invertebrates in the near-surface layer of the pelagic zone as building materials and a source of energy. In this connection it should be noted that in some cases deposition of land insects on the surface of a water body has dangerous consequences. For instance, the ants Solenopsis saevissima var. richteri Forel, imported into the USA from South America, multiplied strongly. During the mating season the winged stages of the ants enter ponds, causing mass deaths of the fish feeding on them (Crance, 1965). More frequently, however, land insects serve as a supplementary source of food both for fish and for invertebrates (Zelezinska, 1962; Zaitsev, 1964a).

Travelling by the same aerial route to the surface of the sea come the pollen of anemophilous plants, spores, cysts, squamellae from culicids and butterflies and other tiny particles which V.N. Beklemishev (1944) named "anemoneuston". As these particles and organisms - brought by the wind from dry land - are not neuston organisms and die in the biotope where neuston lives and develops, this term is inappropriate, as is the term "aerial plankton", which was at one time attacked by S.A. Zernov

(1949).

Thanks to their lightness, non-wettability and small size the deposited particles, before sinking to the bottom, remain on the surface for a more or less long time, creating together with the insects an elevated concentration of organic suspended matter of terrigenous origin. This problem has not yet received special study from the hydrobiological aspect. The literature contains only a few passing comments by various authors, and even these are not related to the question of life in the sea-air interface. Pollen, spores and other organic particles constantly amalgamate with suspended matter entering the sea from the atmosphere (Koreneva, 1955; Lisitsyn, 1955). Most widespread is the pollen of conifers, birches, alders, oaks, maples and elms, the spores of Lycopodinae, Filicales, green mosses and other plants, which are found not only close to the coast but also far away from it (Koreneva, 1955). It is known that pollen is consumed by many hydrobionts, especially Noctiluca (Andrusov, 1892).

The quantity of allochthonous organic matter on the surface of the sea can be judged from certain indirect data. Thus, M.V. Fedosov (1958) considers that the suspended matter in the North Caspian consists 30% of aeolian deposits containing an organic fraction. A.V. Rozhdestvenskii (1964) established that pollen storms over the Black Sea in March and April of 1960 resulted in the accumulation of a large quantity of suspended matter on the surface of water. However, in the overall balance of non-living organic matter in the nearsurface layer of the sea, in spite of its topography, the chief role (especially

in areas far from the coast) is played by remains and excretions of animals and plants of aquatic origin in the form of particles of detritus, colloidal and true solutions. Therefore, assuming that the dissolved and colloidal organic substance is produced both by dead and live hydrobionts, it remains only to determine which source should be considered the main one in a particular set of circumstances - the suspended organic matter or the particles of detritus. Hence, a study of the distribution of detritus as a highly important element in the organic suspended matter in the sea may (to a certain extent) be reduced to a study of the distribution of dead hydrobionts in the pelagic zone. /23/

Until recently no special study was made of this question in hydrobiology. The groundwork for a systematic and comprehensive investigation was laid by L.M. Zelezinskaya (1904-1909) of the hyponeuston division. Her researches produced a number of new propositions of considerable neustonological and general hydrobiological significance. We shall examine here only the most important of these.

The formerly held view that dead plankters are deposited on the bottom in a "rain" of bodies is not quite correct. In point of fact some of the dead bodies, especially those of crustaceans, acquire positive buoyancy on decomposing and ascend. The process of flotation which is constantly operating in the sea leads to the same thing. This phenomenon, for which the term "antirain" of dead bodies was proposed (Zaitsev, 1967a), attains significant dimensions and plays an important role in

the water basin.

In the first place, the "antirain" of dead bodies means that live and dead organisms are constantly found together in the water. The ratio may fluctuate considerably in different places and different seasons of the year, and at the boundaries of the ranges of species - for instance where sea and river waters meet - dead specimens may form the major part of plankton and hyponeuston samples (Zelezinskaya, 1966c). It is important to note also that while bodies in advanced stages of decomposition are comparatively easy to distinguish in the samples, diagnosis of bodies in the early stages of decomposition requires special expertise, such as is possessed only by the specialist. Therefore laboratory processing of samples of plankton without careful separation of live and dead individuals, as is usually the case, can sometimes result in serious errors in quantitative evaluation of the pelagic population. However, the compilation for each species of two types of map - one biogeographical for live specimens) and the other necrogeographical or thanatological (for dead specimens), opens up new prospects for the study of biological processes in the sea.

In the second place, as a result of the "antirain", directly affecting the near-surface microlayer of the sea, a considerable part of the dead hydrobionts and fragments of their bodies is concentrated near the surface tension film of water and in the foam.

By studying the chemical composition of foam A.T. Wilson (1959) discovered that it contained an abundance of phyto- and zooplankton remains and concluded that the dead plankton rises

from the midwater to the surface of the sea. According to the data of L.M. Zelezinskaya this process is sustained by the constant presence of a large number of dead hydrobionts in the pelagic zone (Table 2). Tracing the vertical distribution of dead bodies in the water we soon discover that they are confined to the 0-5cm layer. /24/

Zelezinskaya cites data on the distribution in the Chernomorka region in August 1966 of dead Penilia avirostris, which were killed by a fungal disease (Table 3).

Table 2

Quantity of dead specimens of plankton crustaceans (in % of quantity of live specimens) discovered in upper 15-metre layer of water in the north-west part of the Black Sea in the second half of summer 1966 (according to material of L.M. Zelezinskaya)

Вид	Количе- ство	
	От	До
1	3	4
<i>Penilia avirostris</i>	6,7	15,8
<i>Balanus, nauplii</i>	7,4	38,0
<i>Acartia clausi</i> 5		
I-III копепоdit. стадни	8,7	28,2
IV-V " "	7,3	23,2
♀	2,6	46,0
<i>Centropages ponticus, nauplii</i>	4,2	15,3
<i>Oithona minuta</i> , ♀, ♂	6,0	23,0

Key: 1. species; 2. quantity; 3. from; 4. to; 5. copepodite stages I-III, IV-V.

Table 3

Vertical distribution of dead specimens of Penilia avirostris in the Chernomorka region in August 1966 (according to material of L. M. Zelezinskaya)

Горизонт, см 1	Количе- ство, экз/м ³ 2	Биомасса, мг/м ³ 3	% (по весу) 4
0-5	1152	40,32	47,0
5-25	270	9,45	11,0
25-45	367	12,85	15,0
480-500	190	6,65	7,8
1280-1300	315	11,03	12,9
1480-1500	161	5,64	6,3

Key: 1. layer, cm; 2. quantity, spec./m³; 3. biomass, mg/m³; 4. % (by weight)

As shown by the investigations, nearly half of the dead bodies discovered in the 0-15 metre layer were concentrated in the 0-5 cm microlayer. A.P. Kusmorskaya (1954) and E.V. Pavlova (1961) recorded the maximum number of dead bodies of Penilia at depths of 6-12 and 10-15 m. Evidently the results were affected by the fact that the samples were taken by plankton-collector and Juday net, i.e. the 0-5 cm layer was ignored. A certain increase in the number of dead individuals in the vicinity of the thermocline was also noted at a depth of 13 m (Table 3), but it was considerably lower than the one recorded in the 0-5 cm layer.

The vertical distribution of the dead bodies of the most abundant species of copepods (included in the survey were the

naupliar and copepodite stages and adult individuals of Acartia clausi, Centropages ponticus, Oithona minuta, O. similis in the summer of 1966, according to L.M. Zelezinskaya, is shown in Table 4.

Table 4

Vertical distribution of bodies of Copepoda in Chernomorka region in the summer of 1966 (after L.M. Zelezinskaya)

Горизонт, см 1	Количе- ство, экз/м ³ 2	Биомасса, мг/м ³ 3	% (по весу) 4
0—5	16261	75.42	33.9
5—25	6723	64.92	29.2
25—45	5566	40.49	18.2
480—500	3833	18.39	8.5
1280—1300	5400	22.71	10.2

Key: 1. Layer, cm; 2. quantity, spec./m³; 3. biomass, mg/m³; 4. % (by weight).

It is interesting that a similar vertical distribution pattern for copepod bodies was observed by M.A. Kastal'skaya-Karzinkina (1935) in Lake Glubokoye (Table 5). We may assume that if, in this case too, the near-surface microlayer had been taken into account (in fact, Kastal'skaya-Karzinkina sampled the 0 m layer with a bathometer, i.e. some 10 cm from the surface), the number of bodies in ^{the} uppermost layer would have been still greater.

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Table 5

Vertical distribution of live specimens and dead bodies of Copepoda in Lake Glubokoye on 16.IX.1932 (Kastal'skaya Karzinkina, 1935)

Горизонт, м	Общее количе- ство в пробе	Жи- вые особи	Трупы
1	2	3	4
0	57	37	20
3	46	29	17
6	16	7	9
8	1	—	1
10	5	1	4
20	1	—	1
29	—	—	—

Key: 1. Layer, m; 2. total no. in sample; 3. live individuals; 4. dead bodies.

On the basis of the count of live and dead copepod crustaceans in net hauls of hyponeuston and plankton from the underlying layer of water made by Zelezinskaya, we can determine the absolute number of dead organisms near the surface of the sea.

Assuming that the number of species of Copepoda counted in the north-west part of the Black Sea in summertime is twice as high as in the remaining coastal and open waters of the sea, which is close to the average long-term figures given by Zenkevich (1963), and that the mortality over the entire water area is approximately of the same order of magnitude (the latter is derived from a comparison of hauls from different areas of the sea made by Zelezinskaya), then the average weight of dead

copepods in the 0-5 cm layer of the Black Sea will be $75.42/2 = 37.71$ mg/m³. This means that in every volume of water, which can be imagined in the form of a prism with a base of 20 m and a height of 5 cm, there are 37.71 mg of dead copepod bodies, and that under 1 m² of sea surface in the 0-5 cm layer there are $37.7 \text{ mg} / 20 = 1.8855$ mg of dead bodies.

Assuming the surface of the Black Sea to be equal to 423,000 km² (Stepanov, 1961), or $423 \times 10^9 \text{ m}^2$, the total weight of dead bodies in the near-surface 5 cm layer of the entire water body will be $1.8855 \times 423 \cdot 10^9 = 797,500$ kg, or roughly 8,000 centners. For comparison, the annual catch of mackerel in the Black Sea ranges from 2,000 - 35,000 centners (Borisov and Bogdanov, 1955).

In like fashion we can estimate that the total weight of dead copepod bodies in the 5-25 cm layer of the Black Sea is 27,000 centners, in the 25-45 cm layer - 17,000 cent., in the 480-500 cm layer - 7,800 and in the 1,280-1,300 cm layer - 9,400 centners. /20/

Assuming that the area of all the microlayers studied is equivalent to the surface of the sea, then for the investigated water column of the 0-13 m layer the number of dead copepods will be as follows: in the 0-45 cm layer - roughly 52,000 cent., in the 45-500 cm layer - roughly 275,000 (counting 2,400 cent. per 20cm microlayer of this layer). Thus, in the 0-13 m layer of the Black Sea the number of dead copepods totals some 670,000 centners, which is approximately 1.5 times the annual catch of the most numerous fish in the sea - the anchovy (Rass, 1965).

These rough calculations, obtained by the author in August, when, according to Zelezinskaya's data, the number of dead crustaceans in the water is higher than at the beginning of summer, but lower than in autumn, can give only a rough idea of the order of magnitudes characterizing natural mortality in the water column and the "antirain" of dead bodies. It is clear that, taking into consideration the remaining species of Black Sea copepods and all other groups of animals whose dead bodies remain suspended in the water column and concentrate near the surface, such quantitative data will interest not only hydrobiologists, and particularly neustonologists, but also other specialists studying the distribution and transformation of organic matter in the sea.

Thus, using crustaceans as an example, we established the fact that dead individuals concentrate in the 0-5 cm layer. The surfacing of dead decomposing fish, birds or mammals is a widely known occurrence. Dead crustaceans proved to behave in similar fashion, and this^{is} probably due in large measure to the exoskeleton, under which are trapped bubbles of gas formed as the soft tissues decompose. This is confirmed on the one hand by the presence of gas bubbles in their dead bodies, and on the other by the absence, or relative absence, near the surface of dead organisms with soft and weak integuments, such as jellyfish, worms, eggs and larvae of fish, etc.

However, dead organisms are not the only source of detritus in the sea. A no less important, and in the opinion of many authors an even more important, role in this is played by plants.

But what is their density in the near-surface layer of the sea? It is especially important to ascertain the fate of dead cells of phytoplankton, the biomass of which in the World Ocean, as calculated by V.G. Bogorov (1965), is 7.5 times greater and the production 2,750 times higher than the biomass and production of the benthic macrophytes distributed in the shallow-water areas of the shelf. There is even less published information on this topic than on dead animals, since the study of phytoplankton, and particularly the laboratory processing of samples, is done with the aid of ordinary optical devices, without allowing for the pathological state of the cells.

Research in this field was begun in the hyponeuston division in 1966 by D.A. Nesterova (1968, 1969) with the aim of determining the character and degree of participation of protozoan algae in the life of the near-surface microlayer of the pelagic zone.

Using a special technique, sedimentary and net samples of phytoplankton were taken from the 0-3 cm layer and from various depths in the water column down to 18 m. All the hauls were subjected to luminescence analysis by the method of S.V. Goryunova (1952), which made it possible to divide the cells from each sample into the following categories: live, dying and dead. In addition, empty bivalve shells were examined.

The results of processing the first 500 samples, obtained from various water masses at different seasons of the year in the Chernomorka region, led D.A. Nesterova to conclude that the water always contains live, dying and dead cells. Dying and dead cells and empty shells usually concentrate under the surface

tension film (Table 6).

Table 6

Vertical distribution of *Nitzschia seriata* (in thousands of cells per litre of water) in April-May 1967 in the Chernomorka region (from the material of D.A. Nesterova)

Горизонт, см 1	Физиологическое состояние 2. клеток			Общее количество 6
	живые 3	отмирающие и мертвые 4	пустые створки 5	
0-3	65	3462	73	3600
25	39	2933	73	3045
45	16	2927	55	2998
500	29	997	34	1060
1000	11	363	12	359
1800	108	1291	59	1458

Key: 1. Layer, cm; 2. physiological state of cells; 3. live; 4. dying and dead; 5. empty shells; 6. total.

Thus, study of the microdistribution of dead animal and plant organisms revealed their elevated density beneath the surface tension film of the water. Here they continue to decompose, disintegrate and enrich the biotope with "young" (to use the expression of J. Krey, 1967) detritus, which is the most valuable form for nutrition. The particles of detritus formed are devoured by the animals in the near-surface layer of the pelagic zone, and the remainder gradually sink. Data on the "antirain" of bodies agree well with the conclusion of S. Nishizawa (1966) that particles of detritus form fastest in the surface film of the sea and that the speed of formation of these particles is

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approximately 10 times greater than the rate of photosynthesis of phytoplankton in this same layer. In his latest paper D. Bernal (1969) stresses that all planktonic organisms after death come to the surface for a while, where their remains form a thin film with a very high concentration of organic substances.

As already remarked, in addition to suspended particles the sea contains a large quantity of colloidal and dissolved organic matter formed as the result of intra-vitam and post-mortem excretions of pelagic and benthic plants and animals. It is supposed that the principal sources of dissolved organic matter are benthic macrophytes in the coastal zone and plankton in the open sea (Skopintsev, 1950). It is also supposed that the quantity of organic matter of vegetable origin is greater than that of animal origin.

The chemical composition of dissolved organic substance is very complex and variable. Thus, H. Harvey (1955) notes that it contains organic nitrogen and phosphorus, polypeptides and many amino-acids, and also traces of thiamine, biotine, vitamin B₁₂ and others. Just as rich and complex is the chemical composition of the organic matter of fresh water (Maistrenko, 1965; Shevchenko, 1966), but in this case river storm runoff and aeolian deposits may play a relatively greater role than in the seas and oceans.

Because the importance of dissolved organic matter in the production of the sea is very great, particular attention has been devoted recently to determining the pattern of its

distribution in the pelagic zone. Of great interest to neustonology are the latest data on the concentration of dissolved organic matter in the area of the surface tension film of water. Without dwelling on the special problems forming the subject-matter of the corresponding branches of oceanology, let us examine this phenomenon briefly from the viewpoint of the habitat in the near-surface microlayer.

By studying the chemical composition of foam collected from the surface of the Caspian, B.A. Skopintsev (1939) established, in particular, that it differs from sea water in having a higher (10-30 times) oxidizability, a very high content of salt ammonia and phosphates, and a higher (again 10-30 times) content than in water of organic nitrogen and phosphorus. The number of bacteria in one of the samples of foam received was, according to the figures of B.A. Skopintsev, 140,000 per millilitre as against 440 in sea water. Skopintsev also explained /29/ the mechanism of foam formation: on the air bubbles appearing in the water are adsorbed surface-active substances, especially hydrophilic colloids and semi-colloids, which, rising to the surface, form foam. Notwithstanding all the conclusiveness of the work done by Skopintsev, it did not receive its full due and failed to be further developed in research on hydrochemistry and marine microbiology. Surface samples from the "zero" layer for chemical and microbiological analyses were, as before, collected by bathometers, the design of which virtually excluded the possibility of their picking up any of the surface organic film or foam.

The concentration of dead organic matter on the sea surface was determined for the second time at the beginning of the sixties, and this time the volume of factual material was so considerable that more rapid progress began to be made with the problem.

The researches of S. Nishizawa and G.A. Riley (1962), E.R. Baylor and W.H. Sutcliffe (1963), G.A. Riley (1963), W.H. Sutcliffe, E.R. Baylor and D.W. Menzel (1963), G.A. Riley, P.J. Wangersky and D. Van Hemert (1964), R.T. Barber (1966a,b) and other scientists demonstrated that the gas bubbles forming as the result of waves, photosynthesis, decomposition etc., permeating the pelagic zone, absorb organic substances and transport them to the surface. In the process a change occurs in the degree of dispersion of the organic matter in the organic membranes of the gas bubbles: from true or colloidal solutions are formed particles or aggregates whose composition and size allow them to be consumed by heterotrophic hydrobionts. It has been demonstrated experimentally that even such comparatively large crustaceans as Artemia salina devour these aggregates (Baylor and Sutcliffe, 1963).

The evidence of the part played by gas bubbles in adsorption, aggregation and redistribution of dead organic matter in the sea with its deposition on the surface gave rise to questions about the existence and distribution of these bubbles in the water column, their lifespan, the speed with which they rise, and other facts. These questions have been partially dealt with in some published papers.

Working in Saanich Inlet (British Columbia) with echo-sounders operating at frequencies of 12.50 and 200 kc/sec, McCartney and Bary (1965) studied bubbles of gas rising from a muddy bottom saturated with hydrogen sulphide from a depth of 197 m. The measurements showed that the diameter of the bubbles near the bottom was 0.9-1.6 mm and continued to increase as they rose. The rate of ascent of the bubbles ranged from 16-30 /30/ cm/sec.

An important source of bubble formation is oxygen dissolved in the water (Ramsey, 1962). The bubbles of oxygen formed as the result of water temperature fluctuations constantly expand, migrate towards the surface and transfer to themselves the adsorbed organic film. W.L. Ramsey showed that the stability of bubbles in water is due precisely to the presence of an adsorbed film containing fatty acids and protein substances and playing the role of a diffusion barrier. This barrier prevents the gas escaping from the bubble into the water (i.e. reverse dissolution), and ensures that it reaches the surface. Here the adsorbed organic membrane is retained even if the contents of the bubble are released.

In addition to dissolved oxygen the water contains other sources of gas bubbles, and numerous investigations of the propagation of sound in the sea have furnished direct proofs that they are constantly present in large quantities in the pelagic zone.

Thus foam - one of the most characteristic features of the sea surface - is the product of the ascent of dead organic matter

from the midwater and bottom which is constantly taking place in all the seas and oceans. The foam is also enriched by aeolian deposits of organic material originating from the land, and is itself in a continual state of transformation. On the surfaces of detritus particles formed from the dead bodies of hydrobionts or aggregates, new portions of organic matter in solution are vigorously adsorbed (Krey, 1961). In the process a mass of heterotrophic bacteria is immediately formed, these being the chief consumers of dead organic matter in the sea.

Thus foam is an important constituent element in the surface biotope, and its ecological significance is extremely great. It does not form a dense uniform layer, but accumulates mainly in zones of current convergence, at river hydrological fronts, in storm belts. In calm weather it disperses, forming distinct slicks or calm-weather bands of organic film retaining remains of animals and plants (Babkov, 1965), but in waves it again forms clumps.

A large amount of foam is blown on shore by the wind. In exceptional cases, as on the Pacific coast of Japan, the mass of sea foam thrown up on shore may damage electrical transmission lines and even hinder the movement of trains (Abe and Watanabe, 1965). Opinion exists that the chief source of organic matter in atmospheric precipitation is the sea surface, its organic film (Fonselius, 1959; Wilson, 1959). In the tidal strip foam fills porous bottoms and creates conditions for the flourishing of a very rich interstitial fauna on what would seem

to be lifeless deposits of quartz sand.

From all that has been said in this chapter it is clear that inert organic matter accumulating on the surface of the sea and most evident in the form of foam provides a base for the development of abundant life here and, what is especially important, constitutes a direct source of food for heterotrophic organisms. However, sea foam is not merely a collection of food particles whose nutritional value can be assessed by the objective criterion of calorific content. Research done in the hyponeuston division indicates that sea foam possesses clearly defined biologically active properties.

Chapter III. The biological action of sea foam

If we start with the assumption that foam is a concentrate of external metabolites of animals and plants which, as is known, exert a great influence on the functioning of hydrobionts, then we must conclude that the near-surface microlayer of the pelagic zone is an arena of intensive development of the chemical processes within the sphere of interest of marine biochemistry - a new field of biooceanography, the chief subject of which K.M. Khailov (1965) calls the interaction of community members through the aquatic medium. Therefore, to the areas of ocean for which, according to Khailov, study of the metabolic interorganismal links is of greatest importance, i.e. the near-shore shallows, which are rich in beds of macrophytes and benthic fauna, the reef areas, the photic zone, and, to some degree, the benthic layers, we must add the surface tension film.

Furthermore, it is possible that because of the extremely high concentration of external metabolites at the surface of the sea and the role of this biotope in the ontogenetic development of hydrobionts and the ecological processes, study of biocommunications within the near-surface complex of organisms will be of special interest to marine biochemistry and, of course, neustonology.

Recently numerous communications have appeared on the biologically active properties of intra-vitam and post-mortem excretions of marine plants and animals (Bentley, 1959; Jones, 1959; Lucas, 1961; Skopintsev, 1962, Khailov, 1963, and others). These properties are manifest in stimulating or repressing various biological processes occurring in the organisms in question. However, in most cases the external metabolites used /32/ in the experiments were obtained from dense aggregations of plants and then tested for bacteria. Meanwhile foam, with which neuston components come into contact, is a natural mixture of excretions of all organisms - the live and dead plants and animals present in a particular area at a particular time. Therefore, from the viewpoint of neustonology the problem is to determine the biological effect of sea foam on representatives of those organisms which occur in the sphere of its supposed influence, i.e. in the near-surface biotope of the sea.

The composition of foam is very complex and variable. A priori it can be asserted that it varies depending on fluctuations in the rate of ascent of gas bubbles to the surface (which depends in turn on the size of the waves, the photosynthetic activity of

the plants, fluctuations in the water temperature and other factors), on the intensity and composition of the "anti-rain" of dead plankton, the rate of deposition and composition of aeolian deposits and many other factors. Elucidation of the chemical composition of sea foam for each actual case is undoubtedly one of the important routine tasks of marine chemistry. Because there are insufficient conclusive data in the literature on the biological effect of sea foam, and because its ecological significance is sometimes reduced to the mechanical transport of small mollusks, absorption of near-shore insects, reduction of flotation, salinization of dry land, etc. (Hidaka et Baudoin, 1965), such researches were commenced in the hyponeuston division by the author and L.M. Zelezinskaya and developed by N.S. Chilikina (Zaitsev, 1967a; Chilikina, 1969).

The first experiments were performed with certain cereals (oats, barley, wheat). Using germinants of oats J. Bentley (1959) tested the effect of hormones of the auxin type contained in sea water, phytoplankton and zooplankton.

Foam collected from the sea in the Chernomorka region was left to stand in vessels until it formed a thick, transparent, yellowish or greenish liquid. To obtain a rough idea of its composition it was subjected to biological analysis, which revealed the ratio of animal and plant remains in each sample. The cereal seeds were planted in growing vessels filled with quartz sand or soil, and then a 0.2% solution of foam residue in tap-water was poured over them. The concentration of the residue was determined empirically. The control experiment involved the same

number of seeds sown in the same soil in another growing vessel, but watered with pure tap-water. Subsequently both the experimental and control batches of seeds were watered with pure tap-water (Table 7).

Table 7

The effect of sea foam on the length and weight of certain cereals (Chilikina, 1969)

Вариант опыта	Опыт, $M \pm m$	n	Контроль, $M \pm m$	n	$M_{\text{ант}}$
11 Длина ростков, см					
2 Овес на 7-е сутки	$9,0 \pm 0,27$	89	$6,6 \pm 0,17$	92	7,6
3 Овес на 11-е сутки	$14,58 \pm 0,37$	88	$11,82 \pm 0,25$	91	6,0
12 Вес ростков, мг					
4 Ячмень на 6-е сутки	$9,92 \pm 0,18$	87	$8,35 \pm 0,12$	91	7,5
5 Ячмень на 9-е сутки	$145,5 \pm 3,02$	98	$132,8 \pm 2,3$	95	3,4
6 Ячмень на 33-е сутки	$294,0 \pm 13,9$	98	$227,9 \pm 8,7$	95	4,04
7 Пшеница на 17-е сутки	$83,5 \pm 2,3$	92	$64,0 \pm 2,9$	90	5,3
8 Овес на 11-е сутки	$107,5 \pm 1,0$	88	$84,9 \pm 2,2$	91	3,1

Key: 1. Variant of experiment; 2. oats on 7th day; 3. oats on 11th day; 4. barley on 6th day; 5. barley on 9th day; 6. barley on 33rd day; 7. wheat on 17th day; 8. oats on 11th day; 9. Experiment, $M \pm m$; 10 Control, $M \pm m$; 11. Length of shoots, cm; 12. Weight of shoots, mg.

No less stimulating is the effect of sea foam on the development of the root system of cereals. For example, the total weight of the roots of 20 shoots of barley 9 days after sowing was 2057 mg, whereas in the control it was equal to 1172 mg. (Chilikina, 1969). The most striking difference - apparent even to the eye - was in the length of the root system, but it

could not be measured.

The following series of experiments was performed with the blue-green alga Spirulina tenuissima, which develops mainly in the coastal zone, where a great deal of foam normally forms (Table 8). A small square of film of S. tenuissima with an area of 30 mm^2 , removed from the glass of an aquarium, was attached to the wall of a glass vessel filled with a 0.5% solution of foam residue in sea water. The control was a similar square of alga on the wall of another vessel filled with sea water without foam. Every day the area occupied by the growing alga was measured in each of the vessels.

A parallel series of experiments was conducted with animal organisms in the early stages of ontogenesis, developing in hyponeuston. In such cases a 1% solution of foam residue in sea water was used. The experiments showed, in particular, that sea foam is evidently capable of increasing the percentage of hatching of larvae from eggs of Artemia salina. An insufficient number of experiments and the low "germinating capacity" of the batch of Artemia eggs used made it impossible to speak categorically of any stimulation of the embryos of this species by the foam, but such a tendency judged by the criterion

$$t' = \frac{\bar{x}_1 - \bar{x}_2}{S\bar{x}_1 - \bar{x}_2}$$

is completely reliable. In a 1% solution of foam residue shrimp larvae survive longer (Table 9).

Table 8

Effect of sea foam on growth of Spirulina tenuissima (from data of N.S. Chilikina)

День опыта	2	Опыт, $M \pm m$	3	Контроль, $M \pm m$	M_{diff}
1	30		30		
2		$302,7 \pm 0,6$		$259,2 \pm 0,97$	36,2
5		$2495,6 \pm 2,7$		$2175,3 \pm 2,8$	88,8
6		$3142,0 \pm 6,3$		$2625,0 \pm 7,5$	43,8
1	30		30		
2		$110,9 \pm 0,51$		$140,0 \pm 0,37$	-47,7
3		$337,1 \pm 2,1$		$406,0 \pm 1,8$	-24,9
4		$823,5 \pm 2,5$		$680,1 \pm 2,9$	39,7
5		$1644,2 \pm 5,3$		$1244,0 \pm 2,2$	26,3

Note. Area on walls of vessel₂ covered by growth given in mm : number of samples in all cases equals 20.

Key: 1. Day of experiment;
2. Experiment $M \pm m$;
3. Control $M \pm m$.

Table 9

Effect of sea foam on survival of shrimp larvae Palaemon adspersus in experiment (from data of N.S. Chilikina)

1	2 Опыт		3 Контроль	
День опыта	4 Количество личинок			
	жи-5 вых	мерт-6 вых	жи-5 вых	мерт-6 вых
1	54	—	54	—
2	53	1	44	10
5	13	41	5	49
7	3	51	—	54
9	1	53	—	54
11	—	54	—	54

Key: 1. Day of experiment;
2. Experiment;
3. Control;
4. Number of larvae;
5. live;
6. dead.

Experiments with eggs of the goby Pomatoschistus sp., taken from the same batch, showed that foam can accelerate the hatching of larvae and lengthen their lives in experimental conditions (Table 10). The female of Cyclospodium sp. in a hermetically sealed specimen of sea foam with a volume of 10cc fed actively, moulted and was very motile for a period of 98 days. This case may be of interest from the viewpoint of creating

closed ecological systems.

The experiments conducted by Chilikina in the main answer the question touched on in this chapter. Sea foam is able to exert a stimulating effect on various biological processes. Such properties were discovered in more than 80% of the foam samples collected. The remaining samples revealed a more or less clearly defined inhibiting effect on the same processes. It is quite possible that it is not so much a question of whether the composition of foam is harmful to live organisms, as of the doses used in the experiments. At high concentrations of foam (3-5%) all the samples had a negative effect on the organisms under test.

Thus it was established that sea foam - one of the most characteristic elements in the near-surface biotope - is of great ecological importance as a complex external metabolite with biologically active properties.

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Table 10

Effect of sea foam on hatching and survival of larvae of Pomatoschistus sp. (from material of N.S. Chilikina)

1 День опыта	2 Количество				2 Количество			
	3 личинок		4 икринок		3 личинок		4 икринок	
	5 жи- вых	6 мертвых	5 жи- вых	6 мертвых	5 жи- вых	6 мертвых	5 жи- вых	6 мертвых
	7 Опыт				8 Контроль			
1	100	—	—	—	100	—	—	—
2	60	—	40	—	78	—	22	—
3	39	7	52	2	47	16	31	6
4	15	19	62	4	28	26	37	9
5	12	19	63	6	18	30	40	12
6	8	22	59	11	15	30	37	18
8	2	23	44	31	7	36	20	37
9	—	25	12	63	—	43	9	48
10	—	25	—	75	—	43	—	57

Key: 1. Day of experiment; 2. Number; 3. of larvae; 4. of eggs;
5. live; 6. dead; 7. Experiment; 8. Control.

CHAPTER IV

Biotic Factors of Environment

The boundary position of the near-surface microlayer also has an effect on interrelations between the inhabitants of this part of the pelagic zone, and particularly on the relations between predator and prey, consumer and food.

The intense illumination and transparency of the water and absence of natural shelter place the prey in an especially disadvantageous position vis-à-vis the predator. Such shielding objects as pelagic Sargassum, driftwood, etc. occupy on the whole only a small proportion of the surface of the World Ocean, and predator-prey relations are decided here literally "under the open sky". At the same time the prey is at a further disadvantage because of its proximity to the surface. While in the midwater the prey pursued by the predator can theoretically escape in any direction (in one plane) from 0 to 360° (Fig. 6a), and most probably selects the sector from 180-360°, at the surface its choice is reduced by half. Furthermore, if the predator pursues its prey horizontally, the latter's chances of escaping are equally reduced in both the optimum (180-270°) and worst (90-180°) sectors (Fig. 6b). If the predator approaches from beneath, the prey is deprived of its most probable chance of escape (Fig. 6c).

This is one of the aspects of the question, but it is far from exhausting the complexities of the interrelations between consumer and food in the near-surface layer of water.

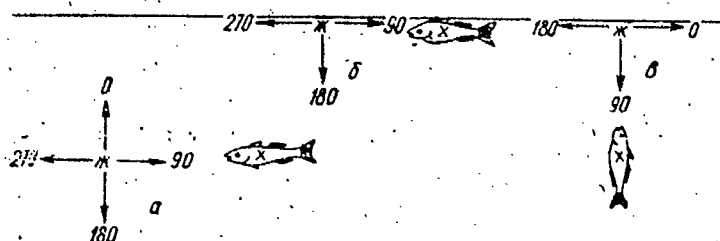


Fig. 6. Interrelations of predator (x) and prey (x̄) in (a) the midwater and (b,c) near the surface (schematic diagram).

The ecological situation here is considerably complicated by the fact that the population of the layer in question is threatened from the air by a large number of feathered foes.

The area of contact between the spheres of ornithology and hydrobiology is yet another "no man's land", encountered by those studying neuston. In most ornithological papers devoted to the biology of nutrition of marine and ocean birds there is no corresponding hydrobiological substantiation. The habits of birds feeding on hydrobionts and the composition and quantity of their food are not compared with the habits of the food items, which a priori must react in some way to the "press" of aerial predators, or with the composition, numbers and distribution of aquatic organisms. Only recently were

investigations of a more comprehensive nature initiated, combining ornithological and hydrobiological studies (Gudkov, 1962; Golovkin, 1963; Golovkin and Pozdnyakova, 1964; David, 1965b).

Study of the largest crustaceans and fish fry making up the neuston revealed a large number of characters with a distinctly "atmospheric" orientation - devices for warding off danger threatening from the air. This focussed attention on birds from the standpoint of neustonology, and during field work some fairly interesting data were gathered (Zaitsev, 1961a, 1964a; Krakatitsa, 1962), together with the published data in the literature gave a general idea of the interrelations between the aerial predator and aquatic prey dwelling no more than 2-5 cm from the surface of the sea. The anatomy, behaviour and feeding habits of a large number of birds revealed that as consumers of hydrobionts they exist chiefly or exclusively on /37/ the animal population of the upper pelagic layer less than 5 cm thick.

One of the most characteristic examples is birds of the scissor-bill family (Rhynchopidae), represented by several species of the genus Rhynchops distributed in the coastal tropical waters of the Atlantic, Pacific and Indian oceans. The main distinguishing feature of the scissor-bills is the knife-like laterally compressed bill, the lower part of which is considerably longer than the upper and provided with numerous tactile corpuscles. These comparatively large birds, with a wingspan of more than 1 m, fly low above the water with the tip of their gonys submerged in the water and seeming to cut the sur-

face of the sea. As can be seen from the picture put together by us from seven consecutive sequences of the documentary film "Galapagos" (produced by West Germany), the depth of immersion of the gonys in the water is normally constant and is independent of the position of the wings (Fig. 7). The resistance of the water to the gonys during flight is reduced and overcome owing to its knife-like form and the strongly developed muscles of the neck. On encountering relatively large fish fry, crustaceans, insects and other animals the tactile corpuscles of the gonys are stimulated and this serves as a signal for the culmen, which seizes the prey. Scissor-bills hunt by day and by night, but mainly during the dark hours, when there is considerably more food on the sea surface.

Far more widely distributed and more numerous than scissor-bills are other birds taking food from the surface of the sea. Let us take some examples.

On June 12th 1962 the scientific research vessel "Akademik Zernov" was stationed in the north-west part of the Black Sea 20 miles from the coast. It was completely calm and in the vicinity of the ship's anchorage there was a "patch" of rich hyponeuston with a predominance of decapod larvae, pontellids, isopods and anchovy larvae. All over the area were sporting dolphins and anchored seiners, catching mackerel. Suddenly Manx shearwaters (Puffinus puffinus yelkouan Acerb.) appeared in the proximity of the ship. The birds flew in flocks of 3-5, but one or two flew on their own. Using binoculars with

a magnification of X 8 from a distance of 40-80 metres, with excellent visibility, it proved possible to observe many details of their behaviour.

When approaching the ship the shearwaters flew at a height of about 0.5 metres above the water and, turning their heads from side to side, appeared to be on the look-out for something. (Fig. 8). At a certain instant the entire flock settled on the water and began to feed. The shearwater buried its beak in the water to approximately eye-level and bending its neck in the shape of an S, moved its head forward so that the beak travelled a certain distance parallel to the surface at a depth never less than 2-3 cm. After each immersion, lasting 2-3 seconds, the bird raised its head above the water and made a swallowing motion. Each bird fed for 5-10 minutes or more in the same spot, and during one minute it was possible to record up to 20-25 immersions of the beak in the water. After a time the birds flew off, only to be replaced by another flock. It proved impossible to catch any of the shearwaters; on being overtaken by the ship the birds took off and brought up the food, which, in the water, from a distance of 4-5 metres looked very similar to net samples of hyponeuston.

The same method of feeding is characteristic of many other bird species. A.M. Sudilovskaya (1951) cites the following data. The food of the Atlantic fulmar Fulmarus glacialis glacialis) consists not only of fish eggs but also of pelagic mollusks, crustaceans and other invertebrates, for which the

bird does not dive but merely submerges its head to eye level. Pelagic crustaceans and young squids are eaten by the Pacific fulmar (Fulmarus glacialis radgersii). The little storm petrel (Hydrobates pelagicus), which is common in the Atlantic and Mediterranean, feeds on small pelagic crustaceans, mollusks, etc., which it snatches up on the wing from the surface of ^{the} sea. The author observed a specimen of Oceanites oceanicus (identified by V.I. Tarashshuk) obtaining its food in this way in the central part of the Gulf of Mexico.

Leach's great fork-tailed petrel (Oceanodroma leucorhoa) in the boreal part of the Atlantic and Pacific oceans eats shrimps, pteropods and copepods. It seizes its food while hovering low over the surface and bowing down to the water every now and then. Sometimes the petrel feeds while floating on the surface.



Fig. 7 - The scissor-bill (Rhynchops sp.) hunting for neuston organisms. Drawn from cine-film.

According to G.P. Dement'ev (1951a) the common little auk

(Plautus alle alle) feeds almost exclusively on Calanus, while the great auk (P. alle polaris) also feeds on amphipods. These crustaceans form the chief food of Ptychoramphus aleuticus. The parroquet auk (Cyclorhynchus psittaculus) in the northern part of the Pacific ocean consumes Calanus, hyperiids and polychaetes.

Some interesting observations are made by L.O. Belopol'skii (1957a,b), who studied the colonial birds of the Barents Sea. The fulmar (Fulmarus glacialis), he notes, takes its food only from the surface of the sea. The kittiwake (Rissa tridactyla tridactyla) can dive to 0.5-1 metre, but as a rule takes its food from the surface. "It catches Calanus in exactly the same way as the fulmar does, i.e. it settles on the water, where there is a mass aggregation of these small crustaceans and starts pecking away furiously. In the stomach of one kittiwake caught in Novaya Zemlya in 1947 we counted nearly 800 crustaceans, belonging mainly to the species Calanus finmarchicus and the remainder to C. arcticus".

According to the data of V.M. Gudkov (1962), birds in the open part of the Bering Sea have been found to eat the following types of food: petrels - Calanoida and young cephalopods, Leach's fork-tailed petrel and the blue-grey petrel - Calanus plumchrus, Metridia pacifica, Parathemisto japonica, Gonatus fabricius, G. magister, puffins - Parathemisto japonica, Gonatus fabricius - small fish, and auks - Calanoida. Typically baleen whales are also found where aggregations of feeding birds form.

According to the calculations of S.M. Uspenskii (1959), the colonial birds on the coasts of the Far-Eastern seas of the USSR consume over 500,000 tonnes of invertebrates and 567,000 tonnes of fish every year, and those of the Barents Sea devour some 100,000 tonnes of invertebrates and the same amount of fish. The chief invertebrates eaten are of course organisms caught in the near-surface layer of the pelagic zone.

/40/

However, only the adult birds can satisfy their hunger on the spot at sea; they still have to deliver food to their young at the nesting sites. While this problem is solved comparatively easily in the case of species consuming large food items such as adult fish, the species enumerated above need some sort of device for storing small items. It is quite obvious that a mere one or two crustaceans brought back in the parent's beak cannot either satisfy the needs of the nestlings or compensate for the energy expended by the parents on obtaining and delivering the food.

Such a device is found in auks, little auks and other birds in the form of the remarkable neck pouches discovered by L.A. Portenko (1948).

An auk with neck pouches is literally a "two-mouthed" bird. When this bird has its beak open it is possible to discern two distinct and almost identical orifices - one above the tongue, and the other, contrary to all preconceived ideas, below it. This second orifice leads to a capacious pouch into which, using a measuring glass, it is possible to pour 16 cc of water

(Fig. 9). In one auk in which a cut was made in the skin along the neck and the left half of the lower jaw removed, a clear view was had of the neck pouch, trachea and oesophagus with a slight dilation. The neck pouch is found in males and females only while they are feeding their young, after which it closes up and the walls grow together until the breeding season the following year.

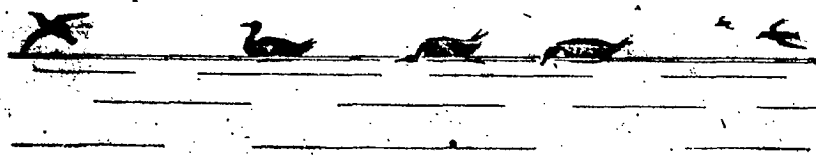


Fig. 8 - Consumption of hyponeuston by the storm petrel (schematic diagram) (Zaitsev, 1964a).



Fig. 9 - Neck pouch of Aethia cristatella (Portenko, 1948).

The biological expediency of such a device is obvious. According to the observations of Portenko, auks, whose diet consists of copepods, mysids, amphipods and other small invertebrates, feed on the surface of the sea several miles from the shore. It can only bring this food back fresh to its young if it has a special receptacle such as the neck pouch. When there is no longer any need for transporting food back to the shore the pouch disappears until it is time to feed nestlings again.

Portenko discovered such organs in the crested auk (Aethia cristatella), the least auk (A. pusilla), the parroquet auk (Cyclorhynchus psittaculus) and the Atlantic little auk (Mergulus alle). Similar devices are also found in land birds feeding their young on small items of food (nutcrackers on mole crickets, etc.). /41/

A specific group of aerial predators is constituted by bats of the family Noctilionidae, which are found in Central America. These animals (representative- Noctilio leporinus), like all bats, are active at night, but hunt over the surface of the sea and water bodies near the sea. With the aid of special apparatus ('radar') bats emit ultrasonic signals directed downward which bounce back off animals on the surface of the water, guiding the predator to its prey (Manteifel', Naumov, Yakobi, 1965). The diet of Noctilio leporinus consists of fish fry, crustaceans and insects. The bats are aided in their search for food by the fact that a huge number of comparatively large invertebrates and young fish, literally ploughing the surface of the water, rise from the lower-lying layers and the

bottom at night near the shore and gain the near-surface layer. Statements in the literature to the effect that the ultrasonic signals, penetrating beneath the water, bounce off the bodies of fish and, weakened nearly a millionfold, are picked up by the amazingly sensitive hearing apparatus of the bat (Griffin, 1961) require verification. It might have been possible to entertain such an idea prior to the discovery of hyponeuston, but now it is clear that N. leporinus has no need to sound for its prey in the midwater when it is present in far greater quantities on the surface and when the backs of crustaceans and fins of fry even project from the water. However, while the conjectural sensitivity of the "sounding devices" of these animals, which are frequently referred to in research papers on bionics, may be exaggerated, their hunting equipment is extremely sophisticated. We can see this in special cine-films (Griffin, 1961). N. leporinus flies at great speed directly over the surface of the sea at night without touching the water. Only from time to time, in response to signals from the sounding apparatus, does it lower its hind legs into the water and, with its long, sharp, curved nails (nothing of the sort is found in their insectivorous kin), dextrously seize their prey (Fig. 10).

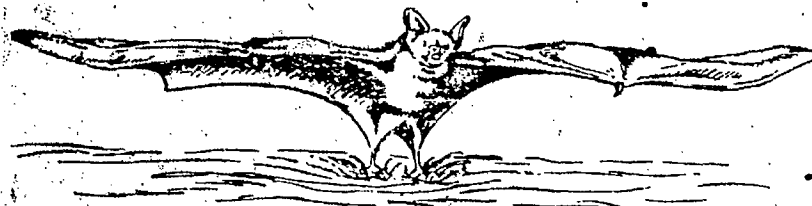


Fig. 10- "Fisher-bat" hunting for neuston organisms. Drawn from sequence of cine-film (Griffin, 1961)

"Fisher-bats" devour a large quantity of hydrobionts, and in the caves where they spend the daytime they deposit thick layers of guano. On Cuba this guano, which they call 'murcielaguina' (from 'murcielago' = bat), is highly valued as a fertilizer.

The examples given, reflecting only part of the biotic links in the near-surface layer of sea, show that it forms a distinctive ecological environment differing from that characteristic of the midwater. Deserving of special attention is the double "press" of predators (aquatic and terrestrial), which cannot help exercising a corresponding influence on the population of this biotope.

Chapter V. The ecological uniqueness of the near-surface biotope of the pelagic zone, determining the development in it of a special biological structure

Although there are still insufficient data characterizing the habitat in the upper microlayer of the pelagic zone, its uniqueness as a biotope emerges quite clearly. It differs most substantially from the midwater in the influx and concentration of non-living organic matter (foam formation, "anti-rain" of dead plankters, aeolian deposits, and so on), the biologically active properties of the foam, the presence of ultra-violet and infra-red radiation of the solar spectrum, and the double press of predators (Fig . 11).

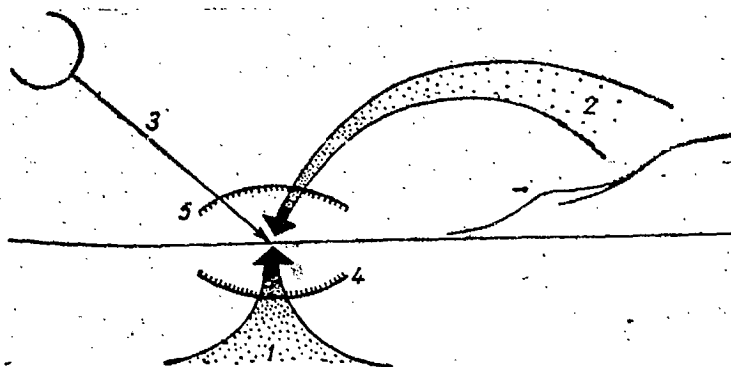


Fig. 11 - Ecological situation in the near-surface biotope of the pelagic zone:

1. - rise of non-living organic matter from midwater and bottom; 2 - deposition of organic matter in aeolian deposits; 3. - solar radiation; 4 - "press" of aquatic and 5 - aerial predators.

This ecological situation has been incorporated in the major current theories of the structure and life of the halosphere, illustrating and amending them.

In effect, as noted by P. Welander (1961), all physical, chemical and biological processes in the sea can be explained chiefly by the fact that the sea has a free surface interacting with the atmosphere. Indeed, the biotope in question here is just below the free surface of the sea and this boundary position explains its most important ecological characteristics. /43/

Discussing the cycle of materials in the ocean, Cooper (1961) arrives at the conclusion that any substance in suspension having the same compressibility as sea water cannot remain long in layers with neutral adiabatic equilibrium. Such substances tend to drop to the lower or rise to the upper density discontinuity. In such a way behave various food particles concentrat-

-ed in the vicinity of the density discontinuities and influencing the distribution of the population of the pelagic zone, while a "biological wasteland" forms between these areas. This is illustrated by the richness of life in pycnocline zones, at hydrologic fronts in rivers, in the vicinity of polar fronts, etc. The area of most contrastive density discontinuity is the surface of the water, and the concentration of organic particles in this zone has the most pronounced effect on the entire pelagic zone.

The great importance of external metabolites in the interrelations between hydrobionts (Lucas, 1961) suggests particularly intensive biological processes in any place where they are concentrated and qualitatively diverse, such as the surface of the sea.

Proceeding from the ecological importance of the factors whose influence is most evident at the surface of the sea - cosmic (solar radiation), trophic (suspended particles of organic substance), biochemical (biologically active properties of external metabolites) and biotic (interrelations between consumer and food) - and also from the interaction between environment and the organisms populating it, we can arrive at the following conclusions.

1. If non-living organic matter and external metabolites constantly concentrate in the near-surface biotope, and if a large number of predators with special apparatus for hunting in it exist, it means that the biotope is rich in life.

2. Since the near-surface biotope is marked in the trophic respect by an abundance of non-living organic matter, it must be populated by reducers and consumers.

3. As the main flow of substances and energy reaches the near-surface biotope from the midwater and bottom, it must be populated mainly by temporary inhabitants. On leaving the near-surface biotope again these organisms must return organic matter to the midwater and bottom, thereby maintaining a certain state of dynamic equilibrium in the sea. In other words, the influx of substances and energy to the surface must be balanced by their outflow. Therefore another stream of substances and energy from the near-surface biotope must flow to the dry land, from which organic particles come in aeolian deposits.

The organisms populating the near-surface biotope must be adapted to its specific conditions and, in particular, to intense solar radiation, ultra-violet rays, the double "press" of predators in the absence of shelter, and so on.

4. Since such an ecological situation forms in virtually all water bodies, the biological structure with the general characteristics enumerated above must be one of the most extensive in the World Ocean. Neuston proved to be such a biological structure, but in order to prove this it was necessary to devise a whole system of special devices and working methods to probe the nearest region of the pelagic zone for biological ends - a region which until now has remained outside the sphere of interest of the researcher.

THE METHODOLOGY OF NEUSTONOLOGICAL RESEARCH

Chapter VI. The impossibility of using existing types of
plankton-sampling gear for neustonological purposes

The life of a particular area of the pelagic zone is usually judged on the basis of samples taken by fishing a specific volume of water. It follows from this that the entire process of obtaining such a specimen should disturb the natural environment of the area as little as possible. If it does not, artificial situations inevitably arise which distort or even completely conceal the true state of affairs.

All efforts to improve existing methods and create new methods of obtaining hydrobiological material are directed essentially towards fulfilling this necessary condition. This also applies to the methodology of sampling neuston in the sea.

The life of any layer of the pelagic zone is studied on the basis of samples taken in that layer. All other things being equal, the representativeness of the samples depends largely on how "cleanly" they were taken, i.e. to what extent admixtures of organisms from neighbouring layers were avoided. As far as the 0-5 cm near-surface layer is concerned, it must be acknowledged that none of the devices used for obtaining samples of "surface" plankton - nets, plankton scoops, plankton collectors, plankton indicators, water bottles etc. - meet this requirement. Until recently it was believed that the pelagic zone was biologically uniform vertically for many metres, so the methodology of taking surface samples of plankton was based on fishing layers

of water of considerable thickness. For example, a sample of surface plankton from the "standard" 10-0 metre layer, obtained with the aid of any vertically operating net, nominally includes the population of ^{the} 0-5 cm layer, which in theory constitutes 1/200 of the entire haul. The IKS-80 conical ichthyoplankton net designed by T.S. Rass (1939), towed horizontally directly beneath the surface of the water, also fishes the 0-5cm layer, but its population theoretically forms only 1/37 of the entire haul. /46/

The plankton scoops (the Bogorov plankton scoop), planktonometers (the Greze planktonometer), plankton recorders (Hardy's continuous plankton recorder), water bottles and other special devices used for collecting plankton are in general not designed for working in the 0-5 cm layer.

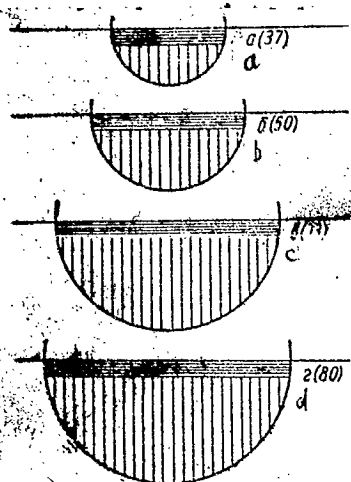


Fig. 12 - The unsuitability of certain common types of conical plankton net for collecting samples of hyponeuston: a) Juday net (mouth diameter given in cm in brackets), b) Jespersen net. c) Hensen net, d) Rass IKS-80 net. The horizontal hatching indicates the 0-5 cm layer, the vertical hatching the underlying layer, whose population forms an "impurity" in samples obtained with conical nets.

Thus, even gear encompassing part of the near-surface layer - vertically and horizontally operating nets - is unsuitable for collecting neuston samples. It is also impossible

to study neuston on the basis of Juday net hauls taken in the 10-0 metre layer, just as it is impossible to examine recent sediments on the strength of a bottom core many metres deep which has first been thoroughly mixed, destroying all traces of stratification. Vertical net samples taken near the sea surface represent something akin to this.

Even when conical plankton nets are only half-submerged and towed horizontally through the water, the "impurity" in the population of the 0-5 cm layer is still too substantial (Fig.12).

For these reasons special types of neuston net with rectangular mouths were devised, the designs of which made allowance as far as possible not only for the dimensions of the microlayer but also for other conditions associated with the life of the 0-5 cm layer.

Chapter VII. Some of the principles on which the elaboration of sampling methods and study of marine neuston are based

When manufacturing gear for neuston sampling allowance must be made for the special requirements of working in the near-surface biotope of the pelagic zone and for the peculiarities of its population. This determines both the actual design and the techniques of using the gear, meaning primarily the nets for collecting hyponeuston.

The direction of fishing and the unit used in counting

As the layer populated by hyponeuston extends virtually in a horizontal direction only, the best method of obtaining net samples is making horizontal sweeps with gear capable of fishing the thin near-surface microlayer. The gear answering the purpose proved to be the pyramidal net, which, unlike the widely used

conical net, has a rectangular mouth. The minimum layer of water that can be fished with these nets with satisfactory precision is 5 cm. Therefore the 0-5 cm microlayer was taken by the author as the conventional biotope of the hyponeuston. The actual thickness of the layer of water occupied by hyponeuston is generally less than 5 cm. In calm weather it is no more than 5-10 mm, i.e. as large as the space occupied by the bodies of the largest components of hyponeuston - fish fry. Pontellid crustaceans, which leap out of the water, may sometimes plunge to a depth of 2- cm on re-entry, and when there is a moderate or rough sea they concentrate in a layer of up to 4-5 cm. The most typical of them remain in this layer while the waves reach a height of up to 5 m and possibly even more.

Thus, as shown by the experience of sampling and visual observations under water, the 0-5 cm microlayer, accepted as the hyponeuston biotope, fully meets requirements of net samples with respect to the zone fished. In other words, fishing of the 0-5 cm layer makes it possible to take sufficiently "pure" hyponeuston with a minimum admixture of organisms from another biotope.

Because of the small thickness of the hyponeuston biotope it is possible to estimate the population density per unit of sea surface. However, the hyponeuston is a part of the pelagic zone population, which for all other layers is rated in units of water volume - cubic metres, litres etc. Therefore, in the interests of comparability the quantity of hyponeuston must also be expressed in units of volume - cubic metres, litres or millilitres of

water from the 0-5 cm layer. Thus, a cubic metre of water from this layer can be represented as a prism 5 cm high with a base area of 20 m^2 . We should not allow ourselves to be confused by this substantial deviation from the usually depicted cube with sides of 1 m, as we are here talking in terms of volume and not form. Moreover, not one type of plankton collecting gear whose haul is subsequently estimated per cubic metre of water "cuts" a regular cube out of the water, nor is it intended to. For example, 1 cubic metre for a Juday net with a mouth diameter of 36 cm is actually a cylinder with a base of 0.1 m^2 and a height of 10 m, while for the "international" net of Ostenfeld and Jespersen (Omaly, 1966) it is a cylinder with a base of 0.2 m^2 and a height of 5 m. For the "continuous plankton collector" widely used in the USA, Britain and other countries in recent years, 1 m^3 is a prism with a base of 1.6129 cm^2 and a height of 6,200.m /sic!/ Thus, a layer thickness of 0-5 cm is no obstacle when it comes to expressing the size of its population in units of water volume. This is a great methodological advantage - the possibility of comparing the numbers and biomass of hyponeuston with those of the plankton in all the underlying layers of the pelagic zone. In case of necessity the number of organisms beneath 1 m^2 of sea surface in the 0-5 cm layer can easily be determined by dividing the figures for 1 m^3 by 20.

Optimum hauling speed

On the speed of the filtering gear through the water depend at least two methodologically important factors. All other things being equal, when the hauling speed is increased the pressure exerted

on the captured hydrobionts by the sides of the net is augmented, and this may lead to mechanical injury to the most delicate organisms and make them unsuitable for investigation. At the same time, when the speed of the net increases the efficiency of catching of the active forms is higher, and this substantially increases the representativeness of the sample. Both these conditions (preservation of specimens and maximum representativeness of the sample) cannot be met in the same collection, so the investigator is compelled to make both slow hauls for the collection and counting of delicate and slowly moving forms and rapid ones for larger and more active specimens.

Examples of passive and delicate forms would be larvae and prolarvae of fish. The need for correct appraisal of the developmental stage and numbers of these important representatives of hyponeuston gave rise to special methodical studies (Zaitsev, 1958a) which revealed, in particular, the following.

The speed of the net through the water is directly proportional to the ratio of undamaged to damaged roe in the sample: when ^{rises} the towing speed/the percentage of damaged roe grows. At a net speed of no more than 20-25 cm/sec there are either no damaged eggs or else the number does not exceed 1-2% of the total. At a single speed of not more than 20-25 cm/sec the extent of the damage to roe in the net depends on the stage of egg development, the specific surface of the roe and the density of the mesh. Prior to the covering of the vitellus (stages I and II according to T.S. Rass), the eggs are damaged much sooner and in greater

quantities than afterwards. At the same stage of development the percentage of damaged roe in the sample is directly proportional to its specific surface, which is greater in the case of small globular and especially ellipsoidal eggs. In nets of No. 21 bolting cloth less roe is damaged than in nets of No. 15 bolting cloth, since the surface of the former is smoother than that of the latter (Fig. 13).

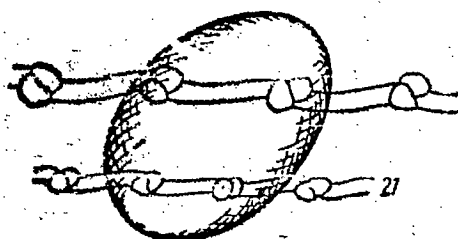


Fig. 13 - Cross-section through threads of weft of bolting silk No. 15 and No. 21 and egg of Black Sea anchovy at same magnification (Zaitsev, 1964).

Hauling at speeds greater than 25 cm/sec results in damage to a larger number of fish prolarvae, which are characterized by low mechanical strength of the integuments, a greater specific area and a body shape that makes it difficult to roll down the side of the net. The prolarval stages are damaged so severely that they may be squeezed out through the mesh. Thus, if eggs and prolarval stages are to be counted correctly nets of No. 21 bolting cloth and above must be used and the speed of hauling must be equal to or less than 25 cm/sec.

And what about the other hyponeuston components? Protozoans and small metazoans (larvae of mollusks, polychaetes, nauplius and copepodite stages of Copepoda, nauplius and cypris larvae of barnacles, small species of adult copepods, cladocerans, and so on),

being relatively slowly moving animals, are overtaken and caught by a net travelling at a speed of 25 cm/sec. Hence, the methods of collecting rae and prolarval stages of fish can also be used for the collection and counting of these organisms.

The larger components of the hyponeuston, such as the larvae of decapods, mysids, isopods, pontellids, and fish fry and larvae, usually flee sluggishly from the oncoming net. For this reason a fairly large body of observations has built up.

/50/

The underwater observations of the author revealed that the plankters visible to the naked eye in the water begin fleeing standard nets (for example, the Juday net) even before the ring connecting the front guys comes near them (Zaitsev, 1964a). The same finding was made by A. Bourdillon (1964). In the Mediterranean the width of the peripheral zone from which adult copepods flee the net varies for different species from 0.3 to 8.5 cm (Fleminger, Clutter, 1965). Fish larvae swim away from fishing gear very actively (Bridger, 1956), and the movement of the net hastens the process. N.M. Voronina (1958) showed that photokinesis (increased activity of organisms in light) occurs in connection with moving objects. It is true that the author worked with freshwater forms, but the same thing is characteristic of marine species also. Through the glass of their face masks divers see clearly how pontellids, decapod larvae, and isopods begin to show signs of unrest and attempt to flee when a motionless object (a pencil, note-pad, the hand of the observer) begins to move. After movement has ceased they stop trying to flee from it. Decapod larvae and some other forms

often settle on a hand quietly resting on the surface of the water. Such forms can be collected very effectively with motionless nets allowed to drift, or with fast moving nets capable of overtaking fleeing organisms. Both these methods were used when devising techniques of collecting hyponeuston.

A net lowered into the sea from an anchored or drifting vessel filters the water because of the current or because of the motion of the ship. It evidently bears some resemblance to various objects floating on the surface (pieces of timber, reeds, bits of algae, etc.) and therefore is easily perceived by organisms, which instead of fleeing allow themselves to be swept inside. It has been established that many hyponeuston organisms feed on the epiphyton of floating objects. Such objects drift with the current or (if they protrude from the water and catch the wind) move slowly relative to the surrounding water.

Collections of drifting plankton were made by Thor Heyerdahl and his companions and by Alain Bombard, all of whom noted how effective this method was. Cushing (1964) collected drifting plankton using nets with an aluminum frame.

Objects moving more rapidly than driftwood are evidently associated with living creatures or predators, and fish flee from them. Therefore active netting of neustonic organisms is done at a speed of about 2 m/sec.

Minimal disturbance of natural stratification of the water and the population density in the collecting area

The lowering of any device into an aquatic environment inevitably disturbs its original state. This is particularly

important when we are dealing with the live objects populating the well-illuminated thin 0-5 cm layer.

The chief factor disturbing the stratification of the water near the sea surface is the moving vessel. Hence, hyponeuston should be collected with the ship standing at anchor. The net at the end of a line is carried away from the ship by the current for a certain distance and collects drifting organisms at a point where the position of the water layers is undisturbed and out of reach of vibrations from the hull of the anchored ship and other noises which scare off animals.

A net operating several tens of metres from the ship is more advantageously placed from the investigator's view-point than the same type of gear operating right alongside the ship. The author often chanced to observe larvae and fry dash away when some device was lowered into the water, or simply when a human being showed himself. On a research vessel it is virtually impossible to create those conditions of complete silence and immobility which would ensure successful collection of all forms of hyponeuston immediately alongside the ship.

The advantage of observing and collecting specimens from small and noiseless vessels such as sloops, rafts and others is evidenced by the researches of seafaring experimenters. Thus, Thor Heyerdahl (1958), in particular, wrote: "The ocean holds many surprises for him who lives on its surface and drifts along slowly and quietly. The hunter crashing through the undergrowth in a forest may return disappointed and report that there wasn't a single

living creature to be seen. Another will sit silently on a tree stump and quietly wait, and soon he will hear a variety of rustling sounds and see curious eyes studying him. The same applies to the sea. We plough across it with engines and pistons thudding away, and then we return and say that the sea is completely deserted"* (p. 78).

Of course, this is no reason to call for the abolition of our present "floating institutes": the laws controlling life in the sea cannot be unravelled on a balsa-wood raft like the "Kon-Tiki". Nevertheless, Heyerdahl's words are undoubtedly true - collections of fauna made from large, powerful ships are /52/ much poorer, than those made from a noiseless small boat. Therefore no opportunity should be lost to observe hyponeuston and epineuston in something approaching natural conditions.

In this connection an interesting experiment was conducted at a biological station in Honolulu. Observations were made through the portholes of a steel cylinder suspended from a small raft drifting with the current for two weeks. A very large number of species of fishes and other animals coming right up to the portholes was recorded. The observers remark on the effectiveness of this method of investigation.

Apart from the ship, the net itself can also cause substantial changes in the distribution of pelagic organisms. Earlier it was stated that hydrobionts strive to escape moving nets and

*None of the published English versions has been cited verbatim for the extract since the original publication was in Norwegian-Translator's note.

that the easiest way of preventing this is to allow the nets to drift. In addition the bridles of the net, being made of thick cordage, set up turbulence currents and eddies in front of the mouth (Clutter, 1966), creating additional obstacles between plankters and the net. These obstacles increase as the net filter becomes clogged and the mesh frays.

Hyponeuston organisms also react to the colour of the net. Very little study has yet been made of the colour perception of pelagic invertebrates. Whereas in the fishing industry the colour of the net webbing is considered one of the factors influencing the catching efficiency of commercial fishing gear, plankton nets are made from material produced to meet the needs of flour mills.

To determine whether the colour of the net influences the hyponeuston catch special experiments were staged (Zaitsev, 1964a). An array of three nets of identical shape and size (red, blue and colourless) was towed during the daylight hours in various parts of the Black Sea. The catches of the three nets (60 samples - 20 hauls) differed only slightly and no pattern of any sort emerged.

Similar results were obtained in a laboratory experiment. Hyponeuston organisms clustered equally well around a dark-red light source ($\lambda = 800$ millimicrons) and a beam of ultra-violet light ($\lambda = 365$ millimicrons). It may be that the same reaction to light rays of different wavelengths reflects adaptation of hyponeuston organisms to a biotope which is characterized by a broad range of the solar spectrum. It is known for example that fish dwelling in the water column at depths where long-wave

radiation does not penetrate, do not perceive dark-red light. (Protasov, 1961).

The investigations showed that hyponeuston organisms flee from nets of all colours, and the idea arose of camouflaging them the colour of objects frequently found floating on the surface of the sea, such as driftwood, the growth on which is eaten by many of the organisms under study. The top hoop of the net was accordingly coloured dark-green like the growth on driftwood. The hauls made with such nets (and later with nets having an olive green and brown hoop) were on average 5-20% higher as regards the larger forms of hyponeuston than in nets with a colourless (white) top hoop. /53/

Some of the technical parameters of nets considered when making filtering devices for collecting hyponeuston

Material. Of the existing filter fabrics used for neuston nets the preferred material is bolting silk, which does not stretch as much as synthetics. Bolting silk nets come in two patterns: openwork and mixed weave (Fig. 14). Openwork nets are considered to be the stronger.

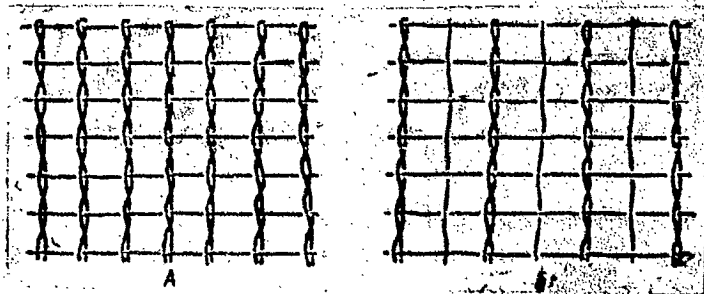


Fig. 14 - Openwork (A) and mixed-weave (B) fabrics used in filtering devices for the collection of hydrobiological material.

Net filtration factor. A serious defect in all types of plankton net in the view of most researchers is their limited filtration capacity, as the result of which the volume of filtered water is always less than expected (Sysoev, 1956; Bourdillon, 1964). The fact that the filtration capacity of the net varies for each tow, depending on the composition and numbers of the plankton captured, makes it impossible to apply any correction factor. But the installation of a water meter at the mouth, which would be useful from the engineering point of view, is undesirable from the biological standpoint, since it sharply augments the already substantial "deterrent effect" of the fishing gear. Therefore present efforts to increase the filtration capacity of the net are being directed chiefly towards raising the filtration factor (F_f), which means the ratio of the total mesh area of the net to the area of its mouth.

The concept of the "filtration factor" was born in recent years when the entire complexity of obtaining representative samples of biological material in the sea became evident. Previously plankton nets had been designed without taking special account of this important technical parameter. The F_f values of two of the most "senior" plankton nets - the Juday net (dating from 1916) and the Rass net (dating from 1939) - which played a prominent part in the collection of zoo- and ichthyoplankton for several decades, were computed by the author. It turned out that a Juday net of No. 38 bolting cloth with a mouth diameter of 36 cm had an F_f value of 4.08, whereas Rass's fish egg net of No. 15 bolting cloth, with a mouth diameter of 80 cm, had a factor of 3.45. The total

/54/

mesh area was determined (under a binocular microscope) on new patterns of fabric, taking into consideration the thickness of the threads of the warp and weft. The total mesh area of the filter bags of these nets is, respectively, 4.08 and 3.45 times greater than the area of their mouths. Many years of collecting experience shows that this is a fairly large reserve of filtration capacity and that these nets generally operate satisfactorily (from the viewpoint of filtration) in the main water mass. In the ideal case all the water in front of the mouth of the net will pass through its meshes if the sum of the areas of the meshes is equal to the mouth area ($Ff = 1$). However, the plankton net does not filter pure water but water rich in suspended matter, and this requires a factor greater than 1. The problem is to determine the optimum value for each type and area of operation.

As regards the near-surface biotope of the pelagic zone (with its abundance of living and non-living suspended matter), hauls have shown that $Ff = 3 - 4$ is insufficient. V.N. Greze (1962), who conducted tests with a self-designed planktonometer using a current meter mounted in front of the mouth of the net, discovered that with a filtration factor of 10.1 the rate of filtration can be kept equal to the towing speed at various values of the latter. Since the planktonometer nets were made of No. 38 and No. 64 cloth and towed close to the surface of the sea at speeds of up to 2.4 m/sec, it can be concluded that $Ff = 10$ is adequate for finemesh plankton nets. This would apply in the

case of a new net (the meshes of old nets become blocked due to untwining of the threads), the absence of medusa aggregations and phytoplankton bloom (particularly Rhizosolenia in the working area, which clog the gear. Therefore a filtration factor of approximately 10 was allowed for when making the neuston nets.

A considerable advantage of nets for the collection of hyponeuston is their rectangular mouth. This design feature not only ensures that the 0-5 cm layer is fished with touching the underlying layer, but markedly augments the filtration factor compared with a conical net having a filter bag of the same size. Thus, if a bag of bolting cloth with a mouth periphery of 160 cm is mounted on a circular hoop with a diameter of 51 cm, we get a conical net with a mouth area of 2020 cm^2 . But if the bag is mounted on a rectangular frame of 60 X 20 cm with the same perimeter, the mouth area of the bag will be 1200 cm^2 . Thus, a pyramidal net of 60 X 20 cm will have a far smaller mouth (in this particular case 40% smaller) and a correspondingly larger Ff value for the same size of the filter portion. This is in accordance with the well-known geometrical proposition that, of all figures with the same perimeter, the circle has the greatest area. /55/

The 60 X 20 X 250 cm pyramidal nets widely used for collecting hyponeuston have $Ff = 11.3$ when made from No. 21 bolting cloth and $Ff = 9.35$ when made from cloth No. 61.

Rigging of the nets. The special purpose of neuston nets and the fact that most of them are towed at low speeds have made redundant such traditional elements of their rigging as the strong bridles of stout cordage and the heavy metal bucket. The side

bridles are absent in the neuston nets, while the front ones are made of fine polyamide fish line with strands 1 mm thick, which has a high breaking strength and is hard to see in the water. The necessity for using bridles made of fish line was confirmed by underwater observations, which convinced the author that stout bridles linked by a metal ring in front scare off plankters visible to the naked eye. The metal bucket has been replaced by one of plastic, which, by lightening the rear end of the filter bag, ensures that the net works in a horizontal plane. A special feature of the neuston nets is the floats. Their number, size and shape differ in the various models.

Maintenance of the net. The problems of net maintenance and depreciation have not been worked out properly yet and require special study. They were touched on partially when devising the methodology of neuston collection.

Bolting silk is made with a special lustrous finish on the threads. While the net is being used, the finish, which is not very elastic, gradually flakes off, baring the threads, which become fluffy so that the original mesh size is sharply reduced. This not only leads to a drop in the filtration capacity of the net but also means that many organisms (e.g. fish prolarvae) are retained on the sides of the net, resulting in accelerated clogging and reduced representativeness of the sample. A high degree of wear may be suffered even by a comparatively little-used net if it is thoroughly washed by hand. Therefore salt must be removed after use by /56/ soaking the nets in fresh water and hanging them up in order to rinse them off. Observance of these rules will ease the passage of

the catch through the net into the bucket and lengthen the net's working life.

Chapter VIII. Gear and, methods of collection and study of marine neuston

This book is not a manual of procedures for the collection of neuston, and so in this chapter we shall leave out a number of details which would be essential in any instruction book. The main aim of the chapter is to demonstrate the specifics of the methodology of studying that new biological structure in the sea which is known as neuston.

The "oldest" gear for collecting marine neuston has barely completed 10 years, and for this reason alone nothing described below can be regarded as a complete and perfected working device. The design of each piece of collecting gear reflects the level of study of the item being hunted - its distribution, mobility, reaction to pursuit - and is constantly being improved. It is typical that whereas previously improvement of the gear was bound up mainly with more successful solutions of particular engineering problems without taking due account of the biological peculiarities of the item being collected, recently more and more attention has been paid to the biology and behaviour of neuston, which have a direct bearing on its collection. This is particularly true of the methodology of neuston collection. In ten years of work in this field many devices have been repeatedly improved or replaced by newer, more effective ones.

Collection of bacteria

The instrument for collecting bacteria in the near-surface

microlayer of the sea was produced by A.V. Tsyban' and M.S. Rozen-gurt and called the "bacterioneuston collector" (BNC). It is designed for collecting water in the 0-2 cm layer and has been tested on research vessels in the Black Sea.

The collecting part of the device is a double-necked glass flask with a capacity of 250 cc (Fig. 15). The length of the flask is 310 mm, the diameter of the body 50 mm, the length of the tubes 20 mm and their diameter 5 mm. The body of the flask is bound with copper rings which act as weights. The flask is kept horizontal by two equal lengths of surgical silk (n, n') /57/ which withstand high temperature and pressure during autoclaving. The ends of the lengths of silk are tied in a single loop. The effective capacity of the device operating in the 0-2 cm layer is about 125 cc.

The BNC is prepared for work as follows. The collecting flask is boiled in distilled water and dried in a special desiccator. Next caps (k, k') of thick X-ray paper are placed over the ends of the tubes, then the rings (KП, KП') and bridles (n, n') are placed into position. After this the device is wrapped in parchment paper and sterilized in an autoclave for 40 minutes at a pressure of 1 atmosphere. On the deck of the boat the BNC is attached to a fishing line which is in turn fastened to a bamboo pole 3-5 metres long. The length of the line depends on the height of the prow of the boat. The caps are removed from the collector and it is lowered onto the surface of the sea, where the flask is immediately filled with water. To avoid pollution from the vessel, the collector is lowered into the water from the foremost point of

the bows while at anchor, but when vessel is moving it is lowered as far as possible from the lee side, at the full extent of the bamboo pole.

Using the BNC, A.V. Tsyban' discovered marine bacteria not caught by the normal hydrological and microbiological water bottles with which marine microbiologists work.

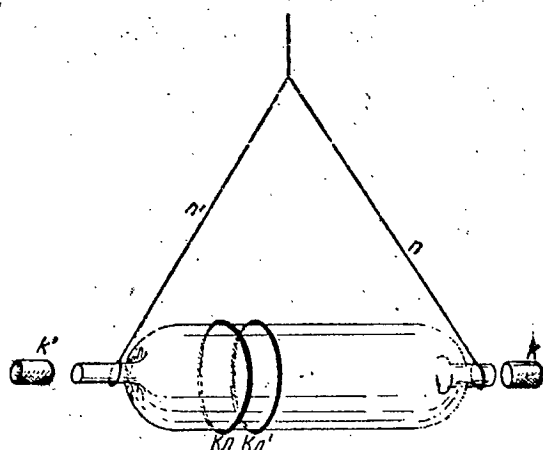


Fig. 15 - General view of the bacterioneuston collector (Tsyban', 1967):
k, k' - caps; K π , K π * - ring weights; n, n' - bridles of surgical silk.

Collecting microphytes

To obtain sedimentary samples of phytoplankton (Ivanov, 1962; Ivanov, 1968; Nesterova, 1969), and also samples of water from the near-surface microlayer for hydrochemical analyses, the hose water sampler is used (Fig. 16). This device was constructed by V.S. Bol'shakov (1963) on the basis of an idea by S.O. Makarov (1894). The intake assembly of the hose water sampler consists of a foam plastic float measuring 20 X 20 X 2 cm with a hole in the middle into which is inserted a tightly fitting glass tube. The bottom end of the tube is 3 cm below the water line of the float, while the top end is connected by a rubber hose to a

bottle. The intake assembly is lowered onto the water with the aid of a bamboo pole, to the far end of which is attached the hose leading to the bottle. The sampler itself is a wide-necked bottle sealed with a stopper and having two glass elbow tubes. The bottom end of one of them extends almost as far as the bottom of the bottle and is connected to the intake assembly; the other - a shorter tube - is connected by a rubber hose to a Komovskii manual vacuum pump. The pump evacuates the air from the bottle and sea water from the intake assembly flows in to replace it. By adjusting the depth of the glass tube passing through the float, water can be obtained from a point 2-3 cm or more below the surface.

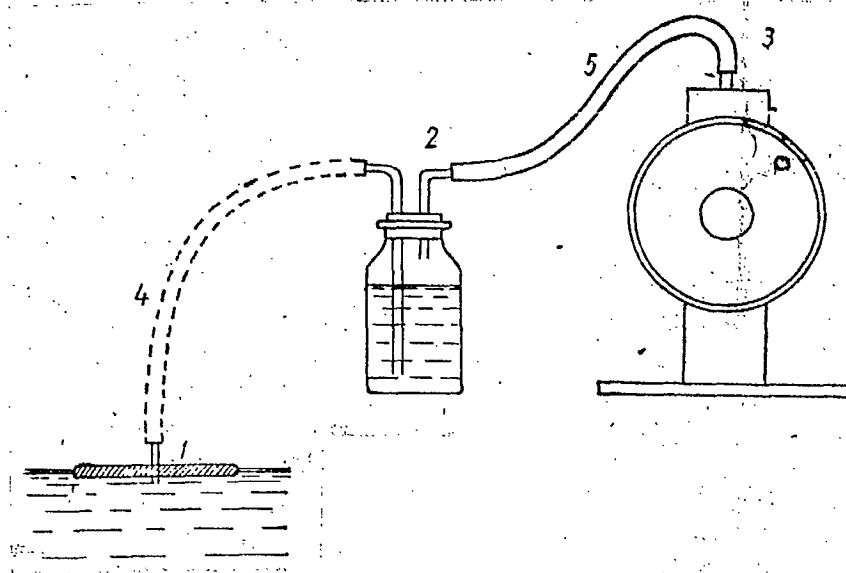


Fig. 16 - The hose water sampler (Bol'shakow, 1963): 1-intake assembly, 2-water sampler, 3- vacuum pump, 4,5 - rubber hose.

From this size group of neuston components up to the largest - the fish fry - samples are no longer collected by extracting devices (with a few exceptions) but with filter devices, and the most widely used of these is the net. Therefore many of the characteristics referred to below relate not only to gear for collecting the very small animals but also to that used for large invertebrates, fish larvae and fry.

The main filter device for collecting neuston is the NC neuston net with a rectangular mouth (Zaitsev, 1959 d,e). The model used most frequently has a mouth frame measuring 60 X 20 cm and a length of 250 cm (Fig. 17). One of the advantages of this net is that it makes the most economical use of the standard width of bolting cloth.

The frame of the net (p) is made of bimetallic wire (steel core, copper sheath) with a diameter of 4 mm, or of bronze with a diameter of 6 mm. The net bag (cm) is attached at its base to the frame and at its apex to the bucket by bands of webbing 10 cm wide (n, n'). The front band is made from dark-green or greenish-brown material in imitation of the growth on driftwood. The bucket (c) is made of plastic. Most suitable for the purpose are the PVC beakers available commercially, with the bottom cut out. They are light, smooth, strong and do not rust.

The neuston net has only front bridles (o,o'), made of stranded fish line 1 mm thick with a breaking strength of 15 kg. The ends of the length of fish line, which is roughly 230 cm long, are

attached to the middle of the short sides of the frame, and in front the line is tied in a loop. Visual observations show that the use of fish line for the bridles and the absence of the metal ring which in all nets connects the bridles at the front, and also the colouring of the front band, reduce the deterrent effect /60/ of the net to a minimum. Foam plastic floats measuring 20 X 10 X 4 cm are fastened to the short sides of the frame.

With this rigging the neuston net is lowered into the water to a depth of some 5 cm, so that 15 cm of the mouth are above the surface. This is necessary to catch such organisms as pontellids, which jump out of the water (the trajectory of the jumps of Black Sea species has been measured) to a height of up to 10-12 cm. The neuston net collects both hyponeuston and epineuston (water measurers, the foam population etc.) and therefore it is more correct to call it a "neuston net" and not "hyponeuston net", though the sample consists mainly of hyponeuston organisms.

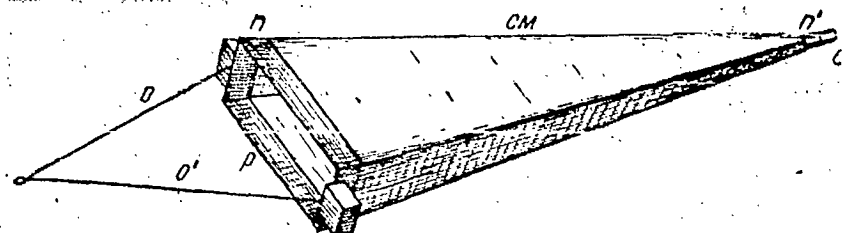


Fig. 17 - Neuston net (Zaitsev, 1964a): o, o' -bridles; n, n' - bands; p- frame; c - bucket; c - net bag.

In appearance the neuston net resembles the pleuston net designed by A.I. Savilov (1963), which can fish the 0-30 cm layer. It is used for collecting the population of the near-surface biotope of water areas whose neuston has been fairly thoroughly studied. For water bodies new in the neustonological respect, and also for simultaneous collection of organisms from the underlying layer of water, multitier assemblies are used - the PNS, or plankton-neuston nets (Zaitsev, patent No. 138422; Zaitsev, 1961b)*.

We give here a brief description of the 5-tier plankton-neuston net PNS-5.

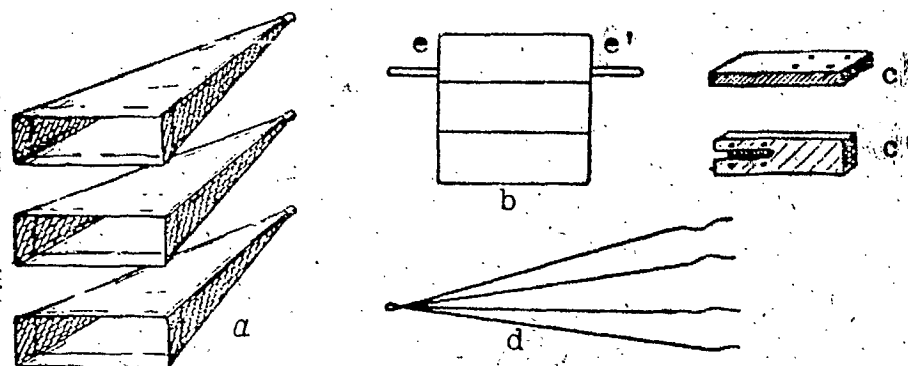


Fig. 18 - Component parts of multitier plankton-neuston net (Zaitsev, 1964a): a - nets; b - connecting frame; c, c' - floats; d - bridles; e, e' - pegs for attachment of floats.

A connecting frame made of 6mm bronze wire and measuring 100 cm high by 60 cm wide is divided into five identical compart-

*When referring to the paper by Y.P. Zaitsev, A.I. Savilov (1963) incorrectly calls the PNS array a "multitier floating net", and G.B. Zevin (1966) - a "plankton-neuston net".

ments of 60 X 60 cm by four partitions of the same material.

15 cm from one end, which then becomes the upper one, pegs (e, e') are welded on, to which foam plastic floats (c, c') measuring 30 X 14 X 4 cm are connected.

Five NS nets, 60 X 20 cm, without frames are mounted on the connecting frame, using fish line. In front four bridles of 1 mm- thick polyamide fish line are fastened to the frame and tied together in a loop. When assembled the PNS-5 is lowered into the water where it assumes its working position (Fig. 19, 20).

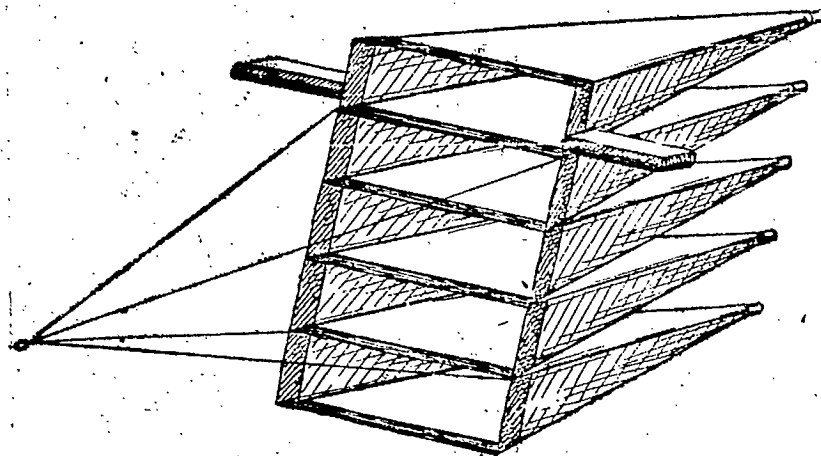


Fig. 19 - General view of the five-tier plankton-neuston net (Zaitsev, 1964a)

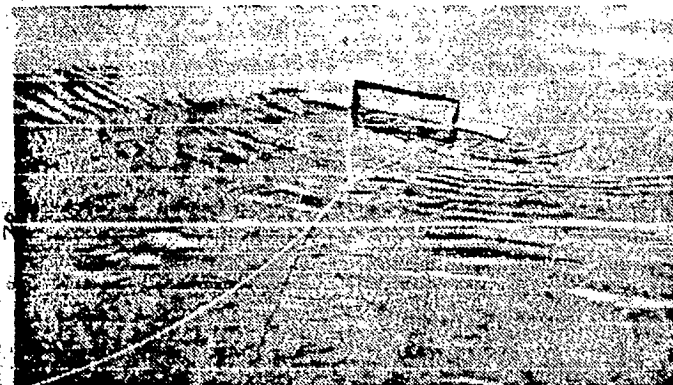


Fig. 20 - Five-tier plankton-neuston net in working position.

The float-planes "hug" the surface of the water and keep the assembly in position. In the north-west part of the Pacific Ocean the model was tested in waves over 4.5 m. high and proved reliable and trouble-free. It is easily assembled and taken apart again, and this makes it easy to transport.

The PNS-5 fishes the following microlayers simultaneously: 0-5, 5-25, 25-45, 45-65, 65-85 cm. A comparison of the samples taken by each of the nets reveals the vertical microdistribution of life near the surface of the sea and provides a comparative description^{of} the neuston and plankton. The net is used in water bodies where the neuston has not been studied in order to determine its composition. Later, when this work has already been done, lighter versions of the multitier assembly can be used, /62/ consisting of four (PNS-4), three (PNS-3) or two (PNS-2) pyramidal nets which are assembled in the same way. The design of the two-tier plankton-neuston net is similar to that of the net used by J. Mundie (1959) to collect chironomid larvae in Lac La Ronge in Canada.

The NS and PNS nets are used as follows. The best spot to operate from is the after deck, since at anchor, when the vessel points into the surface current, the fishing gear, on being lowered into the water, will be swept aft (Fig. 21). The net must be lowered from the side of the after deck and not from the middle of the stern, so that it does not end up in the zone of depauperate neuston formed as the result of the flow of water round the hull of the vessel. The net is also hauled in from the side.

When the vessel heaves to, it lies athwart the wind and drifts (Fig. 21). In that case the net, on being lowered from the aftermost point of the stern, will be swept away up-wind. Under these conditions the zone of depauperate neuston is much wider than when the boat is anchored, and to avoid it the warp must be secured to a boom run out from the stern. On the RS "Miklukho-Maklai" a stout bamboo pole 4 metres long is used, being attached to the aftermost point of the stern. A pole like this can be used when at anchor to run the warp out from the side of the boat in order to avoid that part of the sea surface where the density of the neustonic organisms, under the influence of the ship's hull, is artificially high and easily traced by a strip of foam. /63/



Fig. 21 - Position of the zone of depauperate neuston (hatched) with boat anchored (a) and drifting (b,c) (Zaitsev, 1964a).

So the net is secured ^{to} a marked warp up to 100 metres long. A chlorinated PVC fish line with a diameter of 6mm and a breaking strength of at least 140 kg proved very suitable for the purpose (Andreev, 1962). Every 10 metres foam plastic floats measuring 10 X 4 X 4 cm are attached to the warp to keep it on the surface. Usually from 50 to 100 metres of warp are paid out. The drifting

net drags after it a given length of warp, and at the moment when the warp becomes taut the net takes up its working position and begins to filter the water. From this point until hauling in a check is kept on the fishing time of the net. Hauling can begin immediately after the line becomes taut, but usually it is left for a while (10-20 minutes) to drift. This time is noted down in the log. When there is a heavy sea and the boat is rocking the drifting net tends to jerk, which makes it difficult to retain the collected material and leads to increased wear and tear on the gear. To cushion the effect a rubber shock absorber is used (Fig. 22).

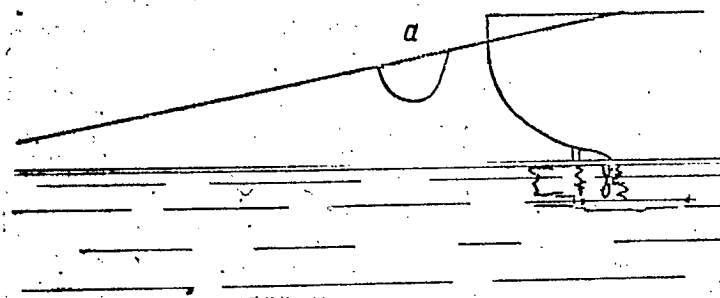


Fig. 22 - Installation of rubber shock absorber (a) on warp (Zaitsev, 1964a).

Hauling is done manually at a speed of about 25 cm/sec. If the gear is light and the towing speed slow this operation is not difficult. Depending on the number of tiers in the PNS assembly and the velocity of the counter-current, the resistance encountered during hauling does not exceed 7-8 kg. The net can be hauled mechanically instead of manually, but the latter method is more even when the boat is rocking.

The volume of water passing through the net is calculated on the basis of the following parameters:

1) The working area of the mouth of the net. For NS nets and the first net of the PNS assembly the figure is $60 \times 5 = 300 \text{ cm}^2$, and for the second and subsequent nets of the PNS it is $60 \times 20 = 1200 \text{ cm}^2$.

2) The linear distance covered by the fishing gear when it is hauled in. This figure is equal to the length of the warp when taut.

3) The linear distance covered by the water mass relative to the net (or through the net) while it is drifting. This is determined by the velocity of the current and the duration of drifting. /64/

4) The linear distance covered by the water mass relative to the moving net (or through the net) while it is being hauled in. When being hauled the net filters not only the volume of water determined by the length of the warp, but also a supplementary volume due to the counter-current.

The third and fourth parameters can be lumped together to denote the distance covered by the water mass relative to the fishing gear (or through it) while it is drifting and being hauled. It is equal to the product of the time from the beginning of drifting to the moment the net is lifted from the water multiplied by the velocity of the current.

The volume of water passing through the net is determined from the formula:

$$V = S(l + l'),$$

where V is the volume of water filtered by the net, in m^3 ; S is the working area of the mouth of the net, in m^2 ; l is the length of line paid out, in metres; l' is the linear distance covered by the water mass while the net is drifting and being hauled, in metres.

The velocity of the surface current in the working area is measured by meter or attached floats, or else judged by the speed at which the net is carried away from the vessel before it is allowed to drift. NS and PNS nets of the described assembly, depending on the number of the bolting cloth, are used to collect various components of the neuston. Thus, for the collection of protozoans and small metazoans, which lie within the size limits of microplankton, mesh Nos. 49-60 are used. For the collection of foraminifers in the near-surface /65/ layer of water in the vicinity of Wellington (New Zealand) R.P. Willis (1963) used a small pyramidal net, with a mouth of 18 X 4 cm and a length of 70 cm, made of No. 78 bolting cloth.

Collecting medium-sized invertebrates, fish roe and prolarvae

Organisms with body sizes placing them in the category of mesoplankton (1-10 mm), or slightly larger, are collected with the aid of neuston nets and plankton-neuston nets of no. 21-23 bolting cloth. They are also captured by nets of coarser material, but the larger admixture of small forms in this case complicates laboratory processing of the samples.

Collecting large invertebrates, fish larvae and fry

The most mobile components of the neuston, such as isopods, large decapod larvae, water-measurers, larvae and fry of fish are also captured by drift nets from time to time, but for quantitative estimates of such organisms active neuston fishing gear is used. In particular, the model MNT fry neuston trawl recommended itself.

The mouth of the trawl is bounded by an ellipsoidal hoop of bronze or brass rod 10-15 mm thick (Fig. 23). The large and small axes of the ellipse are equal respectively to 100 and 50 cm. The frame is connected by a band of closely woven fabric 10 cm wide to a net bag of no. 21-23 bolting cloth, 400 cm long. A rear band connects the net bag to a brass cylindrical bucket. From the frame to the bucket lead four chlorinated PVC fibre bridles with a diameter of 6 mm, forming a loop where they join in front. To either side of the frame are attached prismatic foam plastic floats measuring 25 X 12 X 8 cm. On one of the larger surfaces of each float there is an elliptical groove, 15 mm deep and 15 mm wide, into which the hoops fits, ensuring that it is firmly attached to the float.

The MNT is towed in a circle at a speed of 2 m/sec. The trawl is shackled to a steel winch cable. The vessel circles, the MNT is cast overboard, and the cable is paid out for 50-100 m. Then the winch is braked and the clock stopped. After 10 minutes the trawl is wound in slowly.

Because of the floats, the mouth of the trawl is only half-submerged (to a depth of 25 cm) and a strip 1 metre wide is

fished. Since the boat describes a curve, the fishing gear does /66/ not get caught in the wash and works instead in a zone unaffected (or virtually unaffected) by the mixing influence of the hull and screw.

Together with the large organisms the hauls made by the MNT contain various small forms, but as the result of the high trawling speed many of them are damaged. Thus, most of the fish larvae in the early developmental stages (before the yolk is enclosed) are so deformed that it is difficult to identify them down to the species level.

With the aid of MNT numerous collections were made in different seas and valuable data were obtained. In particular, the use of this gear made it possible for the first time to make a qualitative and quantitative estimate of the early (hyponeuston) mullet fry in the southern seas of the USSR (Zaitsev, 1963a, 1964b; Babayan and Zaitsev, 1964).

Apart from the high-speed gear already mentioned there are other types for the collection of neustonic organisms. The collection of Sargassum in the Atlantic by A. Parr (1939) was done with the aid of a net with a rectangular mouth measuring 61 X 51 cm and a length of 240 cm, made of loosely woven material and towed at a speed of 5 m/sec. In this case the high speed of fishing was dictated not by the activity of the specimen being investigated but by the brief working time available.

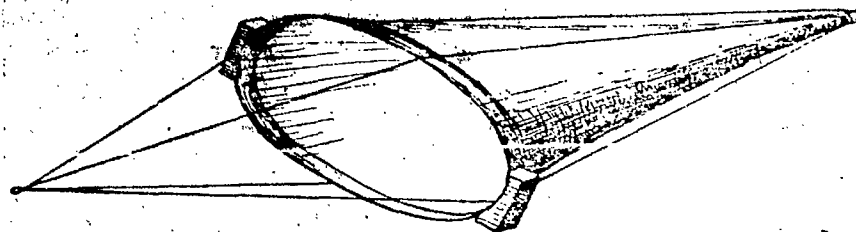


Fig. 23 - Fry neuston trawl (Zaitsev, 1964a).

For the collection of large neuston components consumed by birds, P.M. David (1963) made a pyramidal neuston net measuring 30 X 15 X 370 cm from No. 23 bolting cloth, mounted on a wooden frame like a pair of skis (Fig. 24). This net is towed at a speed of up to 3 m/sec. /67/

Yet another type of high-speed neuston net was used by P. Bieri and T. Newbury (1966). The pyramidal net, 63 X 20 cm and 100 cm long, is designed for a speed of 1 m/sec and towed by small vessels.

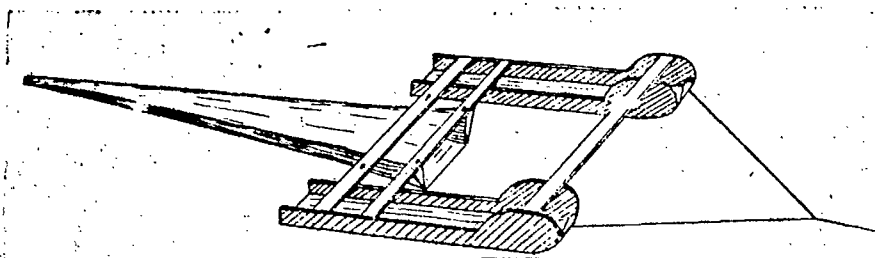


Fig. 24 - General view of neuston net, designed by P.M. David (1963a), in the working position.

As can be seen from the composition of the hauls (this will be discussed in greater detail later on), the collections of

Bieri and Newbury in the Pacific (between Fiji and Samoa), P.M. David in the Indian Ocean and the hauls made by the author with an MNT in the Atlantic and the seas of the Atlantic basin revealed a high degree of similarity, which suggests in particular that the results obtained with the neuston collecting gear described above are comparable and that the neuston of the entire ocean forms a single entity.

Quantitative estimate of young fish for fisheries purposes

The hyponeuston mode of life displayed by the fry of many species of commercial fishes and the demonstrated possibility of collecting them with the aid of MNT nets served as the basis for the manufacture of fishing gear for counting young fish for fisheries purposes. As is known, one of the chief methods of predicting the sizes of fish populations and possible hauls is based on a quantitative estimate of the numbers of young fish. Until recently the principal gear for counting fry in the Black Sea was the pelagic trawl designed by N.I. Revina (1958).

In 1965, N.N. Danilevskii (Azerbaijan Black Sea Research Institute for Fisheries and Oceanography) designed a new trawl intended for fishing the hyponeuston layer. The trawl is made of light synthetic materials and its headline is rigged with eight enclosed rubber buoys ensuring that the net remains half-submerged. The headline length of the trawl is 23 m. At a speed of roughly 125 cm/sec the Danilevskii hyponeuston trawl fishes the layer of water from 0 to 4 m (Fig. 25). /68/

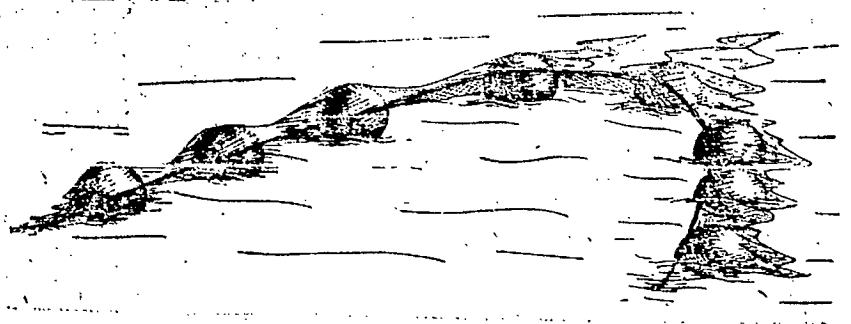


Fig. 25 - N.N. Danilevskii's 23-metre hyponeuston fry trawl in the working position (from photo by Danilevskii).

Over 200 tows made in the summer of 1965 in the Black Sea, 15 of which were parallel, showed that the new trawl has a much higher catching efficiency than the older design of trawl of equivalent size. The fry of different species of mullet, surmullet, sprat and some other species of commercial fishes, which were previously almost entirely absent from the catches, were caught in abundance in the new trawl. Even the catches of juvenile anchovies and horsemackerel, which had been caught in large numbers before, increased by an average of 250% in the neuston trawl. The forecasts of catches based on the data of the new trawl were vindicated. It was found to be broadly suitable in other fishing basins also.

Mass collection of net neuston for radioecological, biochemical and other purposes

Neustonic and especially hyponeustonic organisms became widely known in the very first years after their discovery as important objects for the study of marine radioecology

(Polikarpov, 1964; Polikarpov, 1966; Polikarpov et alia, 1967) and the ecological biochemistry of marine organisms (Vinogradova and Koval'skii, 1962; Kostylev, 1964-1968; Vinogradova, 1967a; Oleinik and Kostylev, 1967), and accordingly the need arose for developing methods of collecting them in masses for analysis. It is particularly important in such circumstances to see that the specimens do not suffer injury or mutilation during collection which could cause (e.g. as a result of the loss of part of their tissue fluid, blood, lymph, limbs etc.) artificial changes in their radioecological and chemical characteristics.

At the present time mass collections of hyponeuston are being made by lift net, fry neuston trawl (MNT) and neuston trawl model "NT". The lift net is most effective in areas of dense hyponeuston concentrations in the vicinity of hydrologic fronts in rivers. The MNT, towed at the lowest speed of slow vessels, is used for collecting relatively large components of the hyponeuston, such as crustaceans and fish fry. A. A. Stroganov (personal communication), when collecting hyponeuston for radioecological purposes, used 2-3 MNT nets simultaneously from one side of the ship.

For the collection of delicate items (prolarval fishes and other strongly hydrated organisms) the neuston trawl depicted in Fig. 26 is used, operating as a drift net. It consists of the following elements: a front frame measuring 300 X 25 cm, made of bamboo poles fastened together at the ends by metal braces; the intake part of the trawl forming a truncated

pyramid with bases of 300 X 25 and 60 X 20 cm and a height of 225 cm, and a cod-end of an ordinary pyramid net 60 X 20 cm and 275 cm long. The total length of the filter part is 500 cm. The trawl ends in a cylindrical bucket 8-10 cm in diameter. The trawl is kept above the surface by five foam plastic floats: two measuring 25 X 10 X 8 cm (at the sides of the front frame, two measuring 15 X 10 X 4 cm (at the sides of a bimetallic wire frame between the intake and cod-end parts of the trawl) and one ring float consisting of two semicircular segments round the bucket. The NT net operates while drifting, on the same principle as the Ns and PNS nets.

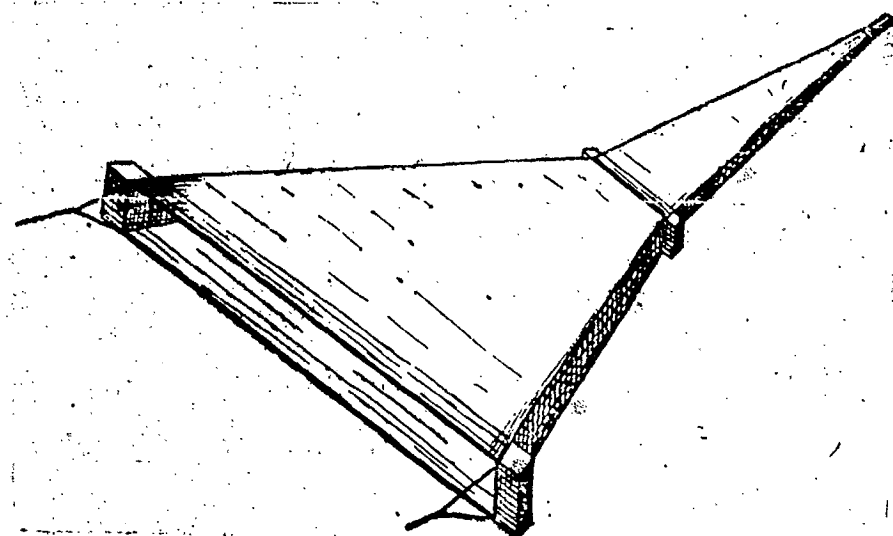


Fig. 26 - General view of neuston trawl (Zaitsev, 1962a)

For collection of neuston in areas of elevated radioactivity, H. Schlichting and J. Hudson (1967) made an experimental radio-controlled model launch out of balsa wood. The length of the model is 95 cm, the width 25 cm, and the overall

weight 6.8 kg. The launch develops a speed of 5 knots (running light) to 3 knots (working). On a radio signal a neuston net is lowered from the launch into the water and fishes the 0-2.5 cm layer. Simultaneously another device selects samples of air at a height of 50 cm above the surface of the water. The launch is designed to operate in calm weather at a current velocity of less than 1.5 m/sec and can be used even in very shallow water basins with a depth of 7-15 cm.

Collecting epineuston

/70/

Quantitative estimates of epineustonic water measurers are rendered difficult by their great mobility, nevertheless, trawling with an MNT net at a speed of 2 m/sec it is possible to count them while it is light, and especially at night. Water measurers are attracted by light, and they can be collected at night alongside the ship with the aid of an electric lamp.

Small epineustonic organisms in clumps of thick foam are collected together with the foam in drop nets of No. 21-23 capron bolting cloth. To remove the foam they are collected and forced through the sides of the net into vessels. Suitable for the purpose are wide glass cylinders. In the vessels the foam settles and the liquid formed on the bottom is used to study the population of the foam or for other experiments, depending on the purpose in mind. The quantitative characteristics relate to one unit volume (1 cm^3) of foam precipitate, which means that the results obtained from samples with different degrees of froth formation can be unified.

V. Garrett (1965) collected organic film from the calm surface of the sea with the aid of a wire net which is lowered onto the water and collects organic matter in its meshes together with its minute inhabitants.

Visual observations of neuston in the sea

Notwithstanding all the technical development of the gear for collecting biological material, direct visual observations by the specialist remain an indispensable method of investigation. They yield information which could not be obtained in any other way.

Underwater observations, which have undergone successful development in recent years, represent a new stage in the evolution of the study of hydrobionts (Manteifel', 1962). As far as the small inhabitants of the pelagic zone are concerned, visual observations of them in nature are only in their infancy.

Through the portholes of the underwater research vessel "Severyanka" N.S. Khromov (1962) saw many large plankters in their natural state and came to the conclusion that visual observations of plankton are far more representative than net hauls. The same conclusion was reached by S.S. Drobysheva and B.S. Solov'ev (1964), who observed Ctenophora and medusas from a hydrostat* in the Barents Sea. Plankton from the depths of the Mediterranean were studied from the bathyscaphe FRNS III by G. Trégouboff (1962). Observations of the migrations of

* Literal translation. The word is obviously formed by analogy with "aerostat" and presumably indicates a diving vessel such as a bathyscaphe. - Translator.

Calanus in the 0-2 m layer off Plymouth were conducted by R. Bainbridge (1952), and H. Ceccaldi (1962), using a face mask and tube, collected Siphonophora and Salpa in the Mediterranean.

Owing to its position in the most strongly illuminated layer of the sea and the comparatively large dimensions of many of its components, neuston is a convenient object for visual observations, and, at the present time, it appears to be the complex of organisms which has been most thoroughly studied visually in the pelagic zone. The results of the observations made it possible to make substantial corrections to information on the biology, distribution and behaviour of the neuston components, and also to the designs of fishing gear and the techniques of its use (Zaitsev, 1964a). /71/

Observations of neuston are conducted both from above and from below water (Zaitsev, 1964a; Vinogradov, 1969), the above-water observations normally being conducted from the deck of a ship. When the ship is drifting a large quantity of neuston organisms collect near its lee side. This occurs because the drifting ship is oriented perpendicular to the direction of the wind and moves across the surface of the sea. In the process the hull of the ship acts like the plow of a bulldozer. As a result a large quantity of neuston organisms and all sorts of driftwood concentrate in the middle of the lee side. From the deck of a ship with low gunwhales (binoculars can be used from the decks of high-sided ships)

the naked eye can easily detect individual neustonic organisms, observe their behaviour and collect them with the aid of a drop net.

One of the first to conduct such observations in the Black Sea was B.S. Il'in (1933). Among the "rubbish" accumulated near the lee side of the paddle-wheel steamer "Sukhum", Il'in observed and netted isopods, small crustaceans, pelagic pipefish, sticklebacks and mullet fry, which he later called the "halistatic biocenosis of the Black Sea". Later it will be shown that this is only part of the hyponeuston organisms of the Black Sea visible to the naked eye, but this example of a perceptive observer and resourceful biologist like Il'in shows how much valuable information can be obtained by above-water observations.

Even more effective are underwater observations. The diving equipment of the observer consists of a mask, air tube and flippers, and the scientific equipment, in its simplest form, includes a note-pad with white celluloid pages, an ordinary pencil attached to the pad by a thread, and a small drop net (diameter 5-6 cm, depth of bag 20 cm, length of handle 30 cm). For examination of objects on driftwood an underwater magnifying glass as devised by Dumas (1961) is used. In this magnifying glass a layer of air between two convex-concave lenses forms a biconcave lens (Fig. 27), which in water refracts light rays just as a biconvex lens refracts them in air. The author also used with similar success a simplified magnifying glass operating on the same principle, /72/

but having instead of the lenses two watch glasses in an airtight cylindrical container with the convex side facing inwards.

A great deal of attention has been paid to the methodology of underwater observations of hyponeuston by A.K. Vinogradov (1969). He constructed a special hyponeuston raft, which facilitates the work of the observer and fixes his position in the water, special paravanes creating a background against which the organisms under observation are more distinctly seen, and other devices.

The methodology of visual observations, like other branches of the methodology of neustonological investigations, is being improved as our knowledge of the objects we are studying deepens. The results of our observations are described in later chapters.

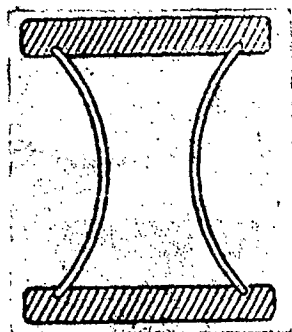


Fig. 27 - The underwater magnifying glass of two watch-glasses operating on the same principle as the glass devised by Dumas.

Laboratory processing of neuston collections
and experimental investigations

Neuston collections are processed in the laboratory in basically same way as plankton collections from the pelagic zone,

but with some modifications. These concern mainly the differentiation of the organisms according to their physiological condition.

The abundance of dead animals and plants suspended in the water column, and particularly numerous in the near-surface biotope, indicated the necessity for counting live and dead organisms in each sample.

Differentiation of the animal specimens was done according to the method devised by M.A. Kastal'skaya-Karzinkina (1935), with some modifications. The organisms are stained with a 5% solution of erythrosine and assigned to one category or another on the basis of the condition of the muscle fibres. The greatest difficulty is experienced in diagnosing the bodies of hydrobionts which have died recently. With the aid of a long series of experiments both in the laboratory and directly in the sea reliable criteria were found for identifying recent dead bodies in fixed samples (Zelezinskaya, 1966a).

Plant specimens are subjected to luminescence analysis by the method of S.V. Goryunova (1952) with the aid of an ML-2 microscope, after which the specimens are differentiated into live, dying and dead cells, and also into empty shells (Nesterova, 1969b).

Differentiated analysis of hyponeuston collections revealed the phenomenon of the "antirain" of dead bodies, suggested the advisability of compiling necrogeographical maps (Zaitsev, 1967a) and made it possible to obtain qualitatively new information on the density and distribution in the near-surface microlayer. /73/

To determine the reaction of hyponeuston organisms to sunlight and rays of different wavelengths special laboratory experiments were conducted (Zaitsev, 1959b, 1964a). The main concern when studying the reaction of the organisms to sunlight was to avoid heating the water in the vessel in the sun as compared to the control in the shade. This was achieved by placing all the apparatus in the vessel in flowing water (Fig. 28) or on the calm surface of a natural water body.

Since there is no single instrument which would satisfy the neustonologist equally in all respects, the choice of gear and collecting methods depends on the particular purpose in mind. The same applies to the periodicity of the collections and to their spatial distribution. For example, seasonal changes in the composition and abundance of hyponeuston of the Black Sea can be clearly discerned in samples obtained at intervals of 2-3 months, and the diurnal dynamics of the organisms of the benthohyponeuston can be computed with satisfactory accuracy after studying collections obtained at intervals of only one hour. /74/

The described equipment and methods for collecting neuston have been used in various regions of the ocean during the past decade (Fig. 29). The collections were haphazard, or systematic, and obtained with the aid of a single piece of fishing gear, or with several. The results of studying these collections give an initial idea of the neuston of various latitudes and in hydrologically differing sea basins. The most complete information is that relating to the southern seas of the USSR, especially

the Black Sea and Sea of Azov. The description of the neuston given in the following chapters is based mainly on the materials of the hyponeuston division and on the published data of other authors who conducted their researches either in conjunction with us or independently.

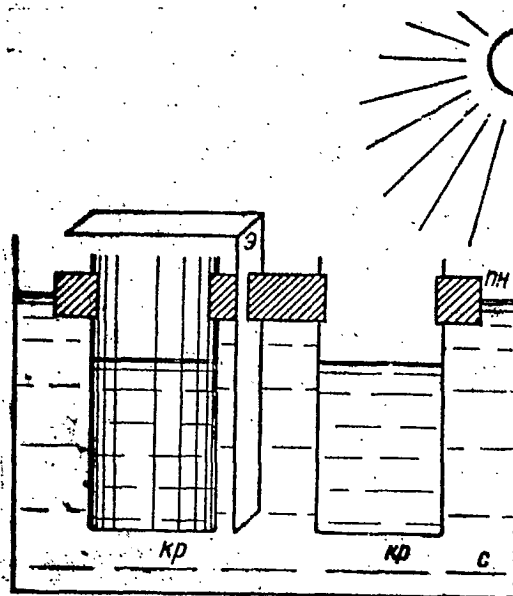


Fig. 28 - Device for studying the reaction of hyponeustonic fish roe to sunlight:

kp - glass vessel coloured on the outside with a black opaque paint (experiment), kp' - vessel of transparent glass (control), 9 - screen of black photographic paper, nh - foam rubber float, c - common vessel containing flowing water (Zaitsev, 1959b).



Fig. 29 - Regions of neustonological investigations conducted by hyponeuston division in 1957-1967.

MARINE NEUSTON, IDENTIFICATION, STRUCTURE, COMPOSITION,
QUANTITY, RHYTHMS AND ECOLOGY

Chapter IX. The birth and development of neustonological
studies in marine water bodies

In the Introduction it was observed that the study of marine neuston began only recently and that specialists approached it by several different paths. The first of these paths, which subsequently proved to be the most fruitful, started out from a study of the habitat of pelagic fish eggs of high buoyancy. A certain similarity can be observed here with the circumstances surrounding the birth of planktonology. As is known, in the seventies of the last century V. Hensen (1887) began his researches by identifying a quantity of roe from flounders and cod in the Kiel Firth. Subsequently, during an examination of the food supply of the emergent larvae, he discovered minute plants and animals suspended in the water, some of which were already known to science. Hensen called these "plankton".

The point of departure in the study of neuston was the roe of the mullet. The problem was to ascertain the places and conditions in which it developed. The difficulty was that the biology of the reproduction of the mullet, which is widely distributed in the seas of the tropical and temperate zones, presented an enigma. Each new generation of these fish was marked by the appearance^{of} large numbers of fry in the surf zone. But where they hatched out and what conditions determined the abundance of the year-class remained a mystery. The statements

in the literature to the effect that mullet reproduce in lagoons, or in the near-shore or pelagic zones of the sea, bore a hypothetical character and were frequently contradictory. The author who, as an ichthyoplanktonologist, was particularly interested in the riddle of the breeding habits of the mullet, favoured the notion that the bulk of the eggs of Mugil saliens in the Black Sea were concentrated at a specific depth in the water column. In support of this argument it was pointed out that they are encountered only singly in the surface hauls made by standard roe nets (Zaitsev, 1955). However, this too was only a hypothesis, and to verify it the hydrostatic method of searching for roe was used, which can be summarized as follows. /76/

By experimental means it was established that the pelagic roe of various species of Black Sea fishes is distinguished by different specific weights (Zaitsev, 1954). The lowest specific weight (1.007-1.0092) was discovered in the eggs of anchovies, the highest (1.0128) in the eggs of the weaver. The specific weights of the roe of other species lay between these two. The eggs of the different species are distributed in sea water at different depths according to their specific weight. Therefore the eggs of the anchovy are usually found right near the surface, and the eggs of other species in the pelagic zone, down to great depths.

Once the specific weight of the eggs of the mullet had been ascertained the depth at which most of them were suspended could be determined. It was found that the roe of M. cephalus

and M. saliens had a specific weight of 1.007-1.008 (Zaitsev, 1959e), i.e. that it was lighter than the most buoyant anchovy roe, so that the bulk of their roe must be situated not in the pelagic zone, as was thought previously, but just below the surface tension film, since the density of the Black Sea water at the surface, except for areas of greatest freshening, does not drop below 1.010. In order to verify this conclusion, which was arrived at by calculation, a deviation was made from the "Instructions" for the collection of fish eggs and larvae (Rass and Kazanova, 1958), which recommended obtaining surface samples by towing a roe net below the surface of the water.

At either side of the hoop of a standard ichthyoplankton net model IKS-80 were fastened two floats, which kept the mouth in a semi-submerged position (Zaitsev, 1959). The very first haul with the semi-submerged roe net, obtained on 22 August 1957 in the north-west part of the Black Sea, confirmed the hypothesis concerning the high concentration of roe in the surface tension film, which is missed by the conventional method of collection. Thus, a sample taken by a net fitted with the floats contained 79 mullet eggs, whereas a haul made by the same net, but fully submerged, the hoop of which passed directly beneath the surface of the water, contained only 3 eggs. This discovered concentration of eggs was called "ichthyoneuston" (Zaitsev, 1958a, 1959e) by analogy with "ichthyoplankton" - the roe and larvae of fish from the pelagic zone.

The fact that the principal objective of the study was to study the habitat of the early developmental stages of fish meant inevitably that it was necessary from the very beginning to conduct a wide complex of investigations, and this in turn helped to disclose the characteristics of the life in the biotope under observation.

After the success which had attended the first hauls in the near-surface microlayer of the sea it appeared necessary to produce fishing gear for studying the various groups of organisms and for other purposes. Several types of net were constructed (Zaitsev, 1960b, 1962a), and the samples obtained with them showed that a hitherto unsuspected rich aggregation of organisms develops in the 0-5 cm layer, constituting the marine neuston (Zaitsev, 1960c). Subsequent analysis revealed that in the Black Sea, as far as metazoans are concerned, the chief component of the neuston is the hyponeuston (Zaitsev, 1961a,c). Operations with the same nets in other marine basins showed that the neuston, in the basic form in which it was discovered in the Black Sea (in the tropical zone, including epineustonic water measurers also), develops everywhere. This provided grounds for considering neuston the most extensive community (or collection of communities) in the ocean (Zaitsev, 1963c, 1964a).

The researches of a number of foreign biologists have confirmed this conclusion.

To study Foraminifera from the near-surface layer of water

R.P. Willis (1963), using the idea of R. Hedley, utilized a small pyramid net with floats (see Chapter VIII). From the RS "Viti" of the New Zealand oceanographical institute, in the region of the Natem islands, Willis caught the same "hyponeuston of Zaitsev" as was described for the Black Sea.

G. Trégouboff (1963) discovered in the hyponeuston layer of the Mediterranean a high concentration of cladocerans.

A start was made on neustonological research by P.M. David (National Institute of Oceanography, England) in the spring of 1962, when, executing the program of the International Indian Ocean Expedition on board the RS "Discovery", he embarked on a study of the near-surface organisms which could serve as food for birds (David, 1963, 1965a, 1965b). Using a high-speed pyramidal net of original design (cf Chapter VIII), and also a three-tier net patterned on the plankton-neuston net, which fished the 0-4, 4-8 and 8-12 inch microlayers, David found that in the pelagic waters of the tropical zones of the Indian Ocean, even in the daylight hours, there is a high concentration and great diversity of species of hyponeustonic and epineustonic organisms. The high-quality colour microphotographs taken by him (David, 1956b) provide valuable material for study of the nature of the pigmentation and adaptations of the marine neuston components to the conditions of their biotope.

A great diversity of neustonic organisms was discovered in the western part of the tropical zone of the Pacific Ocean by R. Bieri and T.K. Newbury (1966), who began in 1965 making col-

col/ lections of neuston with the aid of a high-speed pyramidal net cf. Chapter VIII) from the RS "Te Vega" of Stanford University (USA).

At the XIX Congress of the International Commission for Scientific Exploration of the Mediterranean Sea (C.I.E.S.M.M.) the President of the Plankton Committee, G. Trégouboff (1965), noted the progress and value of the hyponeuston research conducted in the Odessa branch of Institute of South Seas Biology of the Academy of Sciences of the Ukrainian SSR and called for a beginning to similar research in the Mediterranean scientific centres. This call was echoed by the XX Congress of the Commission, held in Bucharest in 1966, at which M. Specchi (1966) delivered a report on the theme "Preliminary observations of the hyponeuston in the Gulf of Trieste". Using a five-tier net, model FNS-5, he made four hauls at different times of the day. Analysis showed that in the Gulf of Trieste, in spite of unfavourable conditions for the development of hyponeuston (freshening of the water, proximity to the shore, etc.), the near-surface layer contained an exceptionally large number of zoöa and metazoöa larvae of decapods.

At the present time various problems of marine neustonology are being worked on in the scientific institutions of France (Station Zoologique Villefranche-sur-Mer, Station Marine d'Endoume), Monaco (Musée Océanographique), in Trieste (Istituto di Zoologia e Anatomia comparata, Università di Trieste), Algeria (Institut Océanographique), England (National Institute of

Oceanography), Canada (Marine Sciences Centre, McGill University, Montreal), New Zealand (New Zealand Oceanographic Institute, Wellington) and in other places.

At present the most comprehensive marine neustonological research is being carried on in the hyponeuston division of the Odessa branch of the Institute of South Seas Biology of the Ukrainian Academy of Sciences. There they are investigating both the ecological conditions of the near-surface biotope of the sea and all the main groups inhabiting it. In addition the hyponeuston division is conducting a significant part of its research jointly with other scientific teams. Fruitful collaboration with the radioecology school of G.G. Polikarpov is yielding particularly valuable results and holds great promise for the future. This is not only because the hyponeuston is one of the most vulnerable aggregations of hydrobionts with respect to the radioecological factor, on which its future directly depends, but also because the methods of radiation and chemical ecology evolved by Polikarpov and his colleagues are an exceptionally effective means of comprehensive and deep study of the biological structures of the sea. Important information illustrating the biochemical composition and biochemical adaptation of hyponeuston organisms has been yielded by the researches of Z.A. Vinogradova et alia on the ecological biochemistry of marine organisms.

The results obtained during the study of marine neuston, and the great interest of a wide circle of specialists in studying life at the sea-air interface give grounds for hoping

that in the not too distant future neustonological research will occupy one of the foremost places in the program of oceanographic investigations.

Chapter X. Neuston and pleuston - the near-surface aggreg-
ations of organisms in freshwater and marine
basins

As factual material was accumulated the careful distinction between "neuston" and "pleuston" which marked the early studies in this field (Schröter u. Kirchner, 1896; Naumann, 1917; Naumann-Lund, 1931) was gradually lost. Representatives of both groups of organisms found their way into the same net and sample, and no special investigations were made to ascertain the similarities and differences between pleuston and neuston. The resulting confusion in the modern literature (glossaries, manuals and text-books) disorients the reader who is attempting to examine the forms of life at the sea-air interface. Let us see how pleuston and neuston are defined in the various reference manuals and textbooks published in the USSR and abroad (Table 11).

As can be seen from the table, a comparison of the definitions of the two terms given by different authors discloses a multiplicity of contradictions, inaccuracies and vaguenesses. In a number of cases these terms are not even mentioned. Only in the manuals of S.A. Zernov and especially A.S. Konstantinov are generally correct definitions of both terms given, but they should be supplemented and amended on the basis of the results of the latest research.

As a result of the terminological confusion and lack of a scientifically based criterion for differentiating between neuston and pleuston there were several cases of an uncritical attitude to the content of these concepts. Thus, E. Hentschel (1933) suggested assigning to the marine pleuston all the organisms "connected in any way with the surface of the water", including adult fish, turtles, birds and even whales. This suggestion received no support in the literature.

An extension of the terms "pleuston" and "neuston" (which was largely responsible for the ensuing terminological confusion) occurred as freshwater and marine hydrobiology developed and particularly ^{as} information on the structure and mode of life of aquatic organisms and aerobionts associated with the surfaces of water bodies broadened and deepened.

Table 11

Definitions of terms "pleuston" and "neuston" given by different authors

Author, year, source	Definition of pleuston	Definition of neuston
1	2	3
S.A. Zernov, 1949, General Hydrobiology	Planktic organisms, part of the body of which protrudes from the water; also called pleustonic organisms (p.41)	Neuston consists of organisms directly populating the surface film of water (p.54)
I.P. Henderson and W.D. Henderson, 1953.	Freely suspended plants	Organisms suspended or floating near the

Dictionary of Scientific terms

N.A. Berezina, 1963.
Hydrobiology

Not mentioned

surface of water or
populating the surface
film

Aggregation of organisms dwelling on the surface film of water: flagellates, bacteria, insects and their larvae, water measurers, gyrenids, larvae of some mosquitoes, some cladocerans (p. 31).

V.B. Bogorad, A.S.
Nekhlyudova, 1963.
Short Glossary of
Biological Terms

Aggregation of plants floating on the surface of a body of water
2. Animals adapted to life in the surface film of water

Not mentioned

D.P. Viktorov, 1954.
Short Glossary of Botanical Terms

Aggregation of plants floating on the surface and not anchored to the bottom of the water basin: in the seas made up of huge concentrations of detached algae (chiefly Sargassum); in freshwater basins pleuston normally consists, for example, of lesser duckweed, Salvinia etc.

Aggregation of organisms floating on surface of water or dwelling in surface films.

R. Husson, 1964. Glossaire de biologie animale

Not mentioned

Aggregation of organisms in surface film of water. Neuston is one of the four elements of seston (neuston, plankton, nekton and tripton)

R.W. Pennak, 1964. Collegiate Dictionary of Zoology

1. Aggregation of macro-organisms floating on the surface of the sea, e.g. siphonophorans, barnacles, isopods, gastropods, etc. Aggregations of micro-organisms associated with the surface film of water e.g. some protozoans, insects, planarians, ostracods etc.

	2. Concentration of algae at or near the surface of fresh water	
M.P. Beregovii et al., 1965. Encyclopedic dictionary of botany	Not mentioned	Biocenosis of surface film of water, made up of plant and animal organisms, using the surface tension film for attachment or movement
R.S. Wimpenny, 1966. The Plankton of the Sea, Glossary	Not mentioned	Organisms living in or on the surface film of water
A.S. Konstantinov, 1967. General Hydrobiology	Planktonic organisms, part of whose body is in the water and part above the surface (p.10)	Plants and animals whose life is associated with the surface film of water (p. 10)

Thus, whereas originally only floating semi-aquatic plants such as duckweed and bladderwort were assigned to the pleuston, the latter was subsequently taken to include the floating foliage of attached plants, such as the water lily, Victoria regia, and even the marine siphonophorans Physalia and Velella, part of the body of which protrudes well above the surface of the water (Hentschel, 1933; Zernov, 1934). Despite the distance between the systematic positions of the freshwater plants and marine coelenterates listed here, there are common features of structure and ecology which unite them in a single group of pleustonic organisms.

The air cells in the leaves of pleustonic plants are so strongly developed that the reserve of positive buoyancy created by them pushes the leaf blades half out of the water.

Still more strongly developed are the air cells in the blade of Velella, while the pneumatophore of Physalia represents a thin bubble filled with gas.

The part of the body of pleustonic organisms which protrudes from the water is capable of withstanding dry air and the direct rays of the sun for a long period without danger. This property, together with the semi-submerged state and the ability to move with the wind, distinguishes the pleustonic forms from all other hydrobionts and aerobionts - both plants and animals. For instance, if ^{the} part of the thallus of the alga Sargassum which floats below the surface is raised above the water, it dries up and dies within a few minutes. The same applies to animal organisms. Only certain crabs and mollusks found in the surf zone can remain out of the water for long owing to reserves of moisture under their carapace or shell, but they cannot swim while half-submerged. As regards pleustonic siphonophorans (Physalia and Velella), these species easily withstand the rays of the tropical sun on completely windless days without the pneumatophore being moistened with water. Even when cast up on the shore and dying they preserve the former shape of the pneumatophore, which, on being squashed, bursts with a pop. This demonstrates that the aerial part of a colony of pleustonic siphonophores has a special histologic structure, and this is not characteristic of the tissues of hydrobionts which do not protrude from the water. In pleustonic plants the protective function is performed by a waxy bloom on the epidermis of the leaf blades.

Recently, thanks to the work of A.I. Savilov (1956a, b; 1958; 1961 and others) a number of pleuston communities have been described for the warm-water part of the Pacific, which are distributed under the influence of the winds according to the structure of the sail. A common feature of the geographical distribution of siphonophores is their confinement to the tropical region of the ocean. According to the materials of Savilov (1961), pleustonic organisms occur at the surface at a temperature of more than 15-17°C. Evidently the chief limiting factor in this case is the air temperature, on which other denizens of the water are not directly dependent. In the case of pleustonic forms, however, most of the pneumatophore comes into contact with the air, and it is probably low air temperatures that limit the latitudinal spread of these species. Therefore, in places where negative air temperatures are observed during the year, pleustonic siphonophorans are not found, and it is only by chance that they may be brought by winds or currents from warmer regions.

A.I. Savilov, in describing the pleuston communities, includes among the secondary members a number of organisms which do not possess the distinguishing features of the pleuston (a semi-submerged position, sails, tolerance to dry air,) but which temporarily use pleustonic siphonophores as a solid substrate or food. These are Ianthina, Glaucus, Idothea metallica, Planes, Halobates and others. In their report "La vie pélagique" J.-M. Pérès and L. Devèze (1963) correctly note that the concept "pleuston" is more limited than is suggested by Savilov, who used the term to cover all animals living on the

surface of the sea (p. 142). All the same, there seem to be special reasons for this in the present case, particularly as several examples are known where the same organisms are included in two or more communities. It should be remembered, however, that in the absence of pleustonic siphonophores, or in the intervals of water surface between them, the organisms in question lead a typically hyponeustonic or epineustonic mode of life, conditioned by their equivalent characters and properties. Thus, when studying the neuston in the Gulf of Mexico and the Bahamas region, the author found only three Physalia and not a single Velella in the 1200 miles the research vessel covered (June 1965). Notwithstanding this, a rich hyponeuston was discovered at all stations, including Ianthina, Glaucus, Planes minutus and the epineustonic gerrids Halobates.

As was shown in the "Introduction", the meaning of the term "neuston" underwent equally substantial changes - from a concentration of single-celled hydrobionts attached to or supported by the surface tension film, to the whole assemblage of hydrobionts and aerobionts populating the aquatic and aerial sides of the interface. The discovery of neuston in the sea showed that this biological structure (like pleuston) is typical not only of fresh waters but also of all inland and marine water bodies.

That it really is an assemblage of neustonic organisms that has been discovered in the area of the surface tension film of the sea is shown by the numerous cases of analogies with the freshwater neuston.

To the water-measurers of the freshwater epineuston - Hydrometra (Hydrometidae), Gerris, Heterobates (Gerridae) - correspond the oceanic water-measurers in the seas and oceans - Halobates (Gerridae). Because of the special conditions of life in the sea the oceanic water-measurers are even more attached to the surface film than their freshwater cousins: they have no wings and are therefore unable to seek refuge or food on the shore.

On the underside of the surface film, like the freshwater Limnaea and Physa, crawl the mollusks Hydrobia Bulva and Glaucus. Like the freshwater hydras (such as Hydra littoralis), which rise to the surface tension film and adhere to it by venting gas bubbles through the aboral pore which remain by the basal disc (Lomnicki, Slobodkin, 1966), behave sea anemones of the family Minyadidae in the sea (David, 1956b). They also secrete bubbles, which accumulate in the centre of the foot. Like the /84/ freshwater crustaceans Scapholeberis, the zoëa larvae of marine crustaceans attach themselves to the underside of the surface tension film by their long spines. Like mosquito larvae the marine hyponeustonic chondrophores Porpita breath air, and the eggs of Black Sea mullet, due to the impermeability of their membrane, are held in position by surface tension forces, as is typical of most forms of freshwater neuston.

Many analogies can be cited which demonstrate the general hydrobiological and not limnological character of neuston, yet it is difficult, and in any case there is no need to look for complete identity of limnoneuston and haloneuston. They are

united by basic characteristics, such as their location in the water body, structure, adaptation of components to the biotope, but there are specific differences of detail caused by the difference between the sea on the one hand and a small pond or pool on the other.

Thus, using as our point of departure the first definitions of the terms we are concerned with and the subsequent modification of their meanings in the light of recent special investigations, the near-surface assemblages of freshwater and marine organisms can be described as follows.

Pleuston - plant and animal organisms of medium and large size, hydrobionts whose bodies are simultaneously in the water and in the air. Free-swimming representatives of the pleuston move under the influence of the wind and in the seas they are distributed in the tropics and partly in the temperate zone. Marine pleuston are represented by siphonophores of the genera Physalia and Velella.*

Neuston - plant and animal organisms of small and medium size, hydrobionts and aerobionts inhabiting the aquatic (hypo-neuston) and aerial (epineuston) sides of the surface tension film of water bodies. Distribution - world - wide. Marine neuston consists of organisms of various taxonomic levels - from plants and bacteria to larvae and fry of fish.

* The secondary members of pleustonic communities are the representatives of the neuston, plankton, pelagic zone and benthos which use the key forms of the communities (pleustonic siphonophores) temporarily as a solid substrate or food.

Chapter XI. The structure of neuston

All the diverse organisms adapted to life in the surface tension film area of marine basins form a number of natural groups, or structural elements, which constitute together the single neuston assemblage. These structural elements are distinguished by two basic criteria: a) their position relative to the water-air interface, and b) the length of the neustonic phase in the life cycle of the species. /85/

On the basis of the first criterion - the topographical one - all neustonic organisms, or neustonts (by analogy with planktons - the components of plankton) (Zernov, 1949; Husson, 1964), are divided into two parts. One part comprises the inhabitants of the lower, or aquatic, side of the surface tension film - the hyponeuston, the other - the inhabitants of the upper, or aerial, side of the film - the epineuston. This division of the organisms into hyponeustonic and epineustonic is quite clear-cut, and only on the level of microorganisms is it technically more difficult to make the distinction, in which case the plain term "neuston" is used. Certain representatives of the hyponeuston and epineuston can change places for a short while. For example, the epineustonic water-measurers are in the water while diving, whereas the hyponeustonic pontellids are in the air while leaping. However, this does not complicate the division of neuston into upper and lower levels, just as the existence of diving birds and flying fish does not obliterate the distinction between birds and fish.

Division of neustonic organisms on the basis of the second criterion is also fairly clear-cut, but there is a difficulty here in that the number of species whose life cycles have been fully analysed is still small. Therefore the division of neuston into permanently and temporarily neustonic organisms will be developed and improved as the study of their biology and ecology proceeds.

Among the components of the hypo- and epineuston, as in the plankton of the pelagic zone, organisms can be distinguished according to whether they spend their entire life or only part of it in the region of the surface tension film. To denote these two groups prefixes were borrowed which are used for the same purpose in planktonology, viz. "eu-" for the first group (organisms spending their whole lives in the neuston) and "mero-" for the second group.

The epineuston includes organisms from both groups and is therefore made up of two elements - euepineuston and meroepineuston. An example of a euepineustonic organism is the water-measurer (Halobates micans) whose eggs are attached to the underside of the abdomen (Chopard, 1959; Savilov, 1967). Usually the water-measurers lay their eggs on driftwood, but their position on a solid substrate has not yet been finally established. Thus, A.I. Savilov asserts that the eggs of H. sericeus and H. micans, which are attached to floating bird feathers, lumps of pumice, wood, remnants and skeletal plates of the pneumatophores of dead Porpita and Velella, remain per- /86/
manently submerged in the water. Accordingly, these species

should in that case be called not euepineustonic but meroepineustonic, since they spend their whole life in the neuston (eggs in the hyponeuston, and larvae and imagoes in the epineuston), and only part (albeit the longer part) of their life cycle, except for the embryonic stage, in the epineuston. However, P.M. David shows a photograph of eggs of Halobates which may be entirely on the upper surface of floating leaves of Thalassia testudinum. The presence of the eggs of water-measurers on top of the surface tension film should apparently be regarded as normal, as is evidenced by their attachment to the abdomen of the females. But this is already a euepineustonic mode of life.

At the same time species of Halobates exist with a firmly established meroepineustonic life cycle. Thus, according to the data of J.L. Herring (1961), the eggs of the coastal species H. hawaiiensis develop while attached to rocks in the surf zone. After 12 days the larvae emerge from the membrane and join the epineuston of the ocean.

The paucity of our knowledge of the mode of life of oceanic water-measurers, and especially of the biology of their reproduction, makes it difficult to arrive at an ecological classification of the epineuston, but such species as H. micans and H. hawaiiensis demonstrate the existence of both permanent and temporary components. Study of the meroepineuston has revealed that the epineustonic phase is characteristic of

larvae and adult individuals, whereas the embryo develops in the other biotope.

Other variants are also known. For example, the thoroughly studied mosquito species Anopheles and Culex lay their eggs on the water. Owing to special floats formed by the exochorion and the impermeability of the membranes the eggs maintain a certain position above the surface tension film, floating at a depth determined by their own weight. Out of the water or under it they fail to develop and die (Beklemishev, 1949). Thus, they are a typical example of epineuston. As is known, mosquito larvae and pupae lead a hyponeustonic mode of life after emerging from the eggs, and the adult individuals are genuine aerobionts. It is not impossible that similar or fairly similar examples also exist in marine water bodies, particularly in coastal waters, where Diptera and other insects are found.

Much more is known about the structure of the hyponeuston, although here too a lack of knowledge of the mode of life of the population of the near-surface biotope of the pelagic zone is a handicap.

The euhyponeuston, or organisms that spend their entire life in the hyponeuston (Zaitsev, 1962b, 1964a), consists of many species of invertebrates and fishes. Among typical representatives are the mollusks Ianthina and Glaucus, most species of copepods of the family Pontellidae, isopods (Idothea stephensi), decapods (Planes and Portunus portunus - the Saragasso crab), fishes (Syngnathus schmidtii), some Antennariidae (Antennarius, Histiog) and others. To the same group belong the

floating Sargasso algae (Sargassum natans and S. fluitans). The ecological position of sargassos, which constitute the main plant mass in the Sargasso Sea, was ascertained by the author on material collected in the Florida Strait.

In the literature these algae are usually called "floating", "drifting" or "pelagic" (Péres, 1961; Zenkevich, 1963), without indicating their vertical position. Sometimes the position of sargassos is specified, but there is no unanimity on this point. Some authors affirm that these algae "float in the water column" (Beregovoii et alia, 1965), others call them "subsurface pelagic" (Woodcock, 1950), while certain writers assign them to the pleuston (Viktorov, 1964; Makkaveev, 1965), i.e. to plants floating half-submerged, but none of the authors cites arguments in favour of assigning sargassos to a particular class of the communities in the pelagic zone.

The first attempt to ascertain the exact nature of the vertical distribution of sargassos in the Sargasso Sea was undertaken by A. Parr (1939). By making comparable horizontal net hauls at various depths he obtained the following quantities of algae by layers: surface - 52.0lbs, 1.5 m - 0.45 lbs, 5-6 m - two small clumps removed from the surface by the net while hauling in, 15-18 m - one small clump from the surface, 35-40 m - no sargassos in the sample. Thus it was shown that the bulk of the sargassos occur in a layer of water which is at any rate less than $1\frac{1}{2}$ m thick. However, this still does not tell us whether their position is below the surface

(hyponeustonic) or half-submerged (pleustonic).

A. Woodcock (1950), on determining the density of S. natans by ballasting the thallus with brass weights before submersion, found that it ranged from 0.905 to 0.955 g/ml and varies according to the composition and quantity of accretions on the thallus. Woodcock was mainly concerned to discover whether sargassos are entrained by downcurrents in zones of convergence of surface waters, and therefore, although his paper is entitled "Subsurface pelagic Sargassum", it does not contain any factual information on the basis of which this species could be assigned to the hyponeuston.

Visual observations in the American Mediterranean* revealed that when the surface is calm parts of the phylloids of sargassos may protrude from the water. Laboratory measurements showed that the weight of the protruding parts does not exceed 0.3% of the weight of the entire thallus. It was demonstrated experimentally that when the projecting parts of Sargassum remain in the air they finally die. Thus, the portions of the phylloids projecting above the surface die within 7-10 minutes after leaving the water, the floats (air bladders) within 20-30 minutes, while the oldest parts of the thallus survive for up to 40 minutes. If only half of the phylloid or float projects above the surface, only this part dies. Frequent (minute-by-minute) moistening with sea water prevents the death of the protruding parts of the thallus. In natural conditions, where oscillations of the water surface are usual, the projecting

* I. e. the Gulf of Mexico plus the Caribbean - Translator.

portions of the thallus apparently die only when the weather is calm. That this does indeed happen is shown by the dead phylloids and floats which are found in almost every clump of Sargassum. The nature of the damage suffered - desiccation, darkening etc.- is the same as in the experiments described above.

The absence of a reserve of "ecological strength" in S. natans and S. fluitans in the half-submerged (pleustonic) position, together with the small proportion ($<0.3\%$) of parts protruding from the water, indicates the hyponeustonic character of this alga. Earlier it was observed that in pleustonic organisms the body parts above water can withstand solar radiation and a dry atmosphere, even in calm weather, for an unlimited length of time without any moistening at all.

It has been established by experiment that the greatest buoyancy characterises the small and medium-sized sargassos with a diameter of 2-3.5 mm, and not the large ones, as might appear at first sight (Fig. 30). This may be due to the deposition of mineral substances in the walls of old floats. The specific weight of the entire thallus without accretions, as determined in one of these experiments, averaged 0.785 - 0.788. It was estimated that the thallus can be buoyant in the hyponeuston in the 0-5 and 0-10 cm layers (depending on its own dimensions), when it has about $1/5$ of its floats. Five times this number of floats constitutes that reserve of buoyancy which prevents the alga sinking when floats are lost as the result of desiccation in the air or burdening of the thallus with deposits of fish roe and settled larvae of sessile

invertebrates. After removal of more than $4/5$ of the floats for an experiment the thallus of a Sargassum without accretions sinks. A thallus covered with accretions sinks when less than $4/5$ of the floats are removed. The specific weight of the /89/ thallus of S. natans without any floats is 1.09. Such a thallus soon sinks in water of normal oceanic salinity.

Thus, S. natans and S. fluitans are hyponeustonic macrophytes whose sub-surface position is due on the one hand to the death of the parts of the thallus protruding from the water, and on the other to a high degree of buoyancy,

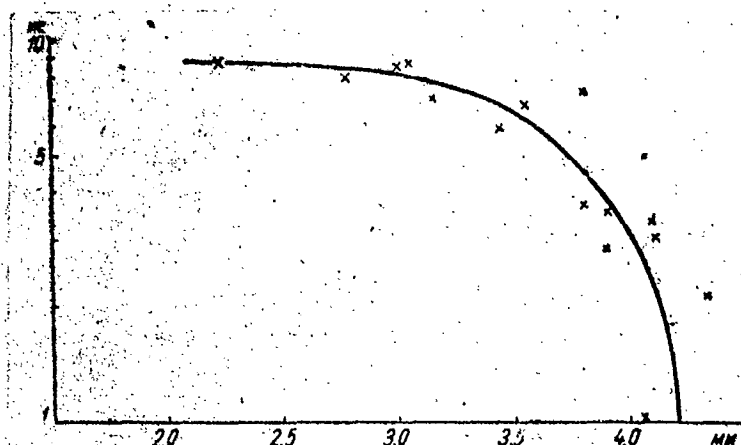


Fig. 30 - Buoyancy of air bladders of Sargassum natans (mg) versus their external diameter (mm).

These species reproduce only vegetatively and therefore belong to the euhyponeuston.

The second hyponeustonic element - merohyponeuston (Zaitsev, 1962b, 1964a) - consists of organisms associated with the near-surface biotope of the pelagic zone in the early stages of

their ontogenetic development. This is the analogue of the meroplankton in the pelagic zone. On completion of the hyponeustonic phase of the life cycle, the merohyponeustonic organisms switch to living in the pelagic zone or on the bottom, becoming components of the plankton (this group can be called planktogenous merohyponeuston), nekton (by analogy, nektogenous merohyponeuston), or benthos (benthogenous merohyponeuston). By virtue of its abundance among metazoans the merohyponeuston constitutes the basis of the hyponeuston. The description of hyponeuston as a highly important sea "incubator" (Zaitsev, 1963c, 1964a) stems from the quantitative predominance of eggs, larvae and young of aquatic organisms in the 0-5 layer. The most numerous groups of merohyponeuston are the larvae of bivalves and gastropods, polychaetes, barnacles, copepods and decapods, echinoderms and fish.

The temporary components of the hyponeuston include a further two groups of organisms - hydrobionts which on attaining adulthood accomplish regular circadian vertical migrations and become part of the hyponeuston when it is dark. They received the appellations "benthohyponeuston" and bathyplanktohyponeuston" (Zaitsev, 1964a).

Before marine neustonological research began the representatives of the benthohyponeuston were assigned to the benthos or nektobenthos. This applied to adult individuals of many species of polychaetes (Nephtis longicornis, Nereis succinea, Platynereis dumerilii and others), amphipods (Nototropis guttatus, Dexamine spinosa, Gammarus locusta, Corophium nobile and others),

cumaceans (Cumella limicola, Pterocuma pectinata), mysids (Gastrosaccus sanctus and others), shrimps (Palaemon adspersus, P. elegans) and others.

In the daylight hours such organisms do indeed dwell on the bottom - at times digging deep into the sediment - and are caught in the conventional types of benthos collecting gear - the bottom grab or drag. At night they rise to the surface. In the pelagic zone these organisms were encountered even earlier, but there were so few of them in the plankton net hauls that the term "tychoplankton"* was proposed for them. Neuston collecting gear disclosed a high density of polychaetes, amphipods, cumaceans, shrimps and mysids in the 0-5 cm layer - the terminal point of their ascent, where they dwell at night.

The researches of V.P. Zakutskii (1963-1968) showed that the occurrence of these organisms near the surface of the sea is not accidental, but regular. Their appearance in the hyponeuston at night (for reproduction and feeding) lasts even in winter at negative values of the surface water temperature. With the coming of dawn they return to the bottom.

Thus, the life of the adult individuals of these species, due to the circadian vertical migrations, passes through benthonic and hyponeustonic phases of roughly equal length every 24 hours. Therefore it was incorrect to call these organisms benthonic, nektobenthonic, tychoplanktonic, benthoplanktonic or tychohyponeustonic. Instead the term "benthohyponeuston" was proposed for them, to reflect their dual mode of life - on the bottom and in the hyponeuston.

*I.e. "chance plankton".

Owing to its tendency to form masses (remember the "swarming" of the palolo Eunic viridis in the Pacific and the similar "swarming" of Nereis longissima in the Black Sea) (Vinogradov, 1962; Zakutskii, 1963), the benthohyponeuston plays an important role not only in the life of the neuston but also in that of the entire shelf zone of the seas and oceans, taking an active part in the redistribution and transformation of substances from the surface down to depths of 100-200m.

A similar mode of life is led by yet another group of organisms, which by day are situated a considerable distance (sometimes hundreds of metres) from the sea surface, forming part of the deep-water plankton, and by night concentrate in the hyponeuston. To this group belong the Nematomorpha (Nectonema agile), copepods (Calanus finmarchicus, C. tonsus, C. cristatus), hyperiids (Parathemisto japonica) and others. For this group the term "bathyplanktohyponeuston" has been suggested, indicating their alternation between the bathyplanktonic and hyponeustonic phases, which are of the same length for each species. /91/

The structure of the neuston is depicted in outline in Fig. 31.

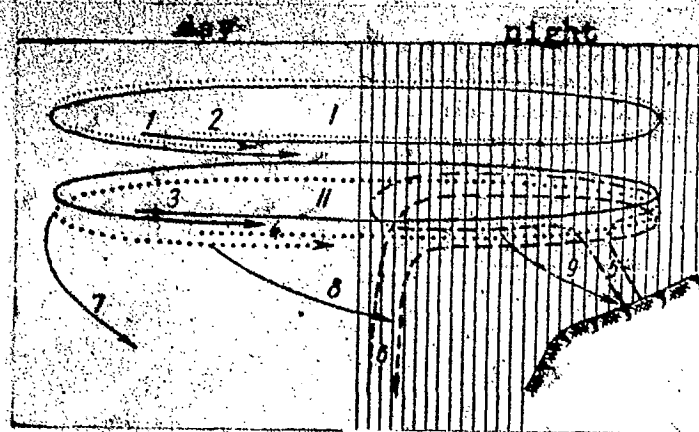


Fig. 31 - Structure of the neuston (schematic diagram):

I. Epineuston: 1 - euepineuston, 2 - meroepineuston. II. Hyponeuston: 3 - euhyponeuston, 4 - merohyponeuston, 5 - benthohyponeuston, 6 - bathyplanktohyponeuston. Transition of fish fry and invertebrates into the nekton (7), plankton (8) and benthos (9) after completion of the neustonic phase (4) of development.

Chapter XII. Composition and abundance of neuston

Bearing in mind that there are as yet no exhaustive lists of the species of plankton in the various seas and oceans, although research in this direction has been going on for a long time, it will be readily understood why it is still premature to say that a satisfactory study has been made of the qualitative composition of the neuston. All the more so as systematic studies in the near-surface layer of the pelagic zone have led within a short space of time to the description of new species for various marine basins. In this chapter the most characteristic of them are described.

The chief criterion by which organisms can be assigned to the neuston, and especially the hyponeuston, is acknowledged

to be their quantitative predominance in the 0-5 cm layer as compared to the lower-lying layers, reflecting the mean seasonal, annual or long-term data. By the same criterion organisms whose numbers in the 0-5 cm layer are only slightly higher, equal or lower compared with the underlying water layers are excluded from the neuston. In chapter XIV it will be shown that neustonic organisms possess special characters and properties appropriate to the ecological environment of their biotope. /92/

The composition and numbers of the marine neuston are examined here in a sequence reflecting the order of the links in the food chains, or trophic levels, in the sea, since the basis of the neuston - hyponeuston - can be used as a model for constructing a typical pyramid of numbers and biomasses indicating the drop in the quantity of hydrobionts in the transition from a lower trophic level to a higher one. After hyponeuston we study the composition of the epineuston and, finally, the phytoneuston, which also forms part of the hyponeuston. Normally plants form the first link in the food chain in a water body, but in the near-surface biotope of the sea the autotrophic element, at any rate as far as we know at present, does not play the same role as in the remainder of the euphotic zone of the open sea.

Micro-organisms

While data on the microflora of the surface of fresh waters can be found even in E. Naumann's papers (1917), and

particularly in the later studies of G.A. Zavarzin (1955), S.M. Drachew, L.E. Korsh and O.V. Mityagina (1957), and L.V. Bogorov (1966), science is indebted chiefly to the recent researches of A.V. Tsyban' (1965-1969), who has been working in the Black Sea since 1962, for its information on the composition and numbers of microorganisms in the near-surface layer of the sea. Before Tsyban', L.N. Pshenin (1964), who studied the distribution of Azotobacter and Clostridium in the eastern half of the Black Sea in August 1956 and found that the quantity of microcolonies and cells of these organisms in the upper 3-5 cm layer is lower, equal or more often 3-100 times greater compared with a depth of 25 m. The large gap between the layers examined meant that Pshenin could not prove at what depth the abundance of bacteria discovered in the near-surface layer begins. In a later paper (1966) he calls this accumulation "microbial hyponeuston", and describes one of its representatives, which proved to be a new species, as Treponema hyponeustonicum n. sp. (Pshenin, 1965). Pshenin's reference (1966) to the fact that "V.A. Vodyanitskii discovered the difference between neuston proper and the population of the near-surface layer of water, which Y.P. Zaitsev (1962) later described as a special pelagic biocenosis - the hyponeuston" (page 164) - is inaccurate not merely because it gives the wrong date for the first description of marine neuston by Zaitsev, but also because much earlier than Zaitsev hydrobiologists working in freshwater bodies proved that the neust-

on is a single near-surface assemblage of organisms of all taxonomic levels from bacteria to fish, consisting of two levels - hyponeuston and epineuston (cf Ch. X, XI).

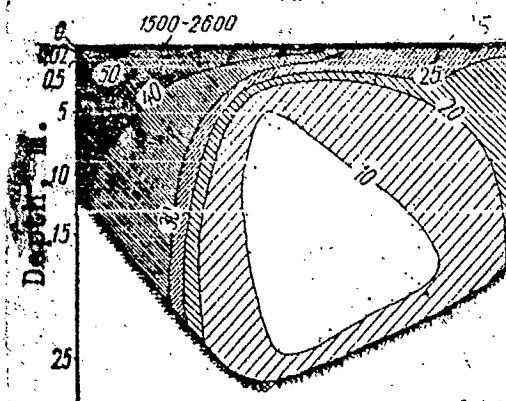


Fig. 32 - Vertical distribution of microorganisms in spring (in thousands of cells per ml of water) on a 30 mile section from Sanzheika to Tendrovskaya spit (Tsyban', 1966a).

The studies of Tsyban', which were done in conjunction with other neustonological investigations, revealed the following important facts.

1. A high density of bacteria on the surface of the sea corresponds to a layer of roughly 0-2 cm, whereas below, at the standard "zero" depth (an actual depth of about 0.5m), their numbers are one to three times less. The same density of bacteria is found at greater depths, as can easily be seen from the vertical profiles of the water column made in the north-west part of the Black Sea (Figs. 32, 33).

This is not a special case. Tsyban' calculated on a "Ural 2" digital computer the average population density of

microorganisms at different depths for the entire north-west part of the Black Sea, where material was collected at 20 permanent stations in winter, spring, summer and autumn in 1963 and 1964. The calculations showed that on average the bacterioneuston is richer than the bacterioplankton by two orders of magnitude (Fig. 34).

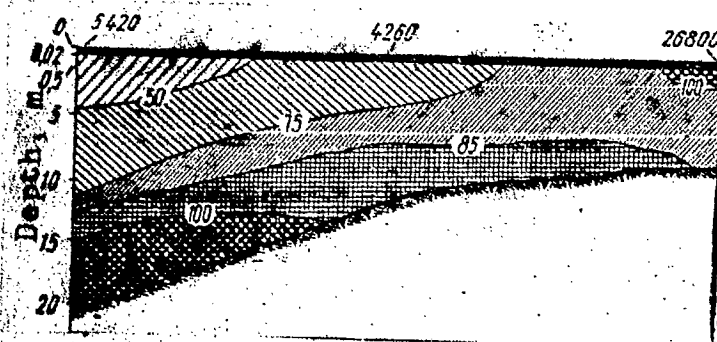


Fig. 33 - Vertical distribution of microorganisms in summer (in thousands of cells per ml of water) in a 12 mile section from Sychavka to Kinobutnaskaya spit (Tsyban', 1966a).

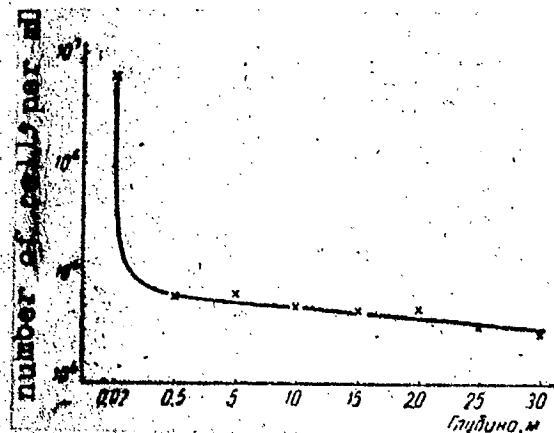


Fig. 34 - Average annual population density of microorganisms at various depths of the water column in the north-west part of the Black Sea (Tsyban' , 1968).

" . A vast quantity of bacteria is to be found in the foam on top of the surface tension film. Thus, both bacteriohyponeuston and bacterioepineuston exist, forming together the bacterioneuston.

3. A high direct correlation was discovered between the bacterioneuston and the organisms of the next trophic level- protozoans and small metazoans. /94/

4. The bacterioneuston was characterized as the first link in the neustonic assemblage of organisms.

According to Tsyban', apart from the sharp increase in the total number of microorganisms in the 0-2 cm layer there is also a greater variety of species, as was also noted by L.N. Pshenin (1964). Thus, for example, in the north-west part of the Black Sea such species as Chromobacterium agarlyticum, Chr. rubidum, Chr. citricum, Micrococcus tetragenus, Sarcina citrinia and Bacillus virgatus were discovered only in the bacterioneuston (Tsyban', 1967 a).

The existence of specific qualitative characters of the Black Sea bacterioneuston is also indicated by its higher biochemical activity and brighter, yellow and orange, pigmentation compared with the bacterioplankton of the pelagic zone (Tsyban', 1969). Tsyban' stresses that the quantity of ammonizing, denitrifying and Thiobacillus bacteria in the 0-2 cm layer is 1-2 orders of magnitude higher than in the pelagic zone. Although they appear paradoxical at first, there is no doubt about the finds made by Tsyban' of sulphate - reducing microorganisms in the bacterioneuston, whose concentration in the 0-2 cm microlayer proved to be no lower than in the near-bottom layers of water. The variation in the qualitative and quantitative composition of microorganisms by layer at 19 stations, embracing the entire north-west part of the /96/

Black Sea, is shown in Fig. 35. So far no special study has been made of the bacterioneuston of other seas. There is only a reference by B.A. Skopintsev (1939) to the effect that in one of the foam samples from the Caspian Sea the number of bacteria cultured on fish-peptone agar immediately after sampling was 14,000 colonies, and in sea water 440 colonies per cubic centimetre. After incubation for three days the number of colonies rose to 2,350,000 in the foam and 820 per cc in the water.

Protozoans

The next link in the chain after bacteria is protozoans - probably the largest consumers of microorganisms. Therefore it was very interesting to learn how the protozoans of the pelagic zone react to the existence of such an exceptional abundance of bacteria as was discovered in the 0-2 cm layer.

The first neustonological studies in the sea (Zaitsev, 1960c) had shown that there was a high density of microplanktonic organisms in the 0-5 cm layer - especially of Noctiluca miliaris (Zaitsev, 1961a). The same was confirmed by L.G. Koval' (1961) on the basis of collections made with a neuston net in the northwestern part of the Black Sea. However, these were isolated cases. Systematic investigations of the microhyponeuston begun by L.N. Polishchuk (1965-1969) yielded more complete information. Data on the average long-term (1961-1965) abundance of Noctiluca miliaris near the surface of the Black Sea are given in Table 12.

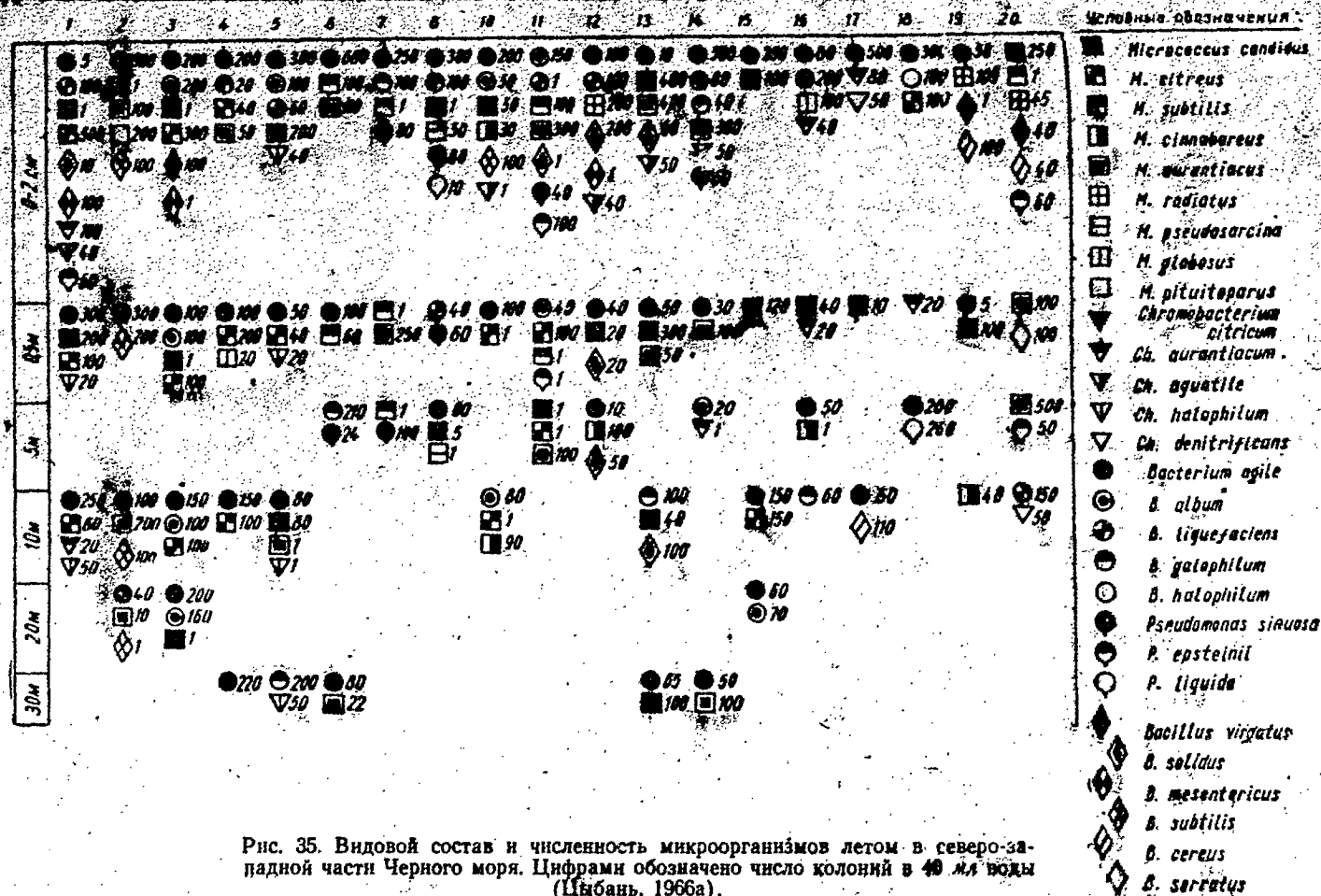


Fig. 35. - Species composition and abundance of microorganisms in summer in the north-west part of the Black Sea. The figures denote the number of colonies in 40 ml of water (Tsyban', 1966a).

Table 12

Average abundance (in spec./m³) of Noctiluca miliaris Suriray near the surface of the Black Sea (from materials of L.N. Polishchuk)

Микрогори- зонт, см	$M \pm m$	Степень на- дежности среднего t_2
I, 0-5	15044,39 ± 176,54	85,21
II, 5-25	6687,80 ± 78,72	84,95
III, 25-45	5198,00 ± 1257,92	4,13
IV, 45-65	4098,00 ± 1019,34	4,02
M_{diff}		
and I и II	I и III	I и IV
	II и III	III и IV
43,25	7,75	10,58
	1,16	0,67

Key: 1. Microlayer, cm; 2. Degree of reliability of average t .

As can be seen from the table, the abundance of Noctiluca miliaris in the 0-5 cm layer differs considerably from its abundance in the lower layers, whereas the differences among the latter are negligible.

The first to direct attention to the abundance and species diversity of tintinnids in the hyponeuston of the Black Sea was O.I. Morozovskaya (1966-1969), who reviewed the taxonomy of this widely distributed group of Infusoria, which plays an important role in the feeding of many invertebrates and fish larvae. The data of Morozovskaya given below characterize the different seasons of the year in the Chernomorka area. The

samples were obtained with the aid of a PNS-4 net, towed for a distance of 10-50 m, and are qualitative: the collections from the various microlayers in each haul are quantitatively comparable one with another.

21 March 1966

0-5 cm layer	<u>Tintinnopsis meunieri</u>	276 spec.
	<u>T. tubulosa</u>	44 "
	<u>Stenosemella ventricosa</u>	52 "
5-25 cm layer	<u>T. meunieri</u>	3 spec.
	<u>T. tubulosa</u>	1 "
	<u>S. ventricosa</u>	44 "
	<u>Coxliella helix</u>	70 "
25-45 cm layer	<u>S. ventricosa</u>	10 "
45-65 cm layer	<u>S. ventricosa</u>	19 "

15 July 1966

0-5 cm layer	<u>T. urnula</u>	16 "
	<u>T. cylindrica</u>	240 "
	<u>T. kofoidi</u>	28 "
	<u>T. meunieri</u>	84 "
	<u>C. helix</u>	164 "
	<u>Helicostomella subulata</u>	104 "
5-25 cm layer	<u>T. tubulosa</u>	22 "
	<u>T. meunieri</u>	9 "
	<u>T. kofoidi</u>	3 "
	<u>H. subulata</u>	16 "
25-45 cm layer	<u>T. cylindrica</u>	18 "
	<u>T. beroidea</u>	1 "
45-65 cm layer	<u>T. cylindrica</u>	9 "
	<u>T. meunieri</u>	17 "
	<u>T. tubulosa</u>	1 "
	<u>C. helix</u>	8 "
	<u>H. subulata</u>	5 "

5 October 1966

0-5 cm layer	<u>T. meunieri</u>	52 "
	<u>T. beroidea</u>	28 "
	<u>T. karajacensis</u>	8 "
	<u>C. helix</u>	102 "

5-25 cm layer	<u>T. karajacensis</u>	28	"	140
	<u>T. meunieri</u>	15	"	
	<u>T. compressa</u>			
25-45 cm layer	<u>T. meunieri</u>	47	"	
	<u>T. tubulosa</u>	2	"	
	<u>C. helix</u>	11	"	
	<u>T. karajacensis</u>	6	"	

Thus, the highest density of tintinnids and their richest species composition were recorded in the 0-5 cm layer. O.I. Morozovskaya (1969) notes that the maximum density of T. kofoidi Hada (7400-7900 spec./m³) was found in the summer hyponeuston of the northwestern part of the Black Sea, whereas the greatest abundance of T. beroidea Stein em. Jørgensen (12,600 spec./m³) was recorded in the spring hyponeuston of the same waters. The 0-5 cm layer is also preferred by T. karajacensis Brandt, while T. urnula Meunier has so far been discovered only in this biotope.

The abundance of tintinnids in the 0-5 cm layer is clearly illustrated by the hose-water-sampler collections made by O.I. Morozovskaya in different areas of the Black Sea in August 1963, compared with collections made with a Juday net of No. 61 mesh (mesh size 0.11 X 0.13 mm) at the same points (Tables 13-15).

Table 13

Abundance of tintinnids (spec./m³) near the surface of the Black Sea in the vicinity of the Bosphorus in August 1963 (from the materials of O.I. morozovskaya)

Вид	Шлангово- 2 метр	Сеть Дюпона
	Сред. 0-5 см	Сред. 0-10 см
<u>Tintinnopsis karajacensis</u>	82 000	0
<u>T. beroidea</u>	4000	0
<u>T. tubulosa</u>	6000	0
<u>Helioecetella rotunda</u>	22 000	52
<u>Stenosemella benticosa</u>	8000	17
<u>Coelothella helix</u>	34 000	65
<u>C. annulata</u>	0	1

(Table 13 continued)

Key: 1. Species; 2. Hose-water sampler; 3. Juday net; 4. Layer.

Table 14

The abundance of tintinnids (spec./m³) near the surface of the Black Sea off Cape Kerempe in August 1963 (from materials of O.I. Morozovskaya)

Вид	Шланг-бато- 2 метр	Сеть Джеда
	Слой 0—5 см 4	Слой 0—10 м 4
<i>Stenosemella ventricosa</i>	16 000	108
<i>Costiella helix</i>	16 000	97
<i>Helicostomella subulata</i>	4000	0
<i>Favella ehrenbergii</i>	2000	0
<i>Tintinnopsis campanula</i>	12 000	0
<i>T. compressa</i>	2000	0
<i>T. meunieri</i>	0	1

Key: 1. Species; 2. Hose-water sampler; 3. Juday net; 4. Layer.

Table 15

The abundance of tintinnids (spec./m³) near the surface of the northeastern deep-water part of the Black Sea in August 1963 (from materials of O.I. Morozovskaya)

Вид	Шланг-бато- 2 метр	Сеть Джеда
	Слой 0—5 см 4	Слой 0—10 м 4
<i>Favella ehrenbergii</i>	26 000	119
<i>Stenosemella ventricosa</i>	44 000	50
<i>Costiella helix</i>	50 000	32
<i>Helicostomella subulata</i>	32 000	0
<i>Stenosemella nacula</i>	10 000	0
<i>Metacyclops mereschkovskii</i>	4000	0
<i>M. ehrenbergii</i>	2000	0

Key: 1. Species; 2. Hose-water sampler; 3. Juday net; 4. Layer.

Of course, there can be no comparison between the data of collections made by water sampler and net - even when the latter is of coarse No. 61 mesh - for such small tintinnids as M. ehrenbergii, St. nucula, T. beroidea and others, but the absence or small numbers of large forms (F. ehrenbergii, C. helix, H. subulata, T. tubulosa and others) in the net hauls can be explained only by concentration of these Infusoria in the hyponeuston layer and low representativeness of vertical net hauls.

The wide geographic distribution of the tintinnid species discovered by Morozovskaya (1968a) in the Black Sea provides grounds for considering this group an important component in the hyponeuston of the ocean. This is also evidenced by the data of L.N. Polishchuk for the Sea of Azov. For instance, the average population density of Tintinnopsis kofoidi Hada as revealed by collections made with a PNS-4 net in August 1962 was: 10,146 spec./m³ in the 0-5 cm layer, 4,073 in the 5-25 cm layer, 4,831 in the 25-45 /99/ cm layer and 3,861 in the 45-65 cm layer. The average abundance of T. cylindrica Daday in the same microlayers in September 1963 was 5,000, 1,257, 124 and 500 spec./m³ respectively. The collections made by Polishchuk with a PNS-2 net in August 1965 showed the following average abundance of the prolific species of tintinnids in the Sea of Azov (Table 16).

Table 16

average population density (spec./m³) of abundant species of tintinnids near the surface of the Sea Azov in August 1965 judged from hauls made with a PNS-2 plankton-neuston net (based on materials of L.N. Polishchuk)

Вид	Слой 0—5 см	Слой 5—25 см
	2	2
<i>Tintinnopsis meunieri</i>	12 000	4099
<i>T. kofoidi</i>	1325	525
<i>T. cylindrica</i>	1383	125
<i>T. rossolimo</i>	1108	16

Key: 1. species; 2. layer

Apart from tintinnids, other species of Protozoa also exhibit their maximum density in the 0-5 cm layer. In PNS-2 and MNT collections from the Gulf of Mexico A.A. Strelkov discovered a much higher abundance of Spumellaria (Radiolaria) than in samples from the pelagic zone. As these Radiolaria were also common in neuston hauls from the tropical part of the Pacific (Bieri a. Newbury, 1966), it may be assumed that Spumellaria are widely distributed /100/ representatives of the oceanic hyponeuston. The same conclusion can be drawn with respect to the Foraminifera encountered in the hauls of Bieri and Newbury, and also Willis (1963) in the vicinity of Wellington. However, protistological study of the marine neuston is still in its infancy, and more detailed information will be obtained in future on the part played by Protozoa in the life of the nearsurface microlayer of the pelagic zone.

Small Multicellular Organisms (Invertebrates)

Small invertebrates whose body size is substantially within the size category of microplankton (0.05-1.0 mm) form the next link in the food chain, since they live to a considerable degree on protozoans and bacteria. It is quite understandable that the division into trophic levels is quite relative and based on average indices. It is known for instance that bacteria and protozoans are also consumed directly by fish larvae, which come very low on the list, while they themselves may be devoured by Balanus larvae, which form part of the same group. Even Noctiluca miliaris may eat fish eggs (Hattori, 1962). Such deviations from the general scheme may be few in number, but small metazoans by virtue of their abundance are the primary consumers, whereas in the hyponeuston layer, where living plants are not of the same relative abundance as in the main mass of water, they consume protozoans, bacteria and detritus. A.V. Tsyban' discovered between the bacterioneuston and small multicellular invertebrates from the 0-5 cm layer a linear relation expressed by a high correlation coefficient ($r = 0.96, \sigma_r = 0.018$), which confirms the fundamental correctness of regarding neustonic organisms as a series of links in a food chain. The systematic composition of this group is complex and in individual cases weakly elaborated, the more so as the larval stages of many classes and types of hydrobionts (merohyponeuston) are included here, the study of which presents special difficulties. /101/

Among the most abundant forms of small multicellular organisms in the marine neuston are certain species of rotifers, the larvae of many species of polychaetes, gastropods and Lamellibranchia, copepods and Cirripedia, echinoderms, certain species of cladocerans and copepods (in adulthood), etc.

Rotifers (Rotatoria) form part of the hyponeuston mainly in the freshened areas of the ocean and are therefore particularly characteristic of such water basins as the southern seas of the Soviet Union - the Black Sea, Sea of Azov and the Caspian. L.N. Polishchuk (1966b) reports that at the end of summer 1963, in the northwestern part of the Sea of Azov, the rotifers Synchaets sp. (vorax?) were distributed among the microlayers (PNS-4 collections) as follows: 245,000 spec./m³ in the 0-5 cm layer, 26,000 in the 5-25 cm layer, 40,000 in the 25-45 cm layer, 22,000 spec./m³ in the 45-64 cm layer.

The confinement of rotifers to the surface tension film in freshwater basins is a known fact. Such rotifers as Monommata, Scaidium, Polyarthra, Filinia and others are capable of making leaps (Zenkevich and Konstantinova, 1956), as the result of which they sometimes find themselves on the surface tension film. Because of their small size they are unable to break through the film to submerge again and they dry out in the sun. The same fate often overtakes Daphnia, ostracods and other small animals with impermeable integuments which leap out of the water and land on the surface tension film (Zernov, 1949). However, it is known that desiccated rotifers are able to revive /102/

in water, and it may be that this property compensates to some extent for the unfavourable consequences of their involuntary epineustonic position.

The larvae of polychaetes also form distinct concentrations in the 0-5 cm layer, and their broad distribution in the halosphere gives grounds for classing them among the most representative of marine merohyponeuston (Table 17). Among the most numerous larvae of the nectochaeta type in Polishchuk's collections, as identified by G.V. Losovskaya, figure representatives of the family Spionidae, and in particular Spio filicornis (O. Muller), Microspio mecznikowianus (Claparede), and - from the family Magelonidae - Magelona rosea Moore. The vertical microdistribution of nectochaetes indicates a distinct and statistically reliable concentration of them in the 0-5 cm layer. Below the hyponeuston biotope the variation in the numbers of larvae along the vertical is insignificant.

Table 17

Average abundance (spec./m³) of Polychaeta larvae near the surface of the Black Sea and Sea of Azov*

Микрогори- зонт, см	$M \pm m$	Степень на- дежности среднего t
I, 0-5	2742,55 ± 26,92	101,87
II, 5-25	931,05 ± 8,05	115,65
III, 25-45	1041,05 ± 139,13	7,48
IV, 45-65	986,05 ± 125,02	7,88
M_{diff}		
I и II	I и III	I и IV
II и III	III и IV	
64,48	12,0	13,74
	0,74	0,29

Key: 1. microlayer, cm; 2. degree of reliability of average t ;
3. and.

*Here and in Tables 18-36 the figures are based on the materials of L.N. Polishchuk.

A similar picture is revealed by the veliger larvae of bivalves (Table 18) and gastropods (Table 19) in all the southern seas of the USSR. The same pattern marks the Balanus larvae (Table 20).

Among the cladocerans the most abundant in the 0-5 cm layer are Evadne tergestina (Table 21). The eggs of Sagitta sp. come next on this list of hyponeustonic organisms (Table 22).

Table 18

Average abundance (spec./m³) of Lamellibranchia larvae near the surface of the Black Sea, the Sea of Azov and the Caspian.

Микрогори- зонт, см	$M \pm m$	Степень на- дежности среднего t 2		
I, 0—5	45907.05 ± 1002.14	45.80		
II, 5—25	25174.05 ± 188.08	133.84		
III, 25—45	5322.05 ± 205.41	25.90		
IV, 45—65	5125.30 ± 226.40	22.63		
M_{diff}				
³ I и II	I и III	I и IV	II и III	III и IV
20.34	39.67	39.69	71.41	0.64

Key: As for Table 17.- Translator.

Table 19

Average abundance (spec./m³) of Gastropoda larvae near the surface of the Black Sea and Sea of Azov.

Микрогори- зонт, см	$M \pm m$	Степень на- дежности среднего t		
		2		
I, 0—5	4703.05 ± 189.04	24.87		
II, 5—25	2851.30 ± 28.51	100.01		
III, 25—45	2029.05 ± 389.54	5.20		
IV, 45—65	2026.05 ± 327.18	6.19		
M_{diff}				
³ I и II	I и III	I и IV	II и III	III и IV
9.68	6.17	7.08	2.26	0.005

Key: As for Table 17 - Translator.

Table 20

Average abundance (spec./m³) of Balanus sp. larvae near the surface of the Black Sea, Sea of Azov and Caspian Sea

Микрогори- зонт, см	$M \pm m$	Степень на- дежности среднего t		
I, 0—5	6103,05±52,68	115,85		
II, 5—25	1702,05±16,61	102,47		
III, 25—45	1227,45±188,06	6,52		
IV, 45—65	977,55±142,31	6,86		
M_{diff}				
$\frac{3}{I \text{ и } II}$	$I \text{ и } III$	$I \text{ и } IV$	$II \text{ и } III$	$III \text{ и } IV$
80,01	24,97	33,78	2,51	1,05

Key: As for Table 17 - Translator.

Table 21

Average abundance (spec./m³) of Evadne tergestina Claus near the surface of the Black Sea

Микрогори- зонт, см	21 $M \pm m$	Степень на- дежности среднего t 2		
I. 0—5	495,05±68,46	7,23		
II. 5—25	221,65±31,54	7,02		
III. 25—45	306,55±45,71	6,70		
IV. 45—65	299,90±42,91	6,98		
M_{diff}				
3 I и II	I и III	I и IV	II и III	III и IV
3,63	2,29	2,41	1,52	0,10

Key: As for Table 17 - Translator.

Table 22

Average abundance (spec./m³) of eggs of Sagitta sp. near the surface of the Black Sea

Микрогоризонт, см. 1	$M \pm m$	Степень надежности среднего t 2
I, 0-5	595,30 $\pm$ 82,15	7,24
II, 5-25	209,65 $\pm$ 33,28	6,29
III, 25-45	204,70 $\pm$ 36,79	5,56
IV, 45-65	361,55 $\pm$ 32,78	7,97
M_{diff}		
3 I и II	I и III	I и IV
II и III	III и IV	
4,35	4,34	3,75
		0,09
		1,15

Key: As for Table 17 - Translator.

The relationship to the 0-5 cm layer of the abundant and widely distributed species of copepods of both sexes proves to be different at the various stages of development. /103/ Thus, in Oithona minuta the copepodite stages and the females are clearly drawn towards the hyponeuston, whereas the males move away from the nearsurface layer (Tables 23-25).

Table 23

Average abundance (spec./m³) of the copepodite stages of Oithona minuta Kric. near the surface of the Black Sea

Микрогоризонт, см	$M \pm m$	Степень надежности среднего t
I, 0-5	5987.0 $\pm$ 225.32	26.61
II, 5-25	3753.80 $\pm$ 158.28	23.71
III, 25-45	3400.05 $\pm$ 522.06	6.51
IV, 45-65	3520.05 $\pm$ 529.28	6.65
M_{diff}		
t_{I-II}	t_{I-III}	t_{I-IV}
8.15	4.56	4.30
		0.64
		0.16

Key: As for the Table 17 - Translator.

Table 24

Average abundance (spec./m³) of females of O. minuta near the surface of the Black Sea

Микрогоризонт, см	$M \pm m$	Степень надежности среднего t
I, 0-5	6017.05 $\pm$ 206.11	29.19
II, 5-25	3389.55 $\pm$ 94.36	35.92
III, 25-45	3645.25 $\pm$ 518.82	7.02
IV, 45-65	4180.05 $\pm$ 576.11	7.25
M_{diff}		
t_{I-II}	t_{I-III}	t_{I-IV}
11.62	4.24	3.00
		0.48
		0.68

Key: As for Table 17 - Translator.

Table 25

Average abundance (spec./m³) of males of O. minuta near the surface of the Black Sea

Микрогоризонт, см	$M \pm m$	Степень надежности среднего t_2
I, 0-5	1312.05 ± 204.00	6.43
II, 5-25	2368.05 ± 135.39	17.49
III, 25-45	690.55 ± 121.38	5.68
IV, 45-55	764.35 ± 118.32	6.46
M_{diff}		
³ I и II	I и III	I и IV
II и III	III и IV	
4.32	2.61	2.32
	9.21	0.43

Key: As for Table 17 - Translator.

Centropages ponticus is clearly a hyponeustonic species at the naupliar stage and less obviously at the remaining stages, though all the age groups give preference to the 0-5 cm layer instead of avoiding it (Tables 26-29).

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Table 26

Average abundance (spec./m³) of naupliar stages of Centropages ponticus Karavajev near the surface of the Black Sea and the Sea of Azov

Микрогоризонт, см	$M \pm m$	Степень надежности среднего t_2		
I, 0—5	47605,05 ± 1745,08	27,27		
II, 5—25	13830,47 ± 131,53	105,15		
III, 25—45	14449,85 ± 2465,22	5,86		
IV, 45—65	7878,95 ± 1238,38	6,36		
M_{diff}				
I и II	I и III	I и IV	II и III	III и IV
19,29	10,97	18,56	0,25	3,06

Key: As for Table 17 - Translator.

Table 27

Average abundance (spec./m³) of IV copepodite stage of C. ponticus near the surface of the Black Sea and Sea of Azov

Микрогоризонт, см	$M \pm m$	Степень надежности среднего t_2		
I, 0—5	3325,05 ± 688,87	4,82		
II, 5—25	1001,95 ± 192,74	5,20		
III, 25—45	1348,15 ± 363,91	3,70		
IV, 45—65	1176,45 ± 296,14	3,87		
M_{diff}				
I и II	I и III	I и IV	II и III	III и IV
3,24	2,53	2,90	0,84	0,42

Key: As for Table 17 - Translator.

Table 28

Average abundance (spec./m³) of females of C. ponticus near the surface of the Black Sea and Sea of Azov

Микрогоризонт, см	$M \pm m$	Степень надежности среднего t		
I		2		
I, 0—5	1267,55±199,60	6,35		
II, 5—25	435,30±72,31	6,01		
III, 25—45	459,55±95,77	4,79		
IV, 45—65	383,55±78,16	4,90		
M_{diff}				
I и II	I и III	I и IV	II и III	III и IV
3,87	3,65	3,95	0,20	0,61

Key: As for Table 17 - Translator.

Table 29

Average abundance (spec./m³) of males of C. ponticus near the surface of the Black Sea and Sea of Azov

Микрогоризонт, см	$M \pm m$	Степень надежности среднего t_2		
I, 0—5	945,55 ± 176,74	5,34		
II, 5—25	411,45 ± 74,35	5,53		
III, 25—45	333,55 ± 72,14	4,62		
IV, 45—65	586,25 ± 129,48	4,52		
M_{diff}				
I и II	I и III	I и IV	II и III	III и IV
2,78	3,22	1,64	0,75	1,70

Key: As for Table 17 - Translator.

The naupliar stages of Acartia clausi form stable aggregations in the hyponeuston. As the copepodite stages develop, their attachment for the 0-5 cm layer weakens, but in the females it is very marked (Tables 30-35).

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Table 30

Average abundance (spec./m³) of the naupliar stages of Acartia clausi Giesbr near the surface of the Black Sea and Sea of Azov

Микрогоризонт, см	$M \pm m$	Степень надежности среднего t_2		
I, 0—5	31480.05 ± 275.42	114.29		
II, 5—25	12991.00 ± 108.85	119.34		
III, 25—45	16210.05 ± 2390.82	6.78		
IV, 45—65	17175.05 ± 2575.19	6.66		
M_{diff}				
t^2 I и II	I и III	I и IV	II и III	III и IV
62.44	6.34	5.52	1.76	0.30

Key: As for Table 17 - Translator.

Table 31

Average abundance (spec./m³) of copepodite stage I of A. clausi near the surface of the Black Sea and Sea of Azov

Микрогоризонт, см	$M \pm m$	Степень надежности среднего t		
I, 0—5	8320.05 ± 1317.23	6.31		
II, 5—25	2641.30 ± 423.76	6.24		
III, 25—45	3650.05 ± 746.21	4.89		
IV, 45—65	3480.05 ± 691.37	5.03		
M_{diff}				
³ I и II	I и III	I и IV	II и III	III и IV
4.10	3.08	3.44	1.17	0.16

Key: As for Table 17 - Translator.

Table 32

Average abundance (spec./m³) of copepodite stage III of A. clausi near the surface of the Black Sea and Sea of Azov

Микрогоризонт, см 1	$M \pm m$	Степень надежности среднего t 2		
I, 0—5	5485.05 ± 1153.84	4.75		
II, 5—25	1535.05 ± 299.33	5.12		
III, 25—45	2250.05 ± 595.83	3.77		
IV, 45—65	1835.05 ± 482.50	3.80		
M_{diff}				
³ I и II	I и III	I и IV	II и III	III и IV
3.31	2.49	2.91	1.07	0.54

Key: As for Table 17 - Translator.

Table 33

Average abundance (spec./m³) of copepodite stage V of A. clausi near the surface of the Black Sea and Sea of Azov

Микрогоризонт, см 1	$M \pm m$	Степень надежности среднего t_2		
I, 0—5	2278.05±506.87	4.49		
II, 5—25	1024.55±245.36	4.17		
III, 25—45	1422.55±450.95	3.15		
IV, 45—65	2032.05±706.75	2.87		
M_{diff}				
³ I и II	I и III	I и IV	II и III	III и IV
2.23	1.26	0.28	0.77	0.77

Key: As for Table 17 - Translator.

Table 34

Average abundance (spec./m³) of females of A. clausi near the surface of the Black Sea and Sea of Azov

Микрогоризонт, см	$M \pm m$	Степень надежности среднего t		
I, 0—5	20445.05 ± 202.67	100.87		
II, 5—25	1410.05 ± 52.22	27.00		
III, 25—45	1760.05 ± 298.02	5.90		
IV, 45—65	2035.55 ± 321.98	6.32		
M_{diff}				
I и II	I и III	I и IV	II и III	III и IV
91.07	5.19	48.39	1.15	0.62

Key: As for Table 17 - Translator.

Table 35

Average abundance (spec./m³) of males of A. clausi near the surface of the Black Sea and Sea of Azov

Микрогоризонт, см	$M \pm m$	Степень надежности среднего t_2		
I, 0—5	3645.05±592.91	6.14		
II, 5—25	1412.05±64.35	21.94		
III, 25—45	2376.05±493.37	4.81		
IV, 45—65	2136.05±420.05	5.08		
M_{diff}				
I и II	I и III	I и IV	II и III	III и IV
3.74	1.64	2.07	1.93	0.39

Key: As for Table 17 -Translator.

One more species which is widely distributed in the seas - /105/
Paracalanus parvus - concentrates in the hyponeuston at the nau-

pliar stage, but is later distributed relatively evenly throughout the pelagic zone (Table 36).

Table 36

Average abundance (spec./m³) of naupliar stages of Paracalanus parvus Claus near the surface of the Black Sea and Sea of Azov

Микрогоризонт, см	$M \pm m$	Степень надежности среднего t		
I, 0—5	3589.45±515.78	6.95		
II, 5—25	1486.05±224.13	6.63		
III, 25—45	1511.35±289.13	5.22		
IV, 45—65	1586.05±295.18	5.37		
M_{diff}				
$\frac{3}{I \text{ и } II}$	I и III	I и IV	II и III	III и IV
3.74	3.51	3.36	0.06	0.18

Key: As for Table 17 - Translator.

The large volume of statistical material cited shows that in consequence of the high concentrations of bacteria and protozoans in the 0-5 cm layer such abundant and widely distributed organisms as the larvae of polychaetes, mollusks and Cirripedia, and the naupliar stages of many copepods, form stable aggregations there. Characteristic of the copepods, but not peculiar to them alone, is the tendency to leave the 0-5 cm layer gradually as the females develop and return to it. This feature of the biology of hydrobionts will be examined in the fifth section of this book in connection with a discussion of the role of neuston in the halosphere. /106/

The clear sequence of the initial links in the food chain creates conditions for the existence of a high concentration of predators in the 0-5 cm layer, and these predators form the next link in the chain.

Large Multicellular (Invertebrate) Organisms

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Large invertebrates measuring more than 1 mm (more often from 3 to 20 mm), and sometimes up to tens of centimetres, form the predator link. These predators feed mainly on the organisms of the preceding link, and also on fish eggs and larvae. In samples of plankton taken from the pelagic zone this group of hydrobionts is represented by solitary specimens, and many ascribe this to the fact that they flee from fishing gear.

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In actual fact, the reason is the failure of researchers to take into account the nearsurface layer of the pelagic zone and the impossibility of fishing this layer with standard plankton nets. Neuston nets, however, which are towed no faster than plankton nets, revealed exceptional diversity and abundance of the organisms constituting this group in the 0-5 cm layer. Whereas even recently the number of such organisms as pontellids in samples of plankton was so small that it was impossible to determine their average weight (Petipa, 1957), now, thanks to neuston samples, not only has this gap been filled (Zaitsev et alia, 1962), but the possibility has been discovered of making mass collections of pontellids and other large invertebrates in the nearsurface biotope, and these have already become customary subjects of biochemical and radioecological investigations.

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The characteristic large invertebrates of the hyponeuston include representatives of all its elements - euhyponeuston, merohyponeuston, benthohyponeuston and bathyplanktonyponeuston.

Among the representatives of the euhyponeuston first place must be assigned to crustaceans of the family Pontellidae. Apparently all nine orders of this highly specialized (Brodskii, 1950) family are represented by euhyponeustonic species. Even Anomalocera patersoni Templ. and Epilabidocera amphitrites (McMurrich), which penetrate into the North Atlantic from the Bering Sea, do not lose their hyponeustonic character. As regards the species of the genera Pontella, Labidocera and Pontellopsis, these comprise the bulk of the pontellid hyponeuston in the tropical and temperate regions of the ocean. /111/

The widely distributed species of the Sapphirinidae family of comparatively large copepods, (Sapphirina angusta Dana, S. nigrimaculata Claus, S. maculosa Giesbr., S. metallina Dana and others) are hardly ever encountered outside the nearsurface microlayer. /112/

Also typical of this group are the isopods, including the widely distributed species Idothea stephenseni Collinge (syn. I. pelagica Leach, I. algerica Lucas, I. ostroumovi Sovinsk, I. met-allica Stephens).

Among the decapods mention must be made of the pelagic crabs of the genera Planes (P. minutus (L.), P. cyaneus Dana) and Portunus (P. portunus), which are especially numerous in the masses of hyponeustonic sargassos.

A group of large hyponeustonic invertebrates is constituted

by mollusks of the genera Janthina (J. janthina, J. fragilis) and Glaucus (G. atlanticus, G. lineatus, G. longicirris).

Among the representatives of the early stages of ontogenesis, the most widely distributed are the large larvae of Decapoda, Euphausiacea and Stomatopoda: protozoa, zoea, metazoea, megalopa, glaucothoe, phyllosoma, alima and others.

In the shelf zone a large part of the hyponeuston consists of adult specimens of benthohyponeustonic invertebrates. Among the representatives of the benthohyponeuston of the Black Sea and Sea of Azov V.P. Zakutskii mentions the following widely distributed species:

Polychaeta: (Phyllodoce tuberculata Bobretzky, Nereis diversicolor O.F. Müller, N. succinea Leucart, N. longissima (Johnston), Platynereis dumerilii Aud. et M.-Edw., Nephtis longicornis Perejaslavzeva).

Isopoda: Eurydice spinigera Hansen, L. pontica (Czern.), /113/
Sphaeroma serratum (Fabr.), S. pulchellum (colosi).

Amphipoda: Bathyporeia guilliamsoniana Bate, Nototropis guttatus (Costa), Gammarus locusta L., Dexamine spinosa (Mont.), Gorophium nobile G.O.S., Caprella acanthifera (Leach).

Cumacea: Bodotria arenosa (Goodsir), Cumopsis goodsir (Beneden), Cumella pygmaea G.O.S., Pterocuma pectinata (Sovinsky), P. gracilloides (G.O.S.).

Mysidacea: Siriella jaltensis Czern., Gastrosaccus sanctus (IV. Ben.), Mesopodopsis slaberi v. Ben., Pseudoparamysis pontica Bacesco, Mezomysis kroeyeri Czern.

Decapoda: Palaemon adspersus Rathke, P. elegans Rathke, Crangon crangon (L.).

The bathyplanktohyponeuston, which is most strongly developed in the oceanic region, is represented by a group of large invertebrates forming part of the hyponeuston during the dark part of the day. This group includes: the recently discovered (for the first time in the southern seas of the USSR) hairworm Nectonema agile subsp. euxina (Kir'yanova and Zakutskii, 1967), Sagitta euxina Molt., Calanus finmarchicus (Gunner), C. tonsus Brady, C. cristatus Kroyer, and , apparently, a considerable part of the hyperiid species (eg Parathemisto japonica) and euphausiacean species (Thysanoessa inermis, Th. raschii, Euphausia).

Some idea of the numbers of large invertebrates in the hyponeuston near the surface of the pelagic zone can be derived from the following indices computed by the author for abundant Black Sea species and developmental stages from collections made from 1960 through 1965 (Table 37). These indices emphasize the fact that the bulk of the organisms listed in the table are not in the hyponeuston by chance, and so when neustonological investigations were first initiated they only occasionally found their way into the vertical hauls of plankton nets and never figured in the lists of abundant forms of plankton.

As regards the absolute abundance of these species, it varies considerably depending on the conditions. The number of pontellids, equipods and decapod larvae in the 0-5 cm layer of the Black Sea in conditions unpropitious for the development of hyponeuston (freshening, immediate proximity of the shore, and

especially during the cold part of the year) can be reckoned in ones and twos per m^3 . Sometimes, e.g. in the near-shore zone when the wind is adverse, there is no sign of them. More often however, the summer density of these organisms ^{is} several tens or hundreds per m^3 , and in the most favourable conditions (zones of current convergence, hydrological fronts) they number tens and hundreds of thousands per m^3 of water. More than 5 cm from the surface their numbers drop sharply (Table 37). /114/

Table 37

Relative abundance of large invertebrates in the Black Sea as estimated from PNS-5 hauls

Вид	2. Микрогоризонт, см.			
	5—25	25—45	45—65	65—85
<i>Pontella mediterranea</i>	0,01	0,008	0,005	0,002
<i>Anomalocera patersoni</i>	0,04	0,004	0,02	0,001
<i>Labidocera brunescens</i>	0,50	0,06	0,005	0,001
<i>Idothea stephenseni</i>	0,02	0,04	0,009	0,0
<i>Brachyura</i> (zoëa)	0,24	0,24	0,22	0,20
<i>Brachyura</i> (megalopa)	0,03	0,06	0,0	0,0
Amphipoda	0,13	0,09	0,07	0,07
Cumacea	0,09	0,08	0,11	0,07
<i>Palaemon adspersus</i>	0,09	0,01	0,01	0,0

Note: Here and in Table 38 the number of organisms in the 0-5 cm microlayer is adjusted to zero.

The highest density of benthohyponeustonic organisms in the Black Sea is observed over depths of up to 20-30 metres, and, as estimated by V.P. Zakutskii, equals 500-700 specimens in the 0-5 cm layer with a biomass of 2000-2500 mg per m^3 of water.

The number of bathyplanktohyponeustonic organisms in the 0-5 cm layer is also considerable in the high latitudes. For example, in the northwestern part of the Pacific and in the Bering Sea in June-September 1962 (judging by the collections of S.M. Chebanov) the average number of large forms (Calanus tonsus, C. cristatus, Eucalanus bungii, Isopoda, Hyperiididae, Euphausiacea) in the 0-5 cm layer was 529 spec./m³, and in the underlying 5-25 cm layer it was 248 spec./m³. In isolated cases the abundance of hyperiids rose to 60,000 spec./m³ in the 0-5 cm layer and to 10,000 spec./m³ in the underlying 5-25 cm layer. On the other hand, the abundance of calanids was 6000 and 1000 spec./m³ respectively.

Fish Roe, Larvae and Fry

If the composition of the hyponeuston is depicted in the form of the links of a food chain, then the last link will be made up only of developed larvae and fry. The eggs, prolarvae and unformed larvae must be assigned to the preceding links. However, in view of the taxonomic integrity of the group, we can deviate from the normal scheme of things and class fish eggs together with larvae and fry.

As already noted, the search for fish eggs of high buoyancy was one of the important factors giving rise to the birth neustonological research in the sea. The material later accumulated confirmed that in calm weather and a sea state of 3-4 (i.e. during the most intensive spawning of pelagophile fishes)

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the primary concentration of eggs forms under the surface tension film, their specific gravity being lower than the density of the sea water in situ. In this case the vertical position of the egg is determined by Archimedes principle. In a sea state of more than 3-4 the nearsurface accumulation of eggs is dispersed to some degree, but when the waves die down the eggs which survive again collect beneath the surface tension film.

The highest buoyancy characterizes the eggs of different species of Engraulidae, Mugilidae, Pomatotomyidae, Carangidae, Mullidae, Callionymidae, Bothidae, Pleuronectidae, Soleidae, and others. Rich collections of such eggs obtained with the help of neuston nets have served not only to clarify the sites, dates and conditions of spawning, but also to reveal hitherto unknown features of the biology of the reproduction of such species as Mugil cephalus L., M. saliens Risso, M. auratus Risso, Mullus barbatus L., Engraulis encrasi cholum (L.), and others (Zaitsev, 1960c, 1963a, 1963b, 1964b; Zelezinskaya, 1961, 1963; Krakatitsya, 1963; Vinogradov, 1966; Savchuk, 1966b, 1968; Zaitsev and Polikarpov, 1967).

Together with the eggs the 0-5 cm layer also contains a high density of larvae and fry of pelagophile fish species (Engraulidae, Mugilidae, Potamomyidae, Carangidae, Mullidae, Callionymidae, Soleidae and others), and also phytophile, lithophile (Kryzhanovskii, 1949) and others fish species (Bellonidae, Exocoetidae, Atherinidae, Labridae, Blennidae,

Ammodytidae, Gobiidae, Balistidae, Syngnathidae and others newly hatched from demersal eggs. It is typical that whereas the concentration of eggs near the surface is dispersed at wave heights of more than 1-2 metres, larvae and fry remain there at wave heights up to 3-4 metres.

The vertical distribution of certain abundant species of fish eggs and larvae near the surface of the Black Sea (by microlayers) can be judged from the indices computed by the author (Table 38). The quantity of these eggs and larvae in the 0-5 cm layer is normally reckoned in ones or twos and tens of specimens per m^3 of water, but in some cases it reaches 200-300 spec./ m^3 and over.

Table 38

The relative number of fish eggs and larvae in the Black Sea according to PNS-5 collections

Вид	2 Микрогоризонт. см			
	5-25	25-45	45-65	65-85
<i>Platichthys flesus luscus</i> , ova	0,36	0,44	0,33	0,22
<i>P. flesus luscus</i> , larvae	0,40	0,27	0,35	0,20
<i>Scophthalmus maeoticus maeoticus</i> , ova	0,29	0,22	0,22	0,02
<i>Engraulis encrasicolus ponticus</i> , ova	0,52	0,36	0,36	0,35
<i>E. encrasicolus ponticus</i> , larvae	0,23	0,10	0,22	0,11
<i>Trachurus mediterraneus ponticus</i> , ova	0,27	0,23	0,17	0,14
<i>T. mediterraneus ponticus</i> , larvae	0,15	0,19	0,23	0,13
Blenniidae g. sp., larvae	0,15	0,03	0,06	0,08

Key: 1. Species; 2. Microlayer.

Epineuston

Thanks to the recently published report by L. Herring (1961) the species composition of the epineustonic water striders can

be regarded as thoroughly studied. The Estonian naturalist I.F. Escholtz (1822), on the basis of his own collections made in the course of a voyage round the world (1815-1818), described the genus Halobates and three species: H. micans, H. sericeus and H. flaviventris. Later papers by various authors began to include descriptions of new representatives of the genus and by the end of the 1950's there were already 40 species (Chopard, 1959). L. Herring reviewed the genus and established the existence of 38 species. Three years later he described yet another species (Herring, 1964). The complete list of oceanic water strider species of the genus Halobates (Herring, 1961, 1964) is given below:

<i>H. micans</i>	Esch-	1822	<i>H. mjobergi</i>	Hale,	1925
<i>H. scholtz,</i>			<i>H. robustus</i>	Barber,	1925
<i>H. sericeus</i>	Esch-	1822	<i>H. marlannarum</i>	Esaki,	1937
<i>H. scholtz,</i>			<i>H. hawaiiensis</i>	Usinger,	1938
<i>H. flaviventris</i>	Esch-	1822	<i>H. katherinae</i>	Herring,	1958
<i>H. scholtz,</i>			<i>H. fijensis</i>	Herring,	1958
<i>H. sobrinus</i>	White,	1883	<i>H. eschscholtzi</i>	Herring,	1961
<i>H. germanus</i>	White,	1883	<i>H. salotae</i>	Herring,	1961
<i>H. princeps</i>	White,	1883	<i>H. kelleni</i>	Herring,	1961
<i>H. proavus</i>	White,	1883	<i>H. browni</i>	Herring,	1961
<i>H. hayanus</i>	White,	1883	<i>H. nereis</i>	Herring,	1961
<i>H. splendens</i>	Willaczi,	1886	<i>H. tethys</i>	Herring,	1961
<i>H. whiteleggei</i>	Skuse,	1891	<i>H. zephyrus</i>	Herring,	1961
<i>H. regalis</i>	Carpenter,	1892	<i>H. darwini</i>	Herring,	1961
<i>H. alluaudi</i>	Bergroth,	1893	<i>H. peronis</i>	Herring,	1961
<i>H. kudrini</i>	Nasanov,	1894	<i>H. calyptus</i>	Herring,	1961
<i>H. sexualis</i>	Distant,	1903	<i>H. bryani</i>	Herring,	1961
<i>H. formidabilis</i>	(Dis-		<i>H. poseidon</i>	Herring,	1961
	tant),	1910	<i>H. galatea</i>	Herring,	1961
<i>H. maculatus</i>	Schadow,	1922	<i>H. panope</i>	Herring,	1961
<i>H. matsumurai</i>	Esaki,	1924	<i>H. tryane</i>	Herring,	1964
<i>H. japonicus</i>	Esaki,	1924			

Owing to their mobility the number of oceanic water striders is very difficult to determine. In the Gulf of Mexico (by visual observations) there was no more than 1 specimen per 100 m² of water surface, but according to A.I. Savilov (1967), in certain parts of the Pacific they occur in large aggregations of several specimens per m² of water surface.

Apart from Halobates, which has conquered literally the entire ocean, the tropical zone contains other insects associated with the surface of the sea. These are representatives of the same family Gerridae - Hermatobates- and of the family Veliidae - Halovelia (Herring, 1961), which are found in lagoons and bays and on coral reefs. It is quite possible, as assumed by Herring, that both these genera, though exclusively halophilous, are associated with near-shore stations.

In mangrove swamps, on tidal flats and rocky shores, many dipteran species found on the sea-surface near the shore are fairly widespread, but their relationship to the epineuston is not quite clear as yet.

In addition to insects the marine epineuston contains the extremely rich and quite unstudied world of lower organisms populating persistent concentrations of foam. Apart from bacteria a sample of foam obtained in the Chernomorka area at the end of April 1967 (water salinity at the surface 5.5 ‰) was found by D.A. Nesterova to contain a very large quantity of diverse small Flagellata, Protococcaceae (Ankistrodesmus), Cyanophyceae (Microcystis aeruginosa) and diatom valves. In another sample taken at the same place and time O.I. Morozovskaya discovered a similar abundance of Infusoria of the orders Holotricha (Holophrya simplex Shewiakoff, Paramaecium aurelia Müller and others) and Heterotricha, some representatives of Sarcodina, Volvocidae and fungi.

In another sample of foam collected in the same region on the 5th of May 1967, while the water salinity at the surface was

10°/oo, blooming of Chlorella sp. began two weeks after collection and continued into 1968.

At the present time the Hyponeuston Division is busy studying the creatures inhabiting sea foam, which plays an important part in the life of the nearsurface biotope of the pelagic zone.

Phytoneuston

The terms "phytoneuston" and "zooneuston" were introduced a long time ago by Naumann (1917), since both plant and animal organisms take equal part in the formation of neuston. In the sea it is a different matter. In salt water there are no Euglena, Chlamydomonas, Chromulina or other numerous representatives of the freshwater phytoplankton. However, it has already been established that many prolific forms of marine phytoplankton (among diatoms, peridinians and cyanophyceans) are not distinguished by high abundance beneath the surface tension film when alive (Nesterova, 1968, 1969). It may be, as indicated by Nesterova, that there is a sudden proliferation of small flagellates such as Carteria in the 0-2 cm layer, but this problem requires further study. Of interest in this regard are certain Dinoflagellata which withstand high insolation and are capable of abundant development. /118/

Thus, on June 27th, 1965, on Campeche Bank 20 miles north of the Yucatan peninsula in the Gulf of Mexico, abundant development of Gymnodinium brevis was noted - one of the main causes of the "red tide" ("marea roja") in that region.

Carmine-red patches, spread by the wind, in some places covered over half the visible surface of the sea. Samples revealed that the layer of coloured water was no more than a few centimetres deep and that below this the water was of the blue-green colour usual for marine shallows.

However, while the role of microphytes in the formation of the marine neuston still requires elucidation, that of macrophytes is firmly established. The macrophytes in question are the Sargasso algae (Sargassum natans (L.) and S. fluitans Borgensen), the hyponeustonic character of which has been demonstrated experimentally and by observations at sea (see Ch. XI).

The benthic sargassos, in particular S. filipendula Agardh, S. polyceratum Montagne, S. platycarpum Montagne, also float up to the surface, when separated from their substratum, but they have a much greater specific weight and accordingly a smaller reserve of positive buoyancy. This is confirmed by the mineral content in the thallus. Thus, for example, S. natans contains 17.02% ash (converted to dry weight), S. polyceratum 23.15% (Diaz-Piferrer, 1958). According to the same author, Ulva fasci- contains 34.48% ash and Enteromorpha lingulata 39.5%. Hence, the low mineralization of the thallus in conjunction with the well-developed air bladders determines the high buoyancy of the hyponeustonic sargassos, which, forming the unique Sargasso Sea, become the dominant forms in a special biocenosis containing both hyponeustonic animals and some representatives of other classes of communities.

In the remaining parts of the world ocean there are no such vast accumulations of sargassos, but the floating algae of this family occur throughout the tropical and subtropical regions (Pérès, 1961) and we can therefore say that the Sargassaceae are of great importance in the life of the nearsurface layer of the pelagic zone and, in particular, that they influence the evolution of a number of hyponeustonic animals (cf Ch. XIV).

A quantitative estimate of the hyponeustonic sargassos can be given only for the Sargasso Sea, the area and algal stocks of which have been determined by some authors. According to L.A. Zenkevich (1956), the area of the Sargasso Sea exceeds 8,500,000 km², and the total volume of floating sargassos comprises 15-20,000,000 tonnes wet weight. J.M. Pérès (1961) gives an area of 4,400,000 km² and stocks of 4-11,000,000 tonnes. Per unit of sea surface the figures of both researchers work out at about the same, being 1.8-2.35 g/m² for Zenkevich and 0.9-2.5 g/m² for Pérès. These are averaged values and in fact the sargassos are distributed unevenly, forming more or less compact masses separated by intervals of clear water. Their distribution is greatly influenced by wind currents. When the wind is strong the ochre-yellow strips of algae stand out clearly against the blue of the sea in regions of converging currents. /119/

According to the calculations of the author, the densest concentrations of S. natans, as observed on windy days in the Florida Strait, comprise 1.5-2.5 kg beneath 1 m² of sea-surface.

Chapter XIII. Circadian rhythms of the neuston

The composition and numbers of the neuston are greatly influenced by the appearance in the 0-5 cm layer, and departure from it, of the nocturnal components of the near-surface assemblage of organisms, i.e. the benthohyponeuston and the bathyplanktohyponeuston. The significance of the diurnal, or rather circadian (Halberg, 1959, cited by Ashoff, 1964), rhythms of such widely distributed and abundant organisms goes beyonds the bounds of neustonology, being of considerable interest from the viewpoint of radioecology, problems associated with "biological clocks" (Byunning, 1964), the important new branch of biology known as biorhythmology, and other spheres of knowledge.

The examples cited below give a complete picture of the circadian rhythms of neuston in shallow water and over great depths.

The shelf zone is the benthohyponeuston region, where a great number of large invertebrates complete circadian vertical migrations between the extremes of the benthonic and hyponeustonic biotopes.

The studies made by V.P. Zakutskii (1963-1969) in the Black Sea and Sea of Azov proved that the circadian rhythms of the benthohyponeuston continue all year, including the winter months. Furthermore, the winter months are marked by exceptionally high mobility and predation of isopods, abundant cases of copulation by gammarids, and other signs indicative of the year-round activity of benthohyponeustonic crustaceans.

Change in the length of the light day alters the time spent by the benthohyponeustonic organisms in each of the biotopes (Table 39). The biomass of benthohyponeuston in the

Table 39

Time of appearance in the hyponeuston layer and departure for the benthal zone of benthohyponeustonic organisms in the cold part of the year in the northwestern part of the Black Sea (according to data of V.P. Zakutskii)

1. Месяц	Часы 6 появления	Часы 7 ухода
2. Декабрь	17*	9
3. Январь	18	8
4. Февраль	19	7
5. Март	20	7

Key: 1. month; 2. December; 3. January; 4. February; 5. March; 6. time of appearance (in hours); 7. time of departure (in hours).

0-5 cm layer during these months, even in conditions of the lowest water temperature near the shore over depths of 2-3 m, reaches 2000 mg/m³ and more. The density of the abundant benthohyponeustonic representative Gammarus locusta varies hourly in winter (Fig.36). During the warm part of the year the cir-

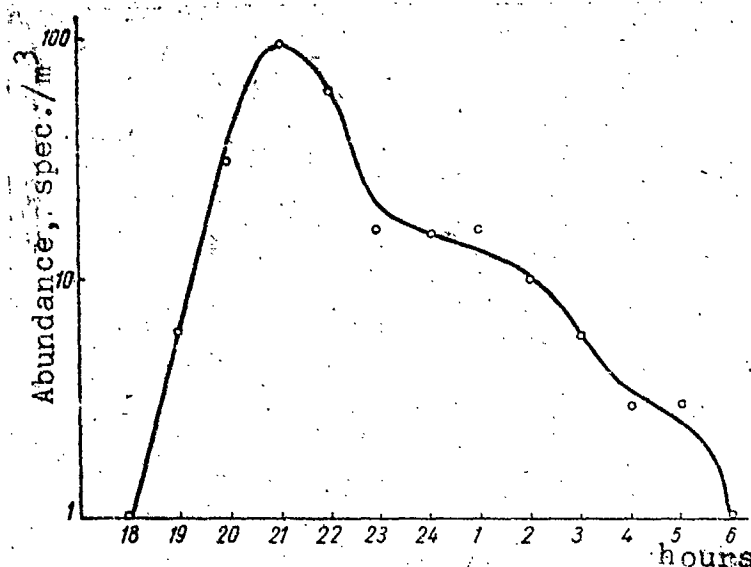


Fig. 36 - Abundance of benthohyponeustonic species Gammarus locusta in the Chernomorka area on the night of the 24-25th of February 1967. Water temperature at the surface ranged from -0.8 to -0.1°C (according to data of V.P. Zakutskii).

cadian dynamics of the benthohyponeuston remain constant (Figs. 37 and 38).

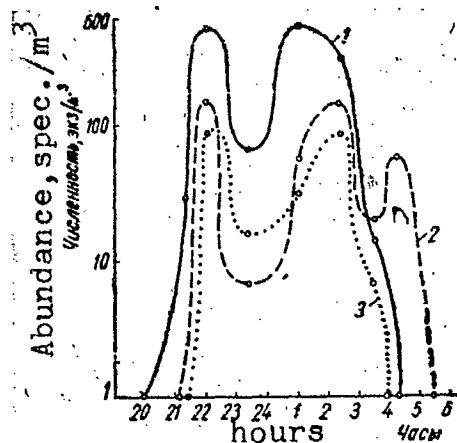


Fig. 37 - Abundance of benthohyponeustonic isopods and mysids near the surface of the Black Sea in the vicinity of the Caucasian coast on the night of the 1st - 2nd of August 1965. Water temperature at the surface 26°C (according to data of V.P. Zakutskii): 1. 0-5 cm layer; 2. 5-25 cm layer; 3. 25-45 cm layer.

The examples cited show that after the sun sets in winter and summer benthic and near-bottom organisms make a concerted ascent to the surface, where they form a distinct density maximum in the 0-5 cm layer. During the night fluctuations occur in the density of immigrants in the hyponeuston /121 biotope, the causes of which have been insufficiently explored as yet, and at dawn they all depart for the benthal zone.

The circadian migrations of benthohyponeustonic organisms bringing to the 0-5 cm layer new generations of eggs and larvae, and on their bodies microorganisms and surface-active substances and food items removed from the nearsurface biotope, play an important role in the life of the neuston and its links with other classes of marine communities.

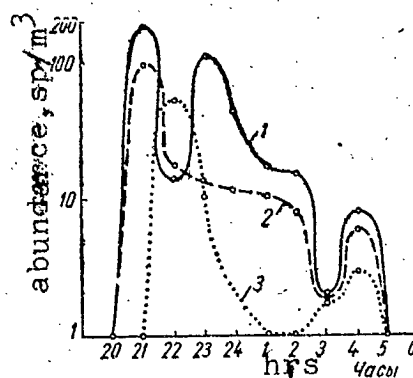


Fig. 38 - Abundance of benthohyponeustonic mysids Mesopodopsis slaberi near the surface in Kazantipskii Bay in the Sea of Azov during the night of 10-11 th of August 1965. Water temperature at surface 24° (from data of V.P. Zakutskii). Legend the same as in Fig. 37.

The circadian rhythms of the bathyplanktohyponeuston were studied by S.M. Chebanov (1963, 1965) and Zaitsev (1964a) on the hyperiids Parathemisto japonica and Calanus tonsus from the northwestern part of the Pacific and the adjacent regions of the Bering Sea.

In the southern part of the Bering Sea, at a point with the coordinates $55^{\circ}45'$ northern latitude and $176^{\circ}35'$ eastern longitude, over a depth of some 3500 metres (station 25) and in waves up to 0.5 m high, samples were taken with a PNS-2 net on July 7-8th at the following times: 17.00 hrs, 19.20 hrs, 22.30 hrs, 04.00 hrs, 0.200 hrs, 07.10 hrs and 10.00hrs. The number of organisms discovered in the 0-5 cm and 5-25 cm layers at various times are shown in Fig. 39.

At 19.00 hrs, when the sun had only just dipped below the horizon, the 0-5 cm layer contained 100 hyperiids per m^3 and the 5-25 cm layer 28. At this time Calanus was represented by a few specimens. At 09.30 hrs the abundance of hyperiids rose sharply

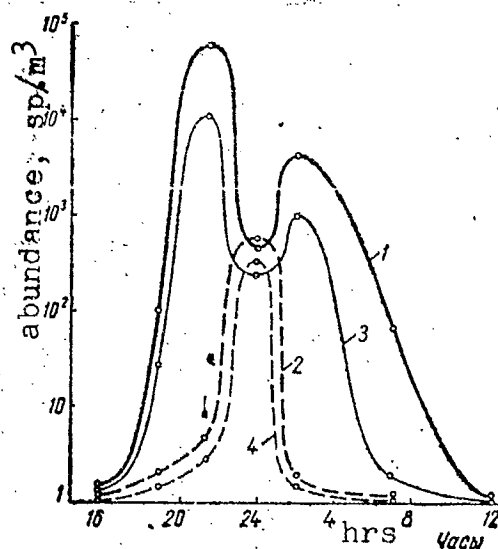


Fig. 39 - Abundance of bathyplanktonic species Parathemisto japonica (1, 3) and Calanus tonsus (2, 4) near the surface of the Bering Sea (station 25) on July 7-8th 1962 (Chebanov, 1965 with additions): 1, 2 - 0-5 cm layer; 3, 4 - 5-25 cm layer.

to 58,200 in the first layer and 10,200 in the second. The number of specimens of Calanus did not exceed 10 per cm^3 . At midnight (24.00 hrs) the number of hyperiids fell to 473 and 245, while the quantity of Calanus rose to 600 per m^3 in the first layer and 380 in the second. At 02.10 hrs comes the second peak in the density of hyperiids - 4001 in the first layer and 1120 in the second, and again only one or two specimens of Calanus. Finally, at 07.00 hrs there were 65 hyperiids specimens per m^3 in the 0-5 cm layer, one entomostracan in the 5-25 cm layer, and no Calanus at all.

Subsequent hauls made in the daytime revealed that these two species are hardly ever encountered near the surface. Sometimes the nets brought in several (less than a dozen) ento-

mostracans, but, according to the observations of S.M. Chebanov (1965), unlike the ones brought up at night they showed no signs of life. Only on one day, when the sky became overcast and the light was dim, were hyperiids caught all day.

As far as can be judged from the results of stomach analyses of more than 150 hyperiids (station 25), their food consisted mainly of copepods, among which could clearly be distinguished the remains of Calanus tonsus (adult individuals and chiefly the fifth copepodite stage), and also other smaller copepods. Each stomach contained up to 2-3 dozen entomostracans. /123/

Of the hyperiids captured at 22.30 hrs, 80% had full stomachs. At 24.00 hrs the number was no more than 25%, while the degree of digestion was high. At 02.00 hrs the number of hyperiids with full stomachs was 74%, and the food was freshly swallowed. At 07.10 hrs 50% of the hyperiid stomachs opened up contained well-digested clanoid remains.

Thus, two nocturnal peaks in the density of hyperiids in the hyponeuston correspond to two peaks in the feeding of these predatory amphipods. It is quite probable that the hyperiids pursue the ascending Calanus, actively devouring it as they go. It may be that this is why adult Calanus do not concentrate in the hyponeuston layer where the bulk of the hyperiids hold sway. Only in the middle of the night, when the hyperiids temporarily leave the surface, does Calanus ascend, only to disappear once more when the second hyperiid maximum occurs.

This rhythmic process of alternation between hyperiids and

calanoids near the surface was observed throughout the entire period of collection of hyponeuston - from June through September. There was merely a time shift in the peaks due to variation in the length of the day and night, as in the case of the benthohyponeuston in the Black Sea.

At lengthy station 11, taken on August 2nd-3rd 1962 in the northwestern part of the Pacific at a point with the coordinates $47^{\circ}47'$ northern latitude and $156^{\circ}23'$ eastern longitude, over a depth of some 5500 metres, the picture was as follows (Fig. 40). At the same ratios of organisms in the first and second layers, the evening maximum of the hyperiids occurred at 21.30 hrs, and the morning one at 05.40 hrs. It may be that the widening of the gap between the two hyperiid peaks and their lower absolute abundance at this point created conditions for a stronger migration of calanoids to the 0-5 cm layer, whereas at the beginning of July, when the peaks and the quantitative ratios between predator and prey were very close, such conditions did not exist.

In the middle of August the first hyperiid maximum comes earlier, and the second later. For instance, at station 34 (August 14-15th) the evening maximum of the hyperiids was observed to occur at 24.00 hrs, and the morning maximum at 06.00 hrs.

S.M. Chebanov notes that at the same time as the neuston collections were being made on the ship experimental catches of salmon were being taken with the aid of gill nets. This revealed that the salmon, when feeding chiefly on hyperiids in the morning and evening (the stomachs of chum and pink salmon were

filled exclusively with hyperiids), concentrate directly beneath the surface and become gilled near the top line of the net. When the nets were visited at dusk, Chebanov indicates, immediately after they had been set, the gleam of salmon could be seen near the top line. From this it was concluded that salmon nets should be set and hauled in during the daylight hours and not late at night as was the usual practice, and that the top line and net webbing must be placed right near the surface of the water. /124/

Thus, the concentration of bathyplanktohyponeustonic organisms in the nearsurface biotope, like the concentration of benthohyponeustonic organisms, brings about substantial changes not only in the life of the neuston but also in a considerable area of the pelagic zone. Even representatives of Scopeliformes, such as Gonichthys tenuiculus (Garm.) (Myctophidae), which keep to considerable depth during the day, rise into the nearsurface biotope at night and feed there on the neustonic organisms Pontellidae, Janthinae and Halobates (Parin, 1968).

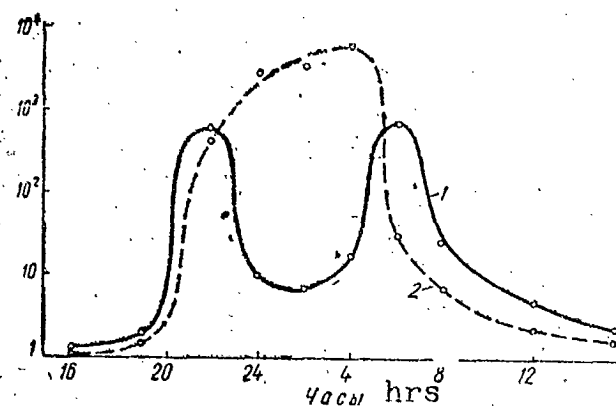


Fig. 40 - Abundance of bathyplanktohyponeuston of species Parathemisto japonica (1) and Calanus tonsus (2) in the 0-5 cm layer in the northwestern part of the Pacific (station II) on August 2nd-3rd 1962 (Chebanov, 1965).

The examples examined, and indeed everything that has been said concerning this point in the preceding chapters, in the first place confirm the well-known truth that many organisms in the epipelagic zone make circadian vertical migrations. In the second place they show that many bottom-dwellers lead a similar mode of life, and thirdly they substantially clarify former ideas on the upper limit of the migrations and abundance of the migrants. The data of neustonology show that the target of the migrants' ascent is the 0-5 cm layer and that they form far higher concentrations there than in the main mass of water. From this it follows that the benthohyponeuston and bathyplanktohyponeuston distributed all over the water-area of the ocean play an important part in the life of the neuston. In addition, the circadian fluctuations of a vast mass of organisms between the surface and the bottom and between the surface and the deep

layers of the pelagic zone, which represent one of the manifestations of the ecological processes (Zaitsev and Polikarpov, 1967a), are a strong factor in the cycle of substances in the halosphere and merit further and comprehensive study.

Chapter XIV. The ecology of neustonic organisms

Although the very fact of the existence of neuston in fresh waters proved that it was possible in principle for rich life to develop in the region of the surface tension film, the data of biological oceanography failed to confirm this. Far more results of different experiments and observations indicated the unsuitability and even danger of the nearsurface biotone of the pelagic zone for inhabitation by hydrobionts. The usual reason given was the sunlight, less often waves, and sometimes temperature and other factors.

R. Bertel (1912) wrote long ago that the number of bacteria in the Mediterranean in the vicinity of Monaco increases with depth and that near the surface they are killed or inhibited by bright sunlight. At night, however, this deficiency is remedied. P. Welch (1935) confirmed the lethal effect of sunlight on bacteria, but as ultraviolet rays are soon absorbed by water their destructive effect is very restricted. Around the same time experiments off the coast of California confirmed that the lethal effect of sunlight is observed on bacteria suspended in sea water down to a depth of 20 cm (Zobell and McEwen, 1935). Summing up the factual data Zobell (1946) came to the conclusion that the intensity of ultraviolet radiation lethal for bacteria is reduced almost by half after passing through a layer of sea

water only 10 cm thick. Zobell also showed that the lethal effect of ultraviolet rays diminishes exponentially to the reduction in the intensity of the light. Thus, if the intensity of the sunlight is sufficient to kill a bacterium near the surface in ten seconds, it will take 100 seconds at a depth of 40 cm and 1000 seconds at 70 cm.

Experts came to the same conclusion with respect to other groups of organisms, especially phytoplankton.

The conclusion that ultraviolet rays harm or kill phytoplankton, especially diatoms (Whipple, 1927; Friedrich, 1961), fits in with the fact that the latter react to strong sunlight /126/ on the systrophe (Moore, 1958) and that when the sun shines brightly photosynthesis is inhibited near the surface (Harvey, 1955). Therefore the region of maximum photosynthesis of the marine phytoplankton is situated not at the surface but in the pelagic zone, and the further the sunlight penetrates into the water the deeper this region is (Steeman, 1954). Thus, in the Black Sea the maximum photosynthetic activity of the microphytes corresponds to a depth of 5-20 metres (Sorokin, 1962). For the tropical zone the figure is roughly 10 m (Steeman Nielsen, 1952), and for the limpid Sargasso Sea 80 m. (Clarke, 1936).

Experimental investigations showed that animal organisms suffer like plants from bright sunlight and ultraviolet rays. In bright light the respiration of *Mysis* is strongly disturbed (Merker, 1926), while in *Calanus finmarchicus* the heartbeat rate is almost halved (Harvey, 1929) and the respiration rate

increases (Marshall, Nicholls and Orr, 1935). It is obvious then that Calanus exhibits negative phototaxis and inhabits the deep layers of water during daytime, like many other species of hydrobionts (Russel, 1925, 1928).

Ultraviolet radiation has a very strong effect on the animal population of the sea, killing crustaceans and fish fry (Klugh, 1929, 1930). For instance, eel larvae are killed by short-wave solar radiation within 18-24 hours, and amphipods within 2-4 days. Ultraviolet rays are particularly harmful to deepwater animals, which rise to the surface only at night (Klugh, 1930). It is no accident that of the species of zooplankton populating the upper 300 metres of water in the region of the Bermuda islands, 75% spend sunny days at depths of more than 80 m, and 50% at depths below 100 m. (Moore, 1949).

On the strength of her experiments and observations A.S. Leshchinskaya (1954) came to the conclusion that solar radiation has a lethal effect on the developing eggs of Azov anchovies, and R.M. Pavlovskaya (1955) confirmed this on the Black Sea anchovy.

This absolute wealth of facts, most of which were irrefutable, created a very definite view of conditions of life at the surface of the sea which was expressed categorically in the pages of many reports, monographs and manuals.

Thus, in "Marine Ecology" by Moore (1958) the author speaks of the "actinic damage" which short-wave solar radiation inflicts in the population of the nearsurface ("the extreme surface") layer of the sea. This layer is generally viewed as some kind

of filter which, at the cost of the destruction of its inhabitants, protects the population of the rest of the pelagic zone from the sun. S.N. Skadovskii notes that "the most harmful ultraviolet rays are absorbed strongly. Water containing organic substances and the metabolic products of aquatic organisms is an excellent screen protecting the aquatic population from the destructive effects of ultraviolet rays" (Skadovskii, 1955, pp 189-190). In his book "La vie pélagique" J.-M. Pérès (1963, pp 11-12) states in this connection that until quite recently some ecologists ascribed the relative paucity of life near the surface to the lethal action of ultraviolet rays. However, measurements showed that 50% of the most dangerous rays with a wavelength of 210-296 millimicrons (particularly 250-280 millimicrons) are absorbed in passing through 10 cm of water, so that below 1 m their effect must be zero.

Thus, directly or indirectly the surface of the sea came to be likened to some sort of desert where life had literally been "burned up" by the sun. The bright blue of the water was the colour of "oceanic deserts" impoverished in life (Berezina, 1963). And the fact that neuston - the richest assemblage of organisms in the pelagic zone - was discovered there seemed at first to be a paradox. However, confirmation of this fact at different taxonomic levels in various regions of the ocean, backed by the data of allied sciences, compelled scientists to recognize it as a reality and reassesses the possibility of development of rich life at the sea-air interface in the light

of this new discovery. In the course of this reappraisal new or little-known facts were brought to light, e.g.:

a) in addition to the bacteria which avoid strong sunlight, the sea contains others which are not inhibited by it;

b) although strong sunlight inhibits photosynthesis, the highest biomass of pelagic algae in the ocean grows near the surface of what is acknowledged to be the most impoverished sea - the Sargasso Sea;

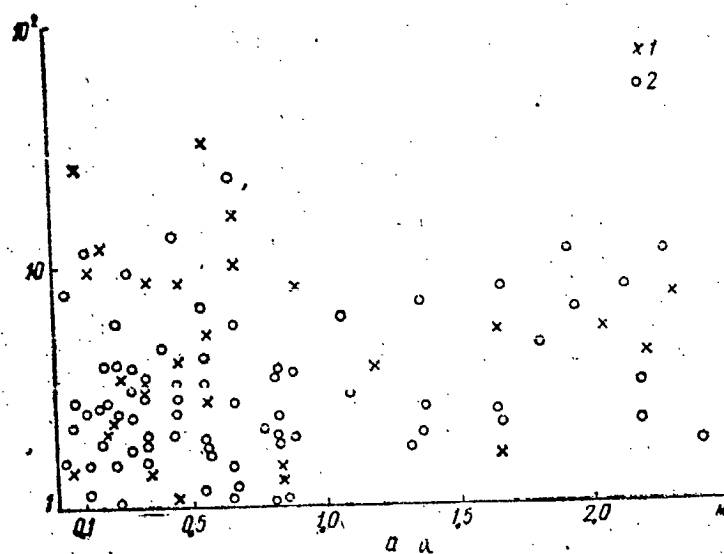
c) regardless of the fact that ultraviolet radiation from the sun is injurious to many planktonic animals, there are a large number of species which live all the year round under the surface tension film.

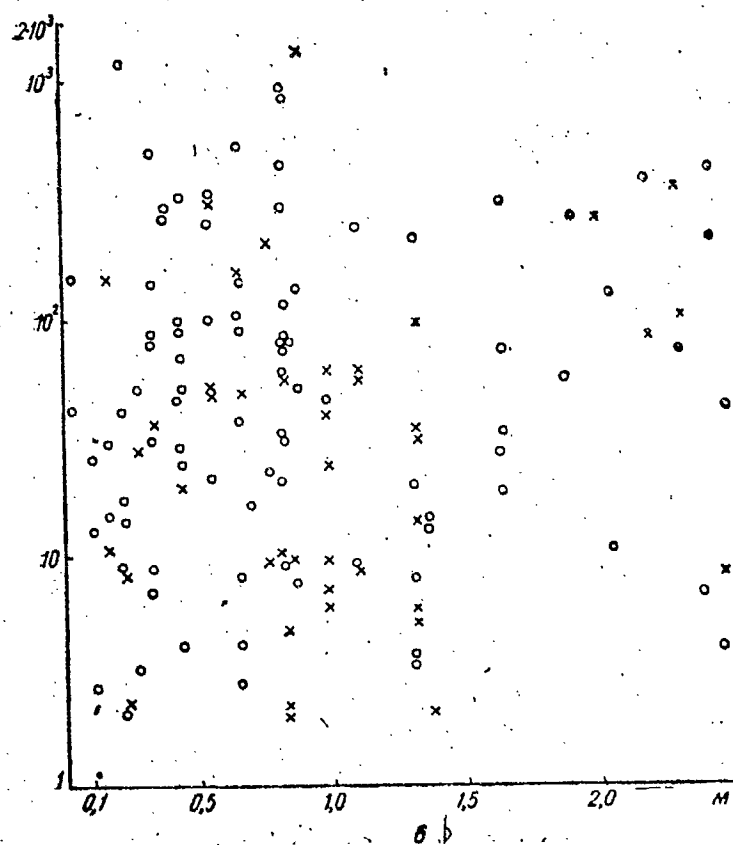
Adaptations enabling neustonts to maintain their position in the region of the surface tension film

The danger presented by waves to the position of neuston near the surface is usually exaggerated a priori. Collections made over many years with plankton-neuston nets reveal that at wave heights of up to 2.5 m the masses of organisms remain in the 0-5 cm layer and maintain a high population density compared with the underlying layer.

To express in quantitative terms the relationship between the density of organisms in the 0-5 cm layer and the wave height we took the ratio of the number of specimens of a particular species in the first tier of the plankton-neuston net (0-5 cm layer) to the number of specimens of the same species in the second tier of the net (5-25 cm layer). If the

vertical distribution of organisms near the surface is even, the number of specimens in the first and second tiers per unit volume of water will be equal and their ratio will be equal to 1. When the distribution is uneven and most of the organisms are concentrated in the 0-5 cm layer the ratio will be greater than 1. The impression is created that in the presence of ^{waves} the difference between the densities of organisms in the first and second tiers will be obliterated, and their ratio will tend to unity. The graphs which have been plotted do not confirm this (Fig. 41 a,b,c).





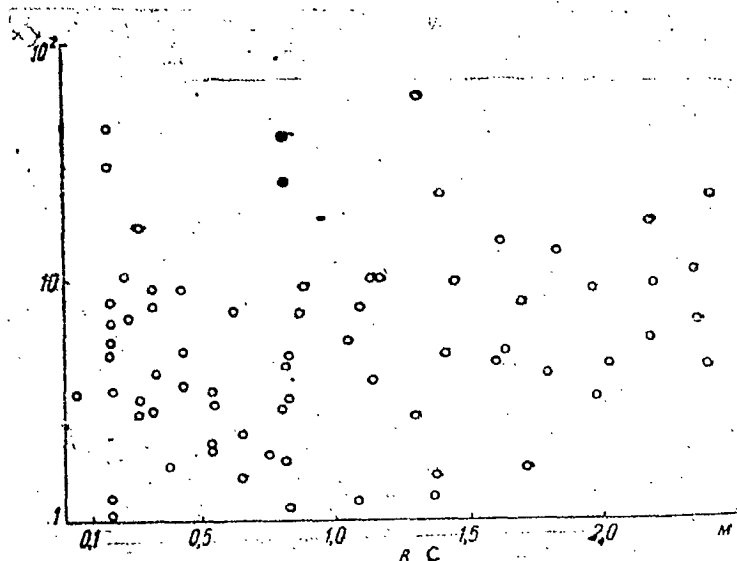


Fig. 41 - Relative abundance (ratio of number of individuals in equal volumes of water in the 0-5 and 5-25 cm layers) and the wave height (m):

a) passive neustonts: 1-eggs of Engraulis encrasicolus ponticus, 2- eggs of Trachurus mediterraneus ponticus; b) active neustonts-invertebrates; c) active neustonts - larvae of E. encrasicolus ponticus. The graphs indicate the absence of any relationship between the values in question.

Hyponeuston representatives of differing motility (from the passive anchovy larvae to the rapidly moving pontellids) do not show any clear tendency to disperse and leave the 0-5 cm layer in sea states of up to 5-6. Since such conditions on the surface can last for a long time, and even permanently in terms of the lifespan of many hydrobionts and certain of their developmental stages, we can conclude that as a rule the organisms of the marine neuston live in the region of the surface tension film. Strong waves may temporarily submerge them to a certain depth, and in the extreme case even destroy them (as for example fish eggs), but after they have died down to

the particular critical level characteristic of each species of organisms the waves no longer prevent their return to their former layer. This constant striving by neustonts to maintain their position in the region of the surface tension film is aided by a number of special adaptations.

In a number of cases the surface position of the organisms is determined by Archimedes principle - the reserve of positive buoyancy in the body. This reserve is acquired in a number of different ways. Two of the most common of these in hydrobionts are the maintenance of a high water content in the body and the presence of oil inclusions. Highly buoyant fish eggs are an illustration of this. Eggs of Scorpaena scorpus ready for fertilization contain 97.85% moisture and those of Mullus barbatus ponticus 94.69% (Vinogradskaya, 1954). The average volume of the oil drop in Black Sea fish species, fulfilling the function not only of a food reserve but also of a hydrostatic device, comprises, according to our data (Zaitsev, 1960a), the following percentages of the volume of the entire egg:

<u>Scophthalmus maeoticus maeoticus</u>	0.36
<u>Gaidropsarus mediterraneus</u>	0.83
<u>Mullus barbatus ponticus</u>	1.76
<u>Trachurus mediterraneus ponticus</u>	2.33
<u>Mugil cephalus</u>	6.10
<u>M. saliens</u>	7.00
<u>M. auratus</u>	7.05

The high moisture content and the presence of oil mean that the egg has a low specific gravity and a large reserve of positive buoyancy. The specific gravity of the eggs of such Black Sea fishes as Engraulis encrasicolus ponticus, Callionymus belenus, Soles lascaris nasuta, Eugil cerhalus, M. saliens, M. auratus, Mullus barbatus ponticus, Trachurus mediterraneus ponticus, Pomatomus saltatrix, Sarda sarda and others ranges from 1.007 to 1.010 at the beginning of development and 1.008 to 1.001 before the emergence of the prolarvae. As a result of this the bulk of the eggs of the above species in water of density normal for the Black Sea, comprising 1.0109 - 1.0109 at the surface on average for August (the month with the minimum density value) (Leonov, 1960), press against the surface tension film and, as it were, "dangle" from it. As the embryo develops the specific gravity of the egg increases, but not to the extent that the egg becomes detached from the film. This detachment will occur only as the result of turbulent mixing processes or of a substantial increase in specific gravity (due, for example, to a change in permeability of the integuments), in which case the further development of the embryo, if indeed it does continue to develop, takes place in conditions considerably different from those at the surface. /131/

The buoyancy reserve of the eggs of many species of fishes in other marine basins is of the same order of magnitude as in the Black Sea, and this explains why they are concentrated in the 0-5 cm layer. Thus, the specific gravity of the fish larvae

found in hyponeuston collections made in the Gulf of Mexico is 1.019-1.022, whereas the density of the water at the surface in that region fluctuates between 1.023 and 1.025 in the summer months.

Whereas fish eggs, which have no organs of active movement, represent a biological model of a hydrostat, Noctiluca miliaris, which also has a globular body with a diameter close to that of the egg, has flagella and is able to alter its position hydrodynamically. However, in this case too hydrostatic adaptations remain important: the protoplasm of Noctiluca contains drops of oil and the cellfluid contains substances of low specific gravity (Denton, 1963).

Interesting adaptations for maintenance of position in the 0-5 cm layer were recently discovered and studied by A.K. Vinogradov (1969) in fish prolarvae. Using the buoyancy of the yolk-sac and the oil drop, and also the external structural features of the body, hyponeustonic prolarvae maintain their position in the nearsurface biotope by hydrostatic and hydrodynamic means.

An effective means of acquiring high buoyancy are the gaseous inclusions in the bodies of hydrobionts. Such adaptations are common among neustonic organisms. According to the data of A.K. Vinogradov, almost all fish larvae developing in the hyponeuston possess a buoyancy bladder, even though they sometimes lose it on reaching adulthood. A complex system of air cells permeates the disc of Porpita, which literally hangs from the surface tension film and may retain the same

position for several years in a solution of formalin (Fig. 42). Air bladders ensure that sargassos maintain their position in the hyponeuston (Fig. 43). Gas bubbles are also to be found in the cavity of the gut in nudibranchs of the genus Glaucus.

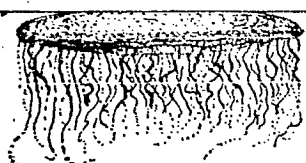


Fig. 42 - The position of Porpita beneath the surface tension film.

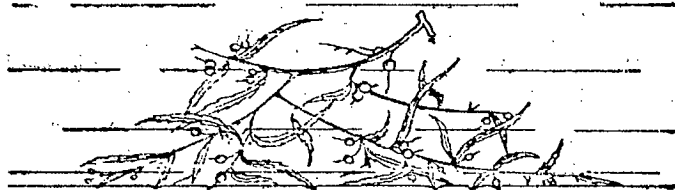


Fig. 43 - Air bladders supporting the thallus of Sargassum natans in the hyponeustonic position.

Some tropical sea anemones anchor themselves to the sur- /132/
face tension film with the aid of a float situated in the
centre of the foot, consisting of gas bubbles enclosed in
an elastic membrane (David, 1965b). Prosobranchs of the genus
Janthina build themselves a special raft consisting of a
mucous mass filled with air bubbles. The raft is put
together at the rate of one bubble per minute (Denton, 1964)

and may have an elongated, rounded or spiral form (Fig. 44).

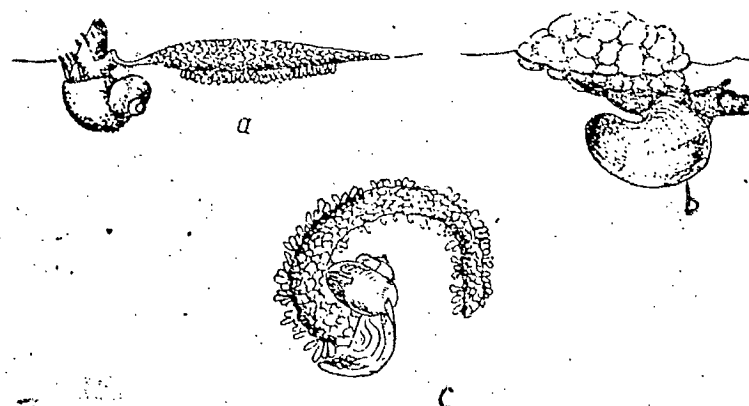


Fig. 44 - Different forms of the raft of Janthina: a- elongated (Trégouboff et Rose, 1957); b- rounded (David, 1965b), c - spiral (viewed from above) (Lindquist, 1965).

Another mollusk-Hydrobia ulva - gives itself a hyponeustonic position in which, unlike Glaucus and Janthina, it stays not permanently but temporarily, with the aid of a raft made of mucus (Fig. 45). This raft also serves Hydrobia as a means of catching food (Newell, 1962). Another species of Hydrobia - H. totteni (H. minuta) - (Davis, 1966) anchors itself to the film in the same way.

Some neustonts in adulthood or various stages of development /13 use extraneous objects floating on the surface of the sea as rafts, and also other animals and plants with a large reserve of buoyancy.

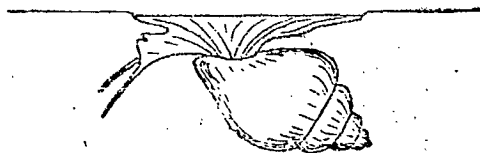


Fig. 45 - Position of Hydrobia ulvae under surface tension film (C.E. Newell and R.C. Newell, 1966).

For example, Halobates attaches its eggs to all kinds of drifting objects. Different scientists have discovered them adhering to pieces of wood, birds feathers, algae and coal, skeletal plates of pneumatophores of Porpita and Velella, the shells of squids and Spirula, patches of fuel oil and even the tail feathers of a live tern Anous stolidus (Herring, 1961; David, 1965b); Savilov, 1967). In 1952, soon after a violent eruption of a volcano near San Benedicto (the Revilla-Hihedo islands in the Pacific) the Skrippsovskii Institute expedition found dozens of floating lumps of pumice with eggs of H. sobrinus (Herring, 1961). In the absence of floating objects, females of the oceanic water striders attach their eggs to the abdomen (Chopard, 1959; Savilov, 1967).

The eggs of Glaucus are deposited straight in the water according to some authors, (David, 1965b), but according to others they are laid on the endoderm lamellae of Velella, which the mollusk eats first (Trégouboff et Rose, 1957; Boshko, Monchenko, 1960). Various floating objects are used

temporarily as floats by hyponeustonic entomostracans, isopods and some decapod larvae, while some forms which are sedentary in adulthood, such as Lepas fascicularis, L. ansifera, L. pectinata, Spirorbis, Membranipora, Diplosoma and others, live on floating objects permanently. There is information to the effect that goose barnacles dwelling on driftwood may build themselves rafts of gas bubbles (David, 1965b).

Highly characteristic of freshwater neustonts is the impermeability of the integuments, which enables these organisms to utilize the energy of the surface tension film of the water. This method of retention in the neuston is more effective in small basins with calm surfaces, and therefore freshwater hyponeustonic forms suspended from the film, such as the air-breathing larvae of the blood-sucking mosquitoes, cannot exist in the open parts of lakes and reservoirs, where waves can wrench them away from the surface. Impermeable integuments are also found in marine neustonts, but in them this feature exists as an auxiliary to the high buoyancy of the body. Thus, the highly buoyant eggs of the Black Sea mullet have an impermeable membrane (Zaitsev, 1964a), thanks to which they are firmly retained by the surface tension film (Fig. 46). This property is preserved by the eggs even when they are fixed with formalin. So far impermeable membranes have not been described for the pelagic eggs of other marine fishes.

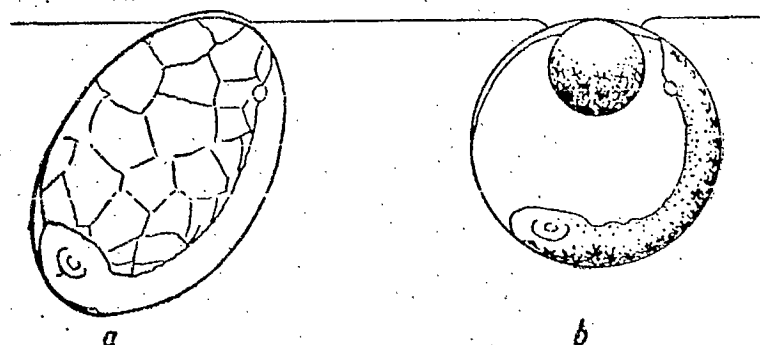


Fig. 46 - Position of hyponeustonic fish eggs near the surface of the sea:
a-anchovy (permeable membrane), b-Black Sea mullets (impermeable membrane).

As shown by visual observations (Zaitsev, 1964a), the impermeable spines of the zoea larvae of decapods serve to attach the animal to the surface film of water (Fig. 47).

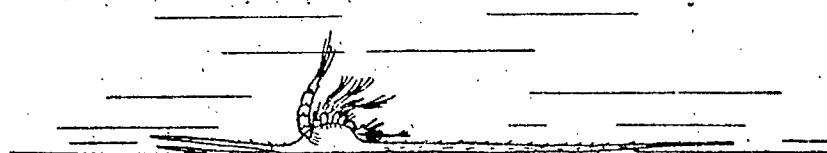


Fig. 47 - The position of metazoea of Pisidia (Porcellana) longicornis under the surface tension film.

The oceanic water striders, like their freshwater cousins, run over the surface of the sea with the aid of impermeable hairs on their legs. Similar hairs cover the body of Halo-
bates, enabling it to take a reserve of air for breathing

when diving below the surface, while at the same time facilitating its return to the epineustonic position.

Interesting adaptations were discovered in the hyponeustonic fry of the Black Sea mullet (Zaitsev, 1964a). The back of fry up to 15-20 mm in length, in the region of the fins, is impermeable and an air sac forms there when the fish moves (Fig. 48). In calm weather schools of striped mullet, grey mullet and golden grey mullet fry look from above like clusters of silver air bubbles against the blue background of the sea. These adaptations facilitate migration of the fry /135/

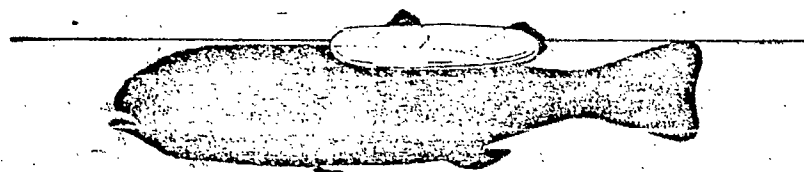


Fig. 48 - Position of the air bladder on the dorsal side of the body of the hyponeustonic Black Sea mullet fry (Zaitsev, 1964a).

from the central parts of the Black Sea where they hatch out to the near-shore shallows where they feed. In addition these bladders fulfil a protective function. Air bladders are also borne on their backs by the fry of Mugil vaigiensis in the Pacific and fry of Atherina in the Panama Canal region (Randall and Randall, 1960). It is possible that they will prove to be a common feature of the fry of all fishes of the order Mugiliformes.

Yet another path leading to the neuston is the transportation of eggs and larvae to the nearsurface layer by egg-bearing females. Thus, the pelagic shrimp Lucifer, bearing developing eggs, rises to the surface when it is time for the larvae to hatch out and the nauplii emerge in the hyponeustonic layer, where they later develop (Woodmansee, 1966).

The females of Sagitta setosa, as was revealed by round-the-clock observations in the Villefranche area of the Mediterranean, deposit their floating eggs before dawn, when in the hyponeuston (Dallot, 1967).

Although the mechanism of the buoyancy of marine neustons has not been sufficiently studied yet, the examples given show that in nature many effective methods exist by which organisms conquer the sea-air interface. Animals and plants in the process of evolution mastered them and became components of the hyponeuston or epineuston, occupying that very region of the pelagic zone where solar radiation was previously regarded as the main danger to life. What is their relationship to this highly important ecological factor?

Adaptations of neustons to solar radiation

The large number of organisms staying continuously in the marine neuston shows that actinic radiation and other perils associated with intensive solar radiation do not on the whole prevent strong development of life at the sea-air interface. It is far more difficult on the basis of our

present knowledge of the neuston to explain the paths and mechanisms of this adaptation, but certain aspects of the problem /136 have already been discussed, particularly in connection with the ichthyoneuston.

According to A.S. Leshchinskaya (1954), whose findings were supported by R.M. Pavlovskaya (1955), the effect of intense solar radiation on the eggs of Azov and Black Sea subspecies of anchovy is lethal. In essence this conclusion confirms that the evolution of the anchovy as a pelagophile species followed a biologically unsuitable path. In giving its eggs high buoyancy and propelling them to the surface into the most strongly lit region of the pelagic zone, the species actually hastens its demise. Since natural selection does not usually permit such serious "miscalculations", and the anchovy, in spite of the buoyancy of the eggs, is one of the most flourishing fish species in the Ponto-Azov (an intensive fishery), Leshchinskaya's findings required additional verification. Accordingly, a series of experiments was conducted (Zaitsev, 1959b, 1964a), using a special device preventing overheating of the water in a vessel exposed to the sun (cf Ch. VIII). It was found that the highly buoyant eggs of Black Sea fishes (anchovy, surmullet, horse-mackerel and sole) develop with equal facility under the direct rays of the sun and in the dark (Table 40). E.A. Pora et alia (1959) came simultaneously to the same conclusion in relation to the eggs of horse-mackerel, and N.I. Revina (1961) also confirmed this in the case of large horse-mackerel.

Table 40

Hatching of normal prolarvae of Black Sea fishes (in %) from eggs developing under direct solar radiation and in the shade (Zaitsev, 1959b).

Условия развития 1	Хамса 4	Барабуля 5	Ставрида 6	Морской язык 7
На свету 2	64—100	69—93	71—96	82—100
В тени 3	67—100	59—96	70—94	82—98

Key: 1 - conditions of development; 2- in light; 3- in shade; 4- anchovy; 5 - surmullet; 6 - horse mackerel; 7 - sole.

From what has been said it follows that eggs developing in the hyponeustonic position are euryphotic. This property is absolutely essential for a hyponeustonic organism that does not make vertical migrations. In the course of their development the eggs experience both periodic (diurnal) and aperiodic (depending on the cloudiness) fluctuation in the intensity of solar radiation. Although, as shown by T.V. Dekhnik (1959, 1961), there is a distinct circadian rhythm to the spawning process, certain embryogenetic stages, particularly the later ones, may occur at different points of the twenty-four hour period, depending on changes in the water temperature and the rate of development. In these conditions only euryphoticity of the embryo and its tolerance to variation /137/ in the intensity of solar radiation can ensure normal development beneath the surface tension film.

To discover the reaction of the embryos of anchovies

to shortwave radiation, eggs were irradiated in an experiment lasting 3-5 hours by a beam of ultraviolet light with an intensity of 365 millimicrons. No visible changes in the course of the development of the embryo or the percentage of prolarvae hatching out were discovered. It is probable that the elevated failure rate of eggs in lighted vessels (from Leshchinskaya's experiments) is due to overheating of the water and the attendant effects (change in the gas regime, pH and so on), whereas these processes occur in a more moderate form in shaded vessels. As regards R.M. Pavlovskaya's discovery (1955) of a slightly lower number of dead anchovy eggs in samples from a depth of 5 metres than in surface samples (on the basis of which it was concluded that the effect of the sun is destructive), it should be borne in mind that collections made with an egg net while the vessel is moving, which causes mechanical damage to the haul, do not provide objective criteria for judging the ratios of live and dead eggs in nature.

It is evident that there are different physico-chemical and physiological bases for the embryo's adaptation to solar radiation. Thus, the defence mechanism against the sun commonly found in nature - pigment - formation - exhibits great variability (judging by ichthyoneuston). For example, anchovy eggs have no pigment whatsoever, and yet this is one of the means of defence against the sun's rays. Like any other glass-like transparent body, anchovy eggs let through the sun's rays with minimal absorption. Very weak development

of pigmentation is characteristic of the hyponeustonic eggs of Ctenolabrus rupestris. According to C. Breder (1962), weak pigmentation or the absence of pigmentation are characteristic of all eggs developing in the upper layers of the sea, and this ensures free passage of solar radiation through the structure of the embryo. This statement is not true in all cases, since intensely pigmented eggs are also found in the hyponeuston, as for example in the case of the Black Sea mullet. In this instance the pigment is obviously able to keep out the sunlight.

An interesting observation was made by I. Sikama (1961), who stated that the oil drop which is always found at the topmost point of the egg suspended in the water, in addition to its hydrostatic and trophic functions, also acts as a converging lens which focuses the incident rays of the sun. The intensity of the beam of light directed at the embryo, according to Sikama, regulates the pigment cells beneath the oil drop, which form a kind of diaphragm. It may be that this is correct, since it has been noted that the /138/ system of melanophores under the drop is particularly well developed in eggs with large oil drops, particularly Black Sea mullet eggs.

In the opinion of T.S. Rass (1937) pigment cells protect the nervous system of embryos and larvae of fish from excessive light and are therefore found in species developing near the surface of the sea, whereas they are absent in those developing in the depths. It is indeed true that the

ichthyoneuston contains more pigmented forms than ichthyoplankton, but there are also contradictory cases such as the already mentioned eggs of the anchovy and tautog on the one hand, and the eggs of haddock and sprats on the other, which, though they develop deep down in summer, are more intensely pigmented than those of the first two species. It has also been established that parts of the diencephalon and mesencephalon (epiphysis and tori longitudinales) in the larvae and adult specimens of anchovy are not covered with pigment at all (Vinnikova, 1965). All this goes to show that among the ichthyoneuston there is no single method of adaptation to the light conditions of the biotope, but various forms of adaptation led to the same result - a capacity for normal development in the 0-5 cm layer.

Invertebrates dwelling in the 0-5 cm layer for twenty-four hours a day behave as pronounced photophils in experimental conditions. For example, while Calanus finmarchicus exhibits a positive reaction to sunlight at a water temperature no higher than 10-13°C, Centropages hamatus preserves this property at temperatures of 25°C and over (Russel, 1928), and moves in the direction of the light source at an average speed of 82 m/sec (Welsh, 1933). It has been noted that females of a number of crustaceans exhibit a more marked tendency to move towards the nearsurface layer than the males.

It has been established experimentally that such abundant inhabitants of the 0-5 cm layer in the Black Sea as the larvae of polychaetes, lamellibranchs and gastropods, nauplii

of Cirripedia and copepods, copepodite stages of Acartia clausi, Oithona minuta, Centropages ponticus, Anomalocera patersoni, adults individuals of A. patersoni, Pontella mediterranea, C. ponticus, O. minuta, O. similis, A. clausi ($\frac{0}{+}$), Podon, Evadne, Idothea stephenseni and others, at a water temperature of up to 28°C exhibit a sharply positive reaction to light and show no apparent preference for the rays of any particular part of the spectrum, including ultraviolet rays of 365 millimicrons (Zautsev, 1962b). In certain cases the experiments lasted up to two weeks and during that time the invertebrates were repeatedly subjected to irradiation by the sun for an hour or more. Adult individuals of A. patersoni, C. ponticus, O. minuta, I. stephenseni manifested a positive reaction every time and did not display any evident changes in behaviour. The larvae behaved differently. Thus, the larvae of the polychaete Microspio mecznicowianus with a length of 1-1.5 mm showed a very active urge to move towards a source of visible and ultraviolet rays. But after a few days (in an experiment lasting many days), when their length had reached 2mm, their attitude towards light underwent a sharp change. The larvae settled on the bottom and, avoiding the light, concentrated in the shaded parts of the vessel. Apparently there is a biological need for photophobia in the transition from larva to the demersal mode of life. /139/

While not giving exhaustive answers to many questions relating to the light preferences of neustonts, these ex-

periments confirm the adaptation of twenty-four-hour dwellers in the 0-5 cm layer to the optical regime of the biotope. There is no doubt that here too an important role is played by the formation of pigment. Thus, in the zoea of Carcinus moenas there is a pronounced diurnal rhythm in the state of the chromatophores which regulate the entry of the sun's rays into the organism (Pautsch, 1961).

It is also typical that far more pigmented invertebrates are encountered in the hyponeuston than in the main water mass: the families Pontellidae and Sapphirinidae, Idothea stephenseni, Portunus portunus, the mollusks Glaucus and Janthina and others - all these are intensely pigmented animals and it may be assumed that in addition to its cryptic significance the rich pigmentation is associated with defence against the sun's rays. P.J. Herring (1956, 1967) assumes that the blue pigment of neustonic crustaceans in tropical waters protects them against solar radiation. This viewpoint is possibly reinforced by the fact that it is the intensely coloured forms which do not make circadian vertical migrations, while the weakly pigmented ones, such as mysids, Calanus and others, appear in the 0-5 cm layer only in the dark hours.

Determination of the ways in which marine bacterioneuston adapts itself to solar radiation is of particular interest, but this is a task for the future. At this stage we can merely affirm that bacteria were able to stimulate a most

powerful burst of development in the very part of the pelagic zone where "bactericidal" solar radiation is present.

This shows once again the exceptional plasticity of micro-organisms and the relativity of the boundaries of action of all sorts of vitacidal factors. Of note is the intense pigmentation of bacterioneustonic colonies observed by A.V. Tsyban' (1967a).

The response of pelagic algae to the solar radiation characteristic of the 0-5 cm layer is apparently negative in most cases. Only the hyponeustonic macrophytes - the sargassos - have adapted themselves well to these conditions. As regards the microphytes, much remains to be explained. The previously noted abundance of diatoms and blue-green algae in the 0-5 cm layer (Zaitsev, 1960 c; 1962, 1968) turned out to be mainly an aggregation of dead and dying cells (Nesterova, 1968).

Various species of microphytes react in different ways to total solar radiation. Thus, whereas for the diatom Biddulphia mobiliensis the optimum light intensity for photosynthesis is 1000 lux, for the green flagellate Carteria it is 3200 lux (Schreiber, 1927). A. Lindquist (1965) points out that green microphytes are able to photosynthesize at a maximum light intensity of 5000-7000 lux, diatoms at 10,000-20,000 lux, and dinoflagellates at 25,000-30,000 lux.

F. Hasle (1950), who conducted round-the-clock observations in Oslo fiord, established that the dinoflagellates Gonyaulax polyedra and Prorocentrum micans ascend towards

the surface by day and descend to the depths at night. The ability of dinoflagellates to move actively towards sunlight has been noted by other authors as well (Pomeroy et al., 1956; Moore, 1958). It is characteristic that it is these microphytes, especially Gonyaulax polvedra, Prorocentrum micans, Gummodinium brevis, and others that participate in the "red tide" phenomenon affecting the uppermost layer of the pelagic zone. Therefore, although it has been established that most abundant species of phytoplankton do not find favourable conditions in for intensive development in the 0-5 cm layer, it is difficult not to concede that in addition to hyponeustonic microphytes the sea may contain hyponeustonic microphytes among, for example, such photophilous species as occur among the dinoflagellates.

Adaptations of neustonts to other abiotic environmental factors

Closely connected with solar radiation is the water temperature. The heat rays of the solar spectrum (ultraviolet) are absorbed in the upper centimetres and the radiation of longer wavelength (infrared) in the upper millimetres of the water mass. As the result of convective mixing however, the heat received from the sun is transmitted to considerable depths in the pelagic zone. Accordingly the temperature regime in the 0-5 cm layer as a whole does not differ from that of the underlying layer to the same degree as does the optical regime. The same applies to the salinity of the water (see Ch. 1). Therefore the adaptations of neustonts

to the thermohaline conditions of their biotope are in normal circumstances probably not marked by any particular specificity. They may become manifest in extreme cases where the surface layer of water is temporarily warmer than the underlying layers, or where pagon forms, but there are no reliable data available on the subject as yet. As shown by the materials of the Hyponeuston Division and an observation of A. Borisenko (1937) made by him in the Gulf of Odessa on February 7th 1937, /141 the pagon of the northwestern part of the Black Sea has failed to reveal abundant representatives of neuston, which complete the hyponeustonic phase of their life cycle at about this time of the year or remain for the winter in the southern areas of the sea.

A more specific factor to which neustonts had to seek ways of adapting themselves was waves. The oscillatory motion of water particles affects a thick layer and waves cannot be described as a physical phenomenon especially characteristic of the 0-5 cm layer. However, by virtue of their biological consequences they represent a specific condition encountered by the population of the nearsurface microlayer. The simplest method of avoiding waves - moving away from the surface - brings in its train a sharp change in environment for neustonts. Judged by the light intensity for example, the descent of a plankton from a depth of 1 m to a depth of 10 m brings a less severe change in conditions than when a neustont descends to a depth of only 1 m. Furthermore, neuston contains a considerably larger number of immobile

(eggs) or slowly moving (bacteria, protozoans, larvae) forms than plankton, and for them departure to the depths is either impossible or difficult. Earlier it was indicated that even relatively mobile neustonts do not leave their biotope. Therefore adaptation to waves is one of the essential conditions of existence for neuston in the sea. As far as can be judged from the available data, there are several ways in which neustonts adapt to this factor.

The most resistant forms, such as fish fry or large invertebrates, can be seen on the surface of the sea in waves of considerable height and, all things considered, survive without great losses. In such cases the bacterioneuston is partially dispersed, but because of the rapid rate of cell division is restored to its former density within a few hours after the critical sea state has ceased to exist (Tsyban', 1967a).

The greatest fears surround the fish egg - a very delicate and passively suspended component of the hyponeuston, for which a sea state even of 4 is injurious (Zaitsev, 1958b, 1959a). One of the effective adaptations to defend eggs from waves lies in the fact that in stormy weather such fishes as the anchovy either do not spawn or else deposit their eggs in places sheltered from the wind (Vodyanitskii, 1930; Smirnov, 1948). Another effective device is the shortening of the period of embryogenesis in species with eggs developing mainly in the hyponeuston. While the embryonic stage in the demersal eggs of the Black Sea goby, atherinid, garfish

and others lasts up to several months, and in the pelagic eggs of the sprat and whiting, which develop in the water mass, 4-8 days then in the eggs of the anchovy, mullet, horse mackerel and surmullet, clustering beneath the surface tension film, it lasts only 30-40 hours, and at a water temperature of 23-25°C it lasts even less. Because of these tempos of development the hyponeustonic eggs have time to complete embryogenesis with the least risk of suffering from critical sea states. Furthermore, spawning at night also helps to avoid waves (Malyatskii, 1940; Dekhnik, 1959, 1961), as the surface of the sea is generally calmer then. Another device is to confine the spawning period of most species to the summertime, when the number of stormy days is minimal.

Thus, losses of hyponeustonic eggs due to wave action can be reduced by a quickened tempo of embryogenesis and by adjustment of the diurnal and seasonal dynamics of spawning of the relevant pelagic species of fishes.

Winds and waves also give rise to the danger that neuston will be swept ashore. As will be shown later, neuston develops mainly at a specific distance from the shore. Fishes with hyponeustonic eggs are characterized by catadromous spawning migrations of varying degrees of intensity within the bounds of the sea, as the result of which the bulk of the eggs are deposited outside the nearshore zone where there is a real danger that the organisms will be swept ashore. For instance, mullets, the eggs, larvae and early fry of which lead a hyponeustonic mode of life for several months, migrate to a point 40-50 miles or more from the shore before spawning.

One of the chief characteristics of the nearsurface biotope of the pelagic zone is its abundance of non-living organic matter (see Ch. II). This factor is one of the most important ecological prerequisites for the occurrence of neuston in the sea, and the wealth of reducers contained in the nearsurface assemblage of organisms must be regarded as an adaptation to it. Bacterioneuston, which consists primarily of heterotrophically feeding microorganisms, is the main means of utilizing the stagnant organic matter in the process of the formation of the nearsurface biological structure of the sea. The role of producers has proved to be far more modest here than in the underlying mass of the sea. Nevertheless, as was noted above this question has not yet been clarified. Dinoflagellates, which are distinguished by a requirement for light and intense bursts of development right at the surface, have proved to be highly sensitive to organic fertilizers as well. Thus, the introduction of nitrogenous and phosphorus fertilizers into Loch Craighlin* in Scotland in 1942 and 1943 was followed in no more than one to three days by a vigorous burst of development of dinoflagellates (up to 8,000,000 kg/l), whereas diatoms failed to react to the fertilizers and the increase in their numbers (up to 7,000 kg/l) bore no correlation with the application of the fertilizers (Aubert, 1965; Wimpenny, 1966). It is possible that the "red tides" caused by these algae are also related to fluctuations in the rate at which non-living organic matter enters the nearsurface biotope of the sea.

*Spelling could not be verified - Translator.

Adaptations of neustonts to biotic factors of
the environment

In Chapter IV it was stated in particular that the uniqueness of the biotic environment, and especially the double "press" of predators (aquatic and aerial), exercises a corresponding influence of the population of the nearsurface biotope of the pelagic zone. If the marine neuston is examined from this point of view this will indeed readily become apparent.

Most neustonts are the prey of larger animals from other biotopes of the sea and the terrestrial environment, and this has laid its stamp on the external appearance and behaviour of these creatures. A very common defensive adaptation in nature is protective coloration. A distinction is made between camouflagic, or cryptic, coloration (cryptism and mimesis) and warning or aposematic coloration, a particular instance of which is mimicry (Naumov, 1963; Kovalev and Oshanin, 1966).

Cryptism is the form of protective coloration used when the animal merges with the background of its usual habitat. Mimesis is imitation of individual elements of the background which cannot be distinguished by the predator, for example dry twigs, leaves etc. The animals, though they stand out against the general background, by camouflaging themselves as an inedible object confuse the predator. Mimicry is also imitation of background elements, but ones which are deliberately avoided by the predator because of their poisonous nature or some other danger.

All these forms of adaptive coloration do not guarantee absolute security of the prey. Movements may betray even an

ideally camouflaged animal. Therefore camouflagic coloration is usually combined with behaviour reinforcing its effect (Naumov, 1963).

In the components of the marine neuston are found various forms of camouflage and behaviour intended for defence against enemies both in the water and in the air.

Cryptism. The colour of the background against which neustonts are clearly visible to animals from another biotope depends on the position of the animal. For hydrobionts it is the silvery white gleam of the aquatic "ceiling", and for aerobionts the various shades of blue of the sea-surface. Accordingly, during the evolutionary process neustonts were given cryptic /144/ coloration as a defence against aquatic and aerial predators. A particularly common type developed was complete or high transparency which enabled a animal to blend with a background of any color, not only at the surface but in the whole water mass. At a body length of 30-35 mm anchovy larvae are almost transparent, and so ~~also~~ at a length of 20-25 mm are the larvae of blennies and weavers, the phyllosoma larvae of Palinurus, the alima larvae of Stomatopoda, young Macropus (Portunus) holsatus crabs, and many megalops and other larvae of decapod crustaceans. The sparse and finely branching chromatophores do not reduce the transparency of these abundant representatives of the hyponeuston. Only the pigment layer of the eyes (tapetum), which is intensely pigmented, betrays the "invisible" creatures.

The calm surface of the sea may, for example, reveal the

following picture. In the upper 3-5 mm of water a pair of black dots can be seen rushing along, pursued by another pair of similar or larger eyes. Both fleeing objects leave traces in the water disclosing their dimensions, but the animals themselves cannot be seen. With the aid of a lift net it is found that it is an anchovy larva some 30 mm long chasing after a blenny larva of 15 mm. It is interesting to note that even when pursued by a predator the prey does not leave the nearsurface layer. This feature - adherence to the biotope under any circumstances - is characteristic of hyponeustonic organisms.

On the whole fish eggs are also transparent, and when viewed through a face mask they are difficult to distinguish in the water. However, it is only man that experiences this difficulty. That fish find them nevertheless, is shown by the discovery of a large number of absolutely transparent anchovy eggs in the stomachs of hyponeustonic surmullet fry captured in the open sea. For example, the stomachs of each of 24 surmullet fry caught in August 1962 at one of the stations situated in the centre of the Black Sea contained in addition to other food 16-249 anchovy eggs. Given the density of anchovy eggs (in the 0-5 cm layer) at this station, which is 243 spec./m³, and taking into account the fact that surmullet fry do not leave this layer, it can be concluded that each of the fish "cleared" up to 20 m² of the nearsurface microlayer of anchovy eggs. This fact merely emphasizes the general biological proposition that the various defensive devices do not guarantee complete security, although they do undoubtedly reduce depredation

of the species (Naumov, 1963).

Another, more common variety of cryptism is exhibited by the organisms which are coloured various shades of blue. The chemical composition of the blue pigment of neustons has not yet been finally established. Some authors call it cyanocrystalline, noting that when acted upon by certain fixatives it turns into a red pigment - crustaceorubin (Brodskii, 1950). For instance, pontellids placed in a solution of alcohol immediately turn red. P.J. Herring (1965) speaks of a chromoprotein complex of carotinoid and albumin displaying a wide absorption band with a maximum at about 640 millimicrons (in Pontella ferra), and D. Fox and G. Crozier (1967) mention a chromoprotein containing astaxanthin (in the crustaceans Velella and Lepas fascicularis).

/145/

Different sea tones - from blue to green - mark species of Pontellidae, shrimps (Parapeneus longipes and Metapenaeopsis sp.), the small crab Planes, a hydromedusa (Porpita), a cirripeace crustacean (Lepas) living on floating objects, and others. These animals merge completely with their background due to their capacity for physiological colour change. Thus, the colour of the Black Sea species Pontella mediterranea and Anomalocera patersoni varies from blue to green depending on the change in the colour of the sea water from the central regions of the sea to the coastal and freshwater regions. The hyponeustonic crab (Planes) is capable of a similar change in colour. When Kreps (1963)

released such small crabs, caught in the Indian Ocean, in a white bath they soon turned a whitish colour. Black Sea pontellids placed in an aquarium also swiftly turn pale.

The inhabitants of the nearsurface layer of the pelagic zone are protected by a variety of devices from deep-sea enemies. Cirripedia attached to floating objects obviously have a few enemies in the water and they stand out fairly clearly against the silvery background of the "ceiling". At the same time they look like a continuation of the substratum to which gulfweed, driftwood or pleustonic siphonophores are attached.

Porpita is reliably protected from below by a bunch of dactylozooids. Things are somewhat different in the case of pontellids. They are not connected to any substratum, have no organs above with stinging cells, and stand out clearly as dark silhouettes against the silvery "ceiling" of the pelagic zone. This defect - from the point of view of concealment - is compensated for by the pontellids' ability to leap from the water, which long ago earned them the nickname of "flying copepods" ("fliegende Copepoden," Steuer, 1910). Visual observations conducted at sea-level revealed that the leaps of Black Sea pontellids attain a height of 15cm and a length of 15-20 cm and may be made singly or in series (Fig. 49). These crustaceans leap for no apparent reason, but their leaps increase sharply in frequency when ^{an} object from the depths approaches, as for example the hand of an observer. As a defensive reaction the leaps of the pontellids are analogous to the flight of flying fish, but are based on a different physical principle. Their result - escape from aquatic enemies - must obviously to some

extent offset the conspicuousness of their pigmentation, which is easily noticeable from beneath the water.

It is possible that the pontellids have yet another protective adaptation. On the dorsal side of the 2nd-4th segments

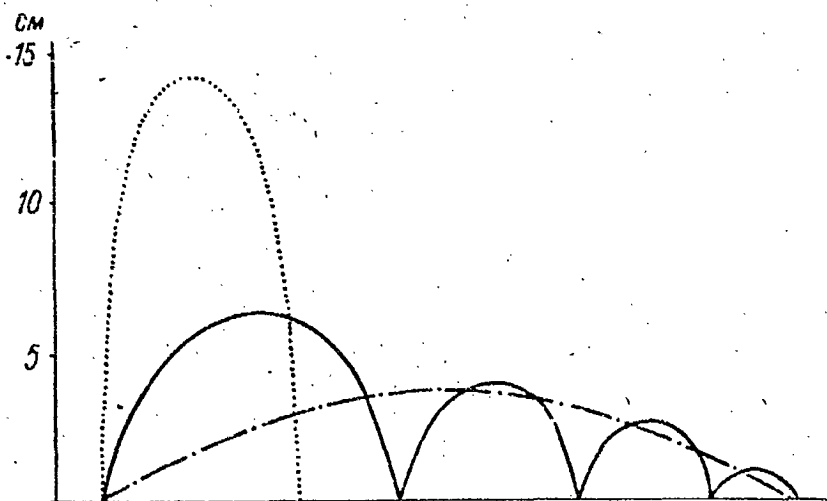


Fig. 49 - Trajectories of different types of aerial leaps of Black Sea Pontella mediterranea (Zaitsev, 1964a).

of the cephalothorax of many species of this family there is a silvery spot resembling the guanine pigmentation of fish. By analogy with other organisms it may be supposed that its purpose is concealment of countershading, but in that case it must be assumed that the pontellids adhere to the surface tension film with their back facing downwards, whereas crustaceans have as yet never been found in such a position in nature.

When evolving the protective coloration the hyponeustonic organisms made wide use of the "countershading principle" (Kott, 1950), according to which the side of the body facing the sun

must be more intensely pigmented than the opposite side. As a result the three-dimensional effect of the animal disappears as it were and this makes concealment easier. In neustonts the countershading is hidden by dark blue pigmentation of the side of the body facing upwards and silvery pigmentation of the underside, though the former need not necessarily be the dorsal side of the body. In the hyponeustonic mollusks Glaucus and Janthina, which "hang" from the surface tension film, the ventral side is blue and the dorsal side silver (Mertens, 1962). The /147/ same pigmentation is found in the catfishes Synodontis batensoda (Rüppell) (Suvorov, 1948) and S. schal (Bloch e. Snelder) (Nikol'skii, 1954), which swim near the surface ventral side up. Far more frequently, however, the dorsal side of the body is pigmented a dark colour and the ventral side is silvery. Such a pigmentation is characteristic of larvae and fry of Augilidae (at a body length of 4-5 mm), the larvae and fry of Gaidropsarus mediterraneus, Mullus barbatus and other species of fishes. It is typical that adult specimens of hake and surmullet, leading a demersal mode of life, have a pigmentation corresponding to the bottom, while their young are coloured tones appropriate to conditions of life in the hyponeuston. Young hake are found in the nearsurface biotope of the Black Sea with a length of 50-54 mm (Vinogradov, 1931; Vinogradova, 1950), and surmullet with a length of up to 60 mm.

In addition to coloration these small fishes possess other cryptic properties. Thus, Black Sea mullet fry are able to change colour by reflection. When waves form in the centre of

the Black Sea in summer and autumn grey mullet and golden mullet fry can be found with silvery backs. These fish, which are unusually light-coloured on all sides, successfully camouflage themselves as patches of foam floating on the surface and hide under them at the sight of a lift net. In general it has been noted that hyponeustonic fish fry react very quickly to the sudden appearance of any object from above. Perhaps there is a definite link between the "window" in the pigment covering of the head of the fry of many fishes and the tori longitudinales in this "window". These parts of the midbrain, being directly connected to the optic nerves and valvula cerebelli, serve as centres for such visual perceptions as must provoke a rapid reflex (Suvorov, 1948).

Black Sea mullet fry caught and placed in a vessel containing ship's water acquire the normal greenish or bluish dorsal coloration within 5-7 minutes (Zaitsev, 1961a, 1964a). According to K. Kott (1950), a capacity for rapid colour change is characteristic of many tropical fishes. In the Bermudas, for example, some 28 fish species have this property. Change of colour is caused by emotions (anger, fear, attack by an enemy), but it is usually connected with imitation of the background.

Yet another protective property of fry with coloration hiding the countershading relates to their body shape in cross-section. Thus, whereas adult surmullet have a cross-sectional shape similar to an isosceles trapezium (Aleev, 1963), the

hyponeustonic fry are flattened at the sides and have a more or less pronounced ventral keel (Krakatitsya, 1963). The cryptic significance of such a body structure, as explained by Y.G. Aleev (1960), is that it eliminates the tell-tale shadow under the trunk of the fish. This feature is highly useful to dwellers in the illuminated zone of the pelagic division and it ^{is} probably for that reason that juvenile surmullet and hake in the hyponeustonic period of their life have, unlike the adults, a laterally flattened and downwardly tapering body. This is not so pronounced a keel as in the "tiulka" (Clupeonella d. delicatula) or "chekhon" (Pelecus cultratus), but in the view of Y.G. Aleev, any tapering of the lower part of the body fulfils a cryptic function. This viewpoint is lent weight by the phenomenon of mimesis (see below) in those hyponeustonic fishes whose bodies are not flattened laterally and which therefore leave a tell-tale shadow in the water. /148/

Yet another form of cryptism is the so-called oblitative shading, when alternation of intensely pigmented and non-pigmented areas breaks up the contours of the body and makes recognition difficult. Oblitative shading is characteristic of larvae of the sole Solea nasuta lascaris (Fig. 50), which, being very conspicuous on the surface of the sea, pretend to be inanimate objects, losing themselves completely among floating debris. This is also a transition to mimesis. Apart from changing colour, Solea larvae take refuge in protective forms of behaviour. If the larva is touched it instantly freezes in an unnatural pose.

(Fig. 50) and begins to sink. Not one pelagic fish will touch such torpid larvae. Once the following case was observed. A Solea larva was pursued by a stickleback, which in the Black Sea are found even in halistatic regions (Il'in, 1933). As soon as the predator touched its prey the latter instantly froze. This produced the desired effect: the stickleback turned away and made off while the torpid larva sank to the bottom. However, it had just come to within 5-7 cm of the bottom (the observations were being conducted close to the shore at a depth of about 2.5 m), when a small goby Pomatouschistus appeared from nowhere and seized its prey. The latter shook itself free and made for the hyponeustonic layer, where it resumed its interrupted mode of life. Evidently pelagic and bottom-dwelling predators behave differently towards these "corpses."

Many more perfect examples of oblitative shading than Solea may be found among hyponeustonic fish fry in the tropical seas.

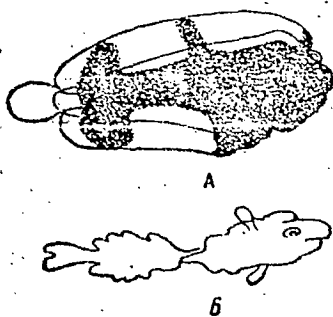


Fig. 50 - Oblitative shading of larvae of Solea nasuta lascaris (A) and contours of the same larva in the event of danger (B) (Zaitsev, 1964a).

Cryptism, although it does not completely eliminate danger from predator-neustophages, undoubtedly reduces the intensity of depredation. However, the protective role of cryptic coloration should not be exaggerated. The specialist neustonologist can now see even with the naked eye much on the surface of the sea that previously escaped the specialist planktonologist. It is a matter not of acuity of eyesight but of knowing where and how to look, and what for. But the eyesight of feathered predator-neustophages is far keener than in man and they have had far more experience than the neustonologist in seeking out and capturing neuston. Furthermore, neuston-eating birds and mammals do not rely solely on eyesight when hunting.

Mimesis. A more perfect form of camouflage than cryptism is mimesis, or the imitation by the intended victim of objects in the biotope which are of no interest to the predator. Although the choice of such objects is more limited for neustonts than for bottom-dwellers, mimesis is common in the world of neuston. The objects imitated are the commonest inedible elements in the nearsurface biotope: air bubbles, patches of foam, all sorts of floating objects and floating algae.

Mention has already been made in this chapter of the fact that mullet fry use an additional hydrostatic device in the form of air bubbles which form above the impermeable portion of the back, and that this character also fulfils protective functions. From above, the mullet fry is visible only as a bubble of air, and its gleaming base - the iridescent back of the fry - acts like a lamp reflector to distract the predator from associations connected with prey. It might be noted that, when evaluating the effectiveness

of mimesis as a protective adaptation against birds, we can rely on our visual sensations (making the necessary corrections), since human sight is close to that of birds.

The fry of Mugil vaigiensis near Tahiti in the Pacific also imitate air bubbles, but with them mimesis is even more perfect than with the Black Sea mullet. When in danger M. vaigiensis fry flex the rear part of the body and freeze. As a result the originally oblong bubble of air becomes round, thereby resembling its natural prototype (Randall and Randall, 1960).

Mortensen (1917, cited by Randall and Randall, 1960) observed Atherina sp. fry in the region of the Panama Canal which also disguised themselves as air bubbles or water drops moving across the surface film of sea. Other fish also imitate air bubbles.

In October 1960 near the Bosphorus, scientists on board R/S "Miklukho-Maklai" observed a school of 25-30 silvery fry some 20mm long which they were unable to catch and identify. /150/

Frightened by an object thrown into the water the school froze as if by command - each individual in a vertical position with its head up. In this position they were carried away from the ship by the current. From above the school resembled a swarm of air bubbles. Surmullet fry on perceiving danger threatening from above (an approaching lift net) also freeze and arch their body, so that they resemble a bird feather. As can be seen, fry of the same species use both cryptism and mimesis for their defence.

While some fish fry imitate air bubbles, and their schools

accumulations of bubbles, Porpita umbella imitates patches of foam. Unlike the blue Porpita from the Indian Ocean depicted in David's coloured photographs (1956b), Atlantic Porpita collected in the waters near Cuba are silvery white on top with a blue border. Translucent air cells enhance the resemblance to patches of foam. White rafts of Janthina imitate patches of foam very effectively.

Another item commonly imitated by neustons is small floating objects of allochthonous origin: chunks of wood, bark, seeds, lumps of pumice, slag and other objects of no interest to predators. All these long-buoyant alien bodies are covered by a film of bacteria and algae and acquire a brown and greenish colour. Many hyponeustonic organisms imitate floating objects, and for this reason are sometimes called "driftwood fauna" (Besednov, 1960; Parin, 1968). It should be borne in mind, however, that they also occur away from accumulations of drifting objects, especially those forms originating from free-floating eggs. But in those regions of the sea where drifting objects usually accumulate (for example, in regions of converging currents), neuston also accumulates under the influence of the same factors, in which case they camouflage themselves not only as floating objects but also as other species.

The fry of the widely distributed barracuda species Sphyræna barracuda (Walbaum), 18-22 mm long, which has been observed in the Pacific (Society Islands), Atlantic (Bahamas) and other places, imitates in coloration and body shape fragments of straight branches and twigs (Randall and Randall, 1960). These

"twigs" drift in a vertical position or at an angle of about 45° to the surface, with the head of the fish touching the surface tension film.

A close resemblance to thin branches is borne by the dark-brown larvae of Strogylura sp. near the Hawaiian islands (Randall and Randall, 1960).

Among invertebrate neustonts Idothea stephenseni imitates floating objects. Their bodies are dark brown and often have a bluish metallic sheen similar to drifting objects coated with encrustations or a film of oil. Idothea often settles on pieces /151/ of floating debris and is able, because its body is flattened dorso-ventrad, to blend entirely with the imitated object (Zaitsev, 1963a). Nevertheless, despite the excellent camouflage, this species in the Black Sea is successfully consumed by dolphins. Kleinenberg (1936, 1937, 1940) used to find I. stephenseni (syn. I. algirica) in Delphinus delphis ponticus and Phocaena relicta and reports cases where the stomachs of dolphins were filled exclusively with Idothea. It may be that the high intelligence of dolphins so widely discussed in recent times plays a part in this, so that they can fill their stomachs with comparatively small and mobile neustonic components without using any filtering device. One rather confusing point here is the absence of selectivity in dolphins pointed out by Kleinenberg, who often found extraneous objects in their stomachs, such as ship's slag, chunks of wood, bird feathers and even paper bags containing cherry stones. Nevertheless, the list of these

floating objects is a weighty argument in support of the fact that dolphins feed intensively in the hyponeustonic layer and can therefore be classed among the active neustophages. In addition to Idothea Kleinenberg discovered a large quantity of a euhyponeustonic species of pipefish (Syngnathus schmidtii) in the stomachs of Black Sea dolphins.

While it may be true that the protective adaptations of I. stephensi are ineffective against predators such as the dolphin, they are much more so against other animals, and this species does not figure in the lists of food items consumed in large quantities by Black Sea fishes. Some of the habits of Idothea are also defence-oriented. If a crustacean in the sea is pursued by some animal (or, for example, the hand of an observer) it often freezes, even before contact, with an unnaturally convex body and straddled limbs (Fig. 51), and begins to sink. The sinking crustacean sometimes chances among dense shoals of fish, for example atherinids, but they do not touch these "prickly" creatures. Once, an isopod of the species Eurydice which was frightened while in the hyponeustonic layer (normally they appear in the nearsurface biotope in the dark hours of the day) rolled itself into a ball and descended to the bottom, only to be swallowed by the first atherinid.



Fig. 51 - Hyponeustonic isopod frozen at sight of danger (Zaitsev, 1964a).

A great resemblance to floating debris is borne by the comparatively large copepods of the family Sapphirinidae, which are coloured dark brown on top with a metallic sheen. Underneath they are whitish in colour. The body is compressed dorsoventrad and is foliate. It may be that this body shape is also among the adaptations appropriate to the laminar layer of hyponeuston. The same type of body is found among the transparent leaf-bodied Phyllosoma larvae too. /152/

Also widely used as object for imitation by neustonts are floating objects of autochthonous origin, above all fragments of benthic algae and aquatic flowering plants. It is known that many benthic macrophytes have in their thallus or leaves various air-filled cavities supporting these anchored plants in the water by their buoyancy. When the plants become detached from their substratum however, under the effect of waves or other factors, they float to the surface into the hyponeuston layer, where they still continue to vegetate for some time. This ability of the algae to vegetate even when detached from the bottom is regarded as one of the means by which macrophytes spread (Vozzhinskaya, 1964). Parts of benthic plants are fairly frequently found on the surface of the sea in the vicinity of the shelf, and also even at considerable distances from the shore. For instance, the leaves of Zostera sometimes form huge concentrations in the halistatic regions of the Black Sea. In the western part of the Pacific 75 species of benthic algae were discovered on the surface. Particularly numerous were various sargassos and

fucuses.

Being objects of no interest to predators and providing a certain amount of cover, floating benthic plants became objects for imitation by many neustonic animals. Characteristically this cannot be said about any of the forms of plankton, since floating macrophytes do not remain in the pelagic zone. They are either only in an anchored state on the bottom, where many fishes and invertebrates are to be found disguising themselves as macrophytes, or else in an unanchored state in the hyponeuston layer, where an abundant group of animals dwell which bear an external resemblance to plants.

The body of the Black Sea larvae and fry of Callionymus belenus, with a length of 4-6 mm, is covered by a dense network of dark-brown melanophores giving them a close resemblance to fragments of the brown sargasso Cystoseira barbata (Fig. 52).

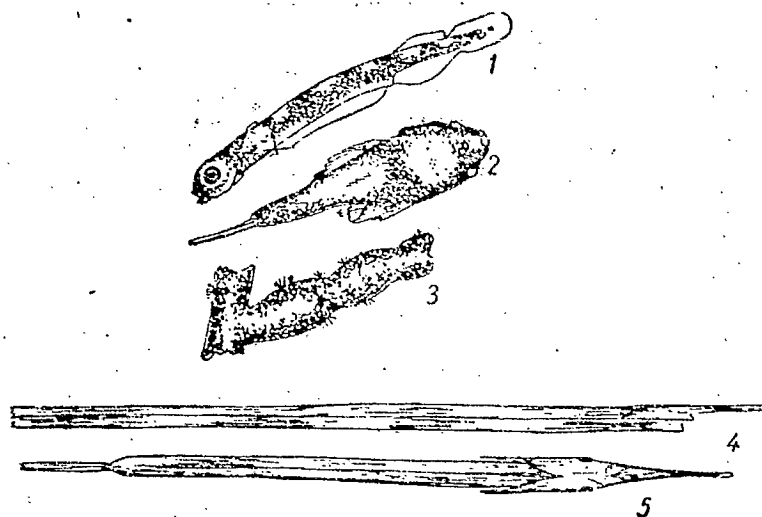


Fig. 52 - Examples of mimesis among neustonts: 1 - Belone belone euxini larva, 2 - Callionymus belenus larva, 3 - fragment, thallus of Cystoseira barbata, 4 - fragment of leaf of Zostera marina, 5 - fry of Belone belone euxini (Zaitsev, 1963c).

An even greater resemblance to Cystoseira is borne by the larvae of the garfish Belone belone euxini, at a length of 10-15 mm. Their oblong body is covered with brown melanophores. In addition light-coloured spots are distributed evenly over the body. These spots are formed by a concentration of guanocytes which create the impression of alternating dilations (air bladders) and contractions on the branches of this alga. The imitation is so perfect that it is extremely difficult to differentiate garfish larvae from fragments of Cystoseira - not only in the sea but also in a small vessel containing a fresh catch made with a neuston net (Fig 52). When they grow, the garfish fry lose their brown pigmentation and turn silvery with a golden back.

Still keeping to the hyponeuston layer they retain their /153/
ability to camouflage themselves as floating fragments of
benthic plants. Now they begin to imitate Zostera leaves:
first Zostera nana, then Z. marina (Zaitsev, 1963c). From a ship
in the middle of the Black Sea it has been observed now juvenile
garfish up to 10-15 cm long invariably stay close to Zostera
leaves. The fish remain strictly parallel to the leaf and,
either ceasing to move or imitating the light bobbing of the
leaf on the surface, it resembles a Zostera leaf (Fig. 52).
After spending some time in this position the fry darts towards
the next leaf and takes up its position parallel to it. The
stomachs of these fry contain 100-200 adult pontellids, many fish
larvae, decapods and other neustonts, and also land insects
from the sea surface. It is probable that mimesis not only protects
young garfish from large predators but also makes it easier
to hunt for the mobile leaping pontellids, fish fry and other
hyponeustonic organisms which, when feeding on the encrustations
on Zostera foliage, carelessly wander close to the "leaf"
(the garfish).

Earlier it was said that fishes without a ventral keel or
downward narrowing of the body leave a tell-tale shadow on the
ventral side. This applies in particular to garfish fry with
their rounded cross-section. Apparently, imitation of the
motionless Zostera leaf, which leaves just such a shadow beneath /154/
it, to some extent offsets this deficiency (from the viewpoint
of camouflage) in the external structure of the fish. Apart
from the juvenile garfish, Zostera leaves are also imitated in

body structure, pigmentation and habits by the pelagic pipefish Syngnathus schmidtii, which is found mainly in the open waters of the Black Sea and Sea of Azov. Typically, representatives of the families Belontiidae and Syngnathidae camouflage themselves in a similar way in other parts of the ocean. The dark-brown larvae of Strongylura sp. near Hawaii imitate branches (Randall and Randall, 1960) and are very similar in external appearance to the larvae of Black Sea garfish.

Fry of Strongylura notata (Goey) and the pipefish Syngnathus pelagicus L., according to the observations of the author in the Gulf of Mexico, imitate floating leaves of Thalassia testudinum, which resemble the leaves of Zostera. Fry of Strongylura raphidoma (Ranzani) and S. timicu (Walbaum) near Florida and the Virgin Islands imitate fragments of the ribbon-like leaves of another marine grass Cymodocea maritima (Randall and Randall, 1960).

Thus, the camouflaging principles of neustonts persist everywhere, and only their bearers and objects of imitation change.

Quite naturally, the hyponeustonic sargassos, which are widely distributed in the warm part of the ocean, large enough to offer refuge to neustonts, and of no interest to predators, have also become an object of imitation by a particular group of neustonts which are sometimes called "the sargasso fauna." The best known representatives of this group - the fishes Histrio histrio (Antennariidae) and Cyphosus sectatrix (Cyphosidae), the small crab Portunus portunus, the shrimp Leander tenuirostris, the isopod Janira minuta and others-imitate sargassos

extremely exactly in colouring and general contours. The bodies of these fishes and crustaceans are speckled with brown, ochre and white spots, which reproduce very faithfully the external appearance of the algae, and H. histrio with its processes and foliate appendages not only conceals itself very cleverly in the thallus, but clings tenaciously to its branches. If a bush of S. natans is thoroughly shaken after removal from the Sea H. histrio will fall out.

As correctly noted by J. -M. Pérès (1961), the perfection of all the adaptations mentioned here is evidence of the antiquity of the hyponeustonic fauna of the Sargasso Sea. He considers that new benthic species no longer migrate to the Sargasso Sea, basing this belief on the fact that the richest fauna both qualitatively and quantitatively is found in the central and eastern parts of this sea, i.e. in the regions most remote from possible sources of occurrence of benthic organisms.

Among the hyponeustonic sargassos floating in the nearshore waters of, say, the Bahamas shelf or the Gulf of Mexico, apart from those animals already listed, there are many other species camouflaging themselves as floating objects - the fry of representatives of the families Balistidae, Exocoetidae, Carangidae, Syn-gnathidae, and so on. /155

Mimicry. Mimicry (in sensu stricto), i.e. the imitation by unprotected organisms of others avoided by the predators, has not become so common among the neuston as the preceding forms of camouflage, possibly because the number of species in

the nearsurface biotope which frighten off predators is very small. The only creatures of this type would probably be the pleustonic siphonophores Physalina and Velella. Although there are indications that these organisms too are devoured by sea turtles, and although they are known to be consumed by the hyponeustonic mollusks Glaucus and also by squids, most animals nevertheless avoid them. On colonies of pleustonic siphonophores, and especially Velella, sit many hyponeustonic organisms exhibiting homochromia with the substratum. For instance, the cirripede crustacean Lepas even "grows" on Velella and takes on the same blue colour. However, the investigations of Fox and Crozier (1967) showed that this is not a chromatic adaptation to the substratum, since the presence of light-blue pigment in the body of Lepas does not depend on whether this crustacean "grows" on Velella or on floating objects of any colour. Since the chemical nature of the light-blue pigment of L. fascicularis is the same as in many crustaceans (Fox, Crozier, 1967), it is clear that this is not mimicry but a case of cryptism which is common among neustonts.

The word "mimicry" can evidently be used to describe the protective adaptations of hyponeustonic fry of Lupus maculatus (Schedophilus maculatus Günth.), which in the words of David (1956b), feed on animals held by the surface tension film as the trout feeds on ephemera falling into the water. These fry hide among the tentacles of Physalia and have blue vertical stripes on the sides of the body similar to the dactylozooids

of that creature (Rass, personal communication; Kreps, 1963).

A small fish that has become widely known is Nomeus albula (Meusch.) (Nomeidae), which is found in the Atlantic, Indian and Pacific oceans among the dactylozooids of Physalia. For this reason it has acquired the English name of Portuguese-man-of-war fish. However, parts of a Physalia colony submerge for more than 20 m and in the absence of accurate information it is difficult to say whether N. albula is a hyponeustonic species, as Schedophilus maculatus probably is, or whether it belongs among the deeper water species of the ichthyofauna of the epipelagic zone.

The examples cited in this chapter provide evidence that the neustonts have acquired many characters and properties appropriate to the ecological environment of their biotope. All the features of their organization and behavioural peculiarities mentioned, such as the positive buoyancy of the body, the auxiliary floats in the form of rafts or air bubbles, the impermeability of the integuments, the ability to develop in bright sunlight and ultraviolet radiation, the blue pigmentation, the leaps out of the water, the imitation of air bubbles, foam, floating objects, sargassos, etc, are biologically expedient only in the region of the surface tension film. At a mere few centimetres from it they lose all their adaptive significance, as the new environment requires neutral rather than positive buoyancy, the impermeability of the integuments is pointless, the light regime is different from that at the surface, the bright blue

pigmentation is conspicuous, aerial leaps are out of the question, there is no foam, no floating objects for organisms to imitate, and so on. Therefore an analysis of the examples of adaptation by neustons to their environment and their degree of perfection leads to the same logical conclusion as has been drawn on the basis of other data: the marine neuston are not a chance and ephemeral conglomerate of organisms, no "concentrated" plankton from the pelagic zone, but something new - a biological structure produced by evolutionary processes which is adapted to life in the specific conditions of the nearsurface biotope of the pelagic zone.

Radioecology of neuston

The radioecology of neuston is a branch of the radioecology of aquatic organisms - a science which studies the factors governing the interaction between hydrobionts and a radioactive environment. Bearing in mind that neuston has a special position with regard to the radioecological factor compared with other classes of aquatic communities, this chapter, which is devoted to ecology, will also give a brief outline of modern ideas in this field.

The author began to tackle the problems connected with the radioecology of neuston several years ago in collaboration with G.G. Polikarpov, who, by formulating the principles of the new oceanographic disciplines of radioecology (Polikarpov, 1964; Polikarpov, 1966) and chemical ecology (Polikarpov, 1967 a, c), demonstrated the necessity, importance and longterm prospects of a comprehensive study of marine neuston from these points of view.

The fundamental propositions of the radioecology of neuston set out below are contained in the papers of Polikarpov and his colleagues published both here and abroad, and also in the papers written by the author of the present book.

The surface of the seas and oceans is a more effective collector of radioactive aerosols than the surface of the land. According to the data of V.P. Shvedov et alia (cited from Polikarpov, 1964), the specific density of deposition of radioactive products /157/ over the Black Sea is 1.5 to 2 times greater than over the littoral. Thus, up to 1961 alone 5.3 microcuries of strontium 90 were deposited in the hydrosphere compared with 1.7 microcuries on land (Report of the Scientific Committee of the UN on the Effects of Atomic Radiation, II, UN Document A/5216, 1962).

Radioactive aerosols falling on the surface of the water obviously create far more radioactivity in the thin layer on top than in the underlying mass of water. Thus, in the foam of reservoirs in 1957 the concentration of radioactive substances amounted to 10^{-8} curies/l, whereas in the water it was 5×10^{-12} curies/l (Drachev and Bylinkina, 1960). Even at a depth of 0.4 m the activity of strontium 90 in sea water near the shores of Japan in 1956 was 13 and 40 times higher than at depths of 5 and 15 m respectively (Hiyama and Ichikawa, cited from G.G. Polikarpov, 1964). Thus, near the surface of the seas and oceans the concentration of radioactive substances is much greater than in the water mass of the pelagic zone. Therefore, in the general complex of marine radioecological investigations special attention

is merited by the inhabitants of the nearsurface microlayer of the pelagic zone, i.e. the neuston, and especially the most important of its components - the hyponeuston (Zaitsev and Polikarpov, 1964, 1965; Polikarpov, 1964; Polikarpov, 1966; Polikarpov, 1967a; Zaitsev, 1967a; Zaitsev, 1968).

Interaction between the radioactive environment and the hyponeuston

a) The accumulation of radioactive materials. To illustrate the capacity of marine hyponeustonic forms and systematically related hydrobionts to accumulate radioactive materials the coefficients of accumulation of fallout and neuston-induced radionuclides (culled from the materials of a number of authors) are given in Table 41. The coefficient of accumulation means the ratio of the concentrations of a chemical element, and especially its radioactive and stable isotopes, in the organism (wet weight) and in the aquatic environment. In those cases where no data existed on radionuclides the available information on the stable isotopes of the same elements were included in the table. Where accumulation is in a state of equilibrium (all other things being equal) the coefficients of accumulation of radioactive and stable isotopes are the same. The maximum values of the accumulation coefficients for most fallout radionuclides in marine organisms are reached very quickly - within a few days (Polikarpov, 1961).

On the basis of the material set out in Table 41 the following conclusions can be arrived at. The first striking point is the insufficiency of the data on most fallout radionuclides. /158/

Table 41

Coefficients of fallout fission products in marine hyponeustonic or systematically related species (Zaitsev and Polikarpov, 1964; Ivanov, 1965; Polikarpov et al., 1967).

1. Организм	Кoeffициент накопления				
	Cs ¹³⁷	Sr ⁹⁰	Y ^{90,91}	Ce ¹⁴⁴	Ru ¹⁰⁶
Одноклеточные водоросли 2	1—3	4—17	—	340—4500	—
Гипонейстонные макрофиты 3					
<i>Sargassum natans</i>	10	41	—	1040	366
<i>S. fluitans</i>	12	35	—	200	310
Простейшие 4	—	110*	—	—	—
Гипонейстонные ракообразные 5					
Pontellidae	6	8	—	51	32
Amphipoda	4	2	—	119	—
Isopoda	5	2	—	37	7
Mysidacea	11	7	—	15	7
<i>Planes minutus</i> , megalopa	5	2	—	58	4
<i>P. minutus</i> , megalopa, панцирь	1	23	—	320	320
<i>P. minutus</i> , juv.	8	10	—	43	22
Рыбы 6					
Гипонейстонная икра 7					
<i>Engraulis encrasicolus ponticus</i>	9	0,8	100—223	—	12
<i>Trachurus mediterraneus ponticus</i>	—	0,9	191—196	495	—
<i>Mullus barbatus ponticus</i>	—	0,8	83	—	—
<i>Scophthalmus maeoticus maeoticus</i>	8,8	1,6	57,1	308	—
Гипонейстонные предличинки 8					
<i>E. encrasicolus ponticus</i>	26,1	—	250	—	26,2
<i>T. mediterraneus ponticus</i>	—	0,8	11—92	538	—
<i>M. barbatus ponticus</i>	—	2,1	114	—	—
<i>S. maeoticus maeoticus</i>	14,1	4,3	91,4	611	—

10 * Кoeffициент накопления стабильного изотопа.

Key: 1. organism; 2. unicellular algae; 3. hyponeustonic macrophytes; 4. protozoans; 5. hyponeustonic crustaceans; 6. fishes; 7. hyponeustonic eggs; 8. hyponeustonic prolarvae; 9. coefficient of accumulation; 10. * coefficient of accumulation of stable isotope.

The accumulation coefficients for caesium 137 in unicellular algae are close to unity. Hyponeustonic sargassos, eggs and prolarvae of fishes, and also the muscles of adult fishes, concentrate this nuclide in quantities up to 10 times greater

than in sea water. Strontium 90 is easily concentrated by microphytes (Carteria sp.), the representatives of which are good accumulators, and also by hyponeustonic sargassos. The concentration of stable strontium in the protozoans Acantharia is 100 times, and in their celestine skeletons 60,000 times, higher than in sea water (Polikarpov, 1966). The pelagic eggs and larvae of fishes are indifferent to the accumulation of strontium, but adult fishes, especially their skeletons, possess a marked ability to concentrate strontium 90 as is revealed by an examination of the accumulation coefficients for the radioisotopes of the rare-earth elements. The fact is that strontium 90 constantly regenerates the daughter radioisotope yttrium 90 which is characterized by high coefficients of accumulation in various marine organisms (Polikarpov, 1960, 1961, 1964), including hyponeustonic eggs and prolarvae of fish (Polikarpov and Ivanov, 1961, 1962a, b; Ivanov, 1965). According to the data of G.G. Polikarpov and V.N. Ivanov (1962a), the coefficient of accumulation of yttrium 90 in the membrane of pelagic fish eggs is 10,000.

The values for the accumulation coefficients for another representative of the rare-earth metals - cerium 144 - are measured in hundreds and thousands. The accumulation coefficients for ruthenium 106 are also high.

Dead hydrobionts have higher coefficients of accumulation than live ones (Table 42). This circumstance acquires serious significance for the radioecology of neustonts due to the existence of the "antirain" of dead organic matter which results

in the concentration of dead animals and plants and their remains in the nearsurface microlayer of the pelagic zone and in foam. A.Y. Zesenko (1967) indicates that yttrium 91, cerium 144, zirconium 95, niobium 95 and ruthenium 106 are present in sea water on particles of organic matter and in colloidal form, and this predetermines their elevated concentration in the region of the surface tension film, and especially in the foam.

Table 42

Coefficients of accumulation (per wet weight) of radionuclides by hyponeustonic organisms dying in the course of an experiment (Polikarpov et alia, 1967)

Физиологическое состояние	Macrura, larvae			Planes minutus, juv.
	Cs ¹³⁷	Sr ⁹⁰	Ce ¹⁴⁴	Ru ¹⁰⁶
2 Живые	0.7	5	7	45
3 Мертвые	3	7	36	1400

Key: 1. physiological state; 2. living; 3. dead.

By concentrating radioactive materials neustonts firstly create in themselves incorporated sources of elevated doses of ionizing radiation, and secondly become themselves the first links in the migration of radionuclides both into the sea and onto dry land. We still do not know the significance for man of the accumulation of strontium 90 by sea fishes.

(Black Sea mullet, surmullet, garfish etc.) during the hyponeustonic phase of their life cycle, when they may, on finding /160, themselves in the nearsurface biotope, accumulate a correspondingly greater amount of radionuclides than the inhabitants of the underlying water mass (Zaitsev and Polikarpov, 1964).

b) The effect of radioactive materials on pelagic fish eggs.

The least radiosensitive organisms are bacteria and unicellular algae, and the most radiosensitive, invertebrates, including fish, particularly in the embryonic stages of development. Taking account of the cosmic background at sea level and the level of the dose yielded by potassium 40 in sea water and hydrobionts, we can expect the beta particles of strontium 90 - yttrium 90 emitted from solution due to external irradiation to have a biological effect on the development of the pelagic eggs of fish and other radiosensitive hydrobionts at an activity of 10^{-8} curies/l or over. At such a concentration the strength of the dose will be ten times greater than the cosmic background, the same number of times greater than the level of the dose of potassium 40 in organisms, and 100 times higher than the background due to potassium 40 radiation in sea water. However, if we also take into account the high coefficients of absorption of yttrium 90, the concentration of strontium 90-yttrium 90 capable of having a radiation effect on pelagic fish eggs will be correspondingly lower. In addition, Academician V.I. Spitsyn (cited from G.G. Polikarpov, 1964) lays special stress on the fact that radionuclides incorporated in chemical and biological

systems are most effective than those irradiated with the same dose, but by external sources.

The determination and quantitative assessment of all kinds of radiation damage to fish embryos and larvae, and of the radiation aftereffects during the transition of the fish to adulthood, is a highly important task to be tackled by radioecologists in the near future (Zaitsev and Polikarpov, 1964). The work done in this direction by A.Y. Zesenko, V.N. Ivanov (1966) and V.G. Tsytugina (1967) convincingly demonstrates its topical interest and importance.

The danger of a reduction in commercial fish stocks due to radioactive pollution of the surface of the ocean.

Generally speaking, the consequences of changes in the neuston assemblage of organisms under the influence of the radiation factor may be of two kinds: on the one hand, inhibition and degeneration of a whole number of fish and other radio-sensitive neustonts, on the other- a burst of development and sudden flourishing of bacteria, microphytes and macrophytes and radioresistant invertebrate forms.

We still do not know the values of the maximum permissible /161/ concentrations of radionuclides in sea water for normal life-function and reproduction of marine organisms -especially fish - in natural conditions. There are still no data on the range of radiation damage to fish, i.e. on the quantitative relations between moribund eggs, dying larvae and fry, and fish surviving to adulthood (both sterile and capable of reproduction), or on the

nature and tempos of radiogenetic change and degeneration of marine fishes. However, the material available does show the high radiosensitivity of the developing eggs of sea fishes and how very close are the concentrations of strontium 90-yttrium 90 increasing the frequency of occurrence of deformed fish larvae and the concentrations of the same radionuclide in the various parts of the Pacific and Atlantic oceans (Polikarpov, 1964; Polikarpov, 1966). It was this circumstance that led to the first step being made towards determining the probable consequences of radiation damage to ichthyoneuston (Zaitsev and Polikarpov, 1964).

Of course, all other things being equal, the essential prerequisite for a reduction in fish stocks is the presence of a chronically acting injurious agent distributed all over the sea or large areas of ocean, i.e. virtually throughout the hydrosphere. Global radioactive pollution fits the bill.

The systematic reduction of fish stocks of a particular species in time under the influence exerted by such a factor on eggs in the 0-5 cm layer can evidently be described as a first approximation by an exponential function (Zaitsev and Polikarpov, 1964):

$$N_t = N_0 e^{-0.693 \frac{t}{T}}$$

where N_0 is the initial number of fish, N_t the number of fish after t years, and T the time (in years) taken for the fish stocks to be reduced by half. The values of $e^{-0.693 \frac{t}{T}}$ can be found in the tables of I.N. Verkhovskaya (1954). For the

nomograms of the decline in fish stocks it is convenient to use a semilogarithmic scale. The results of the computations of T for certain fish species in relation to the percentage of eggs suffering radiation damage (5-100%) are shown in Table 43. It is assumed for the purposes of the calculations that all the eggs of a given species more than 5 cm from the surface of the sea remain unharmed and that the percentage of normal hatched prolarvae is independent of the depth at which development of the embryo took place.

The relationships described are possible only in conditions of chronic radiation acting with uniform intensity. Changes in the content of radioactive materials in the sea water must entail changes in the percentage of hyponeustonic eggs damaged. In other words, on normal variations in the numbers of fish may be superimposed variations in their stocks caused by changes in the intensity of the radioecological factor. /162

From all that has been said it follows that neuston is not only the most extensive assemblage of organisms but also probably the most sensitive on earth to the effects of radioactive pollution. Therefore the continuation or resumption of nuclear weapons testing is out of the question if the marine and oceanic stocks of fish and other organisms are not to be destroyed. Another great danger in this connection is the dumping of radioactive waste into the sea and the risk that nuclear-powered vessels or aircraft will bring about radioactive pollution of the latter.

As the result of a conjunction of certain ecological factors favouring the development of life, the sea-air interface became the focus of highly important ecological processes (Zaitsev and Polikarpov, 1967) occurring in the halosphere, and the neustonic stage is the crucial one. In the atomic age the anthropogenic radioecological factor has invaded the nearsurface biotope, exceeding in biological effect all the natural ecological factors. The spatial coincidence of the region of the sea's most important "incubator", with its high radiosensitivity, and the region of elevated radioactivity, and also the strong links between the neuston and other classes of hydrobiont and aerobiont communities, are evidence of the extreme importance and urgency of comprehensive research on the radioecology of neuston.

Table 43

Relationship between the time required for reduction of fish stocks by half (T) and the percentage of damaged eggs in the hyponeustonic layer (Zaitsev and Polikarpov, 1964).

Поражен- ность, % 1	T, годы 2		
	Кефаль 3	Ставрида 4	Хамса 5
5	63,0	71,0	100,0
10	30,0	35,0	50,0
20	14,0	17,0	24,0
30	9,0	11,0	16,0
40	6,6	8,2	12,0
50	5,1	6,5	9,6
60	4,2	5,4	7,9
70	3,5	4,6	6,8
80	3,0	4,0	5,9
90	2,7	3,6	5,3
100	2,4	3,2	4,7

Key: 1. percentage of damage; 2. years; 3. Black Sea mullet;
4. horsemackerel; 5. anchovy.

PART IV

THE DIFFUSION AND DISTRIBUTION OF NEUSTON
IN THE SEAChapter XV. General characteristics of the diffusion and distribution of neuston in the sea

On the basis of the information accumulated on the structure and composition of neuston, its ecology and frequency of occurrence the present chapter examines some of the general features of the spatial distribution of the nearsurface assemblage of organisms in the sea. On account of an insufficiency of data on many regions of the ocean it is still difficult to formulate the principles of the biogeography of neuston as the resultant of its ecology, diffusion, distribution and origin, but it is possible to analyse a number of environmental factors exercising a considerable influence on this aspect of the life of neustonts. Among them are: the distance from the shore and the depth, the temperature and salinity of the water, currents, piling up and removal effects, and some others.

Distance from the shore and depth

The distribution of the inhabitants of the nearsurface biotope of the pelagic zone is greatly influenced by wind currents. For neustonts this factor offers two alternatives: ejection onto the shore or removal out to sea. Since the first alternative has a lethal outcome it is quite reasonable to assume that shore "phobia" is one of the distinguishing features of the horizontal distribution of neuston components in the sea.

The following case tends to support this. The stations at which collections of hyponeuston were made in the Black Sea in 1960-63 were divided up into six classes according to the distance to the closest point on the coast. For each of these classes the average density of organisms of a given species (in spec./m³) in the 0-5 cm layer was calculated (Fig. 53). As can be seen from the figure, the abundance of pontellids increases markedly with distance away from the shore. In this particular instance no account was taken of the cases where the numbers of this crustacean near the coast increased strongly due to piling up of water or the influence of river run-off. These will be examined separately later. On the whole, Pontella in the Black Sea, as in other basins, behaves as an oceanic species whose abundance generally increases in the direction of the open sea, away from the coastal shallows and into deep-water regions. This much can be

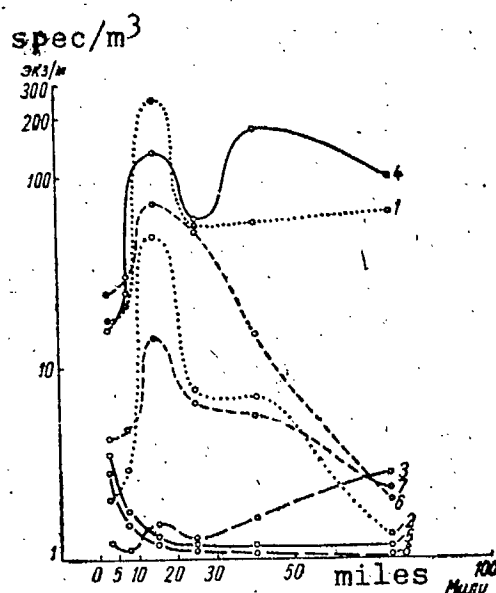


Fig. 53 - Number of organisms in the 0-5 cm layer of the Black Sea in relation to distance from the shore (in miles):
 1 - eggs of *Engraulis*, 2 - *Trachurus*, 3 - *Idothea*, 4 - *Pontella*,
 5 - *Labidocera*, 6 - Decapoda zoea larvae, 7 - *Brachyura megalopa* larvae, 8 - Amphipoda.

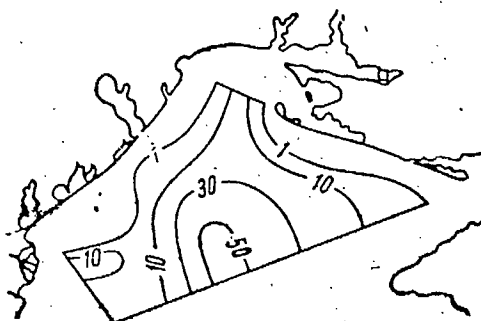


Fig. 54 - Abundance of *Pontella mediterranea* in northwestern part of Black Sea in July 1960 in relation to distance from shore and depth. Number of crustaceans in spec./m³ is indicated by solid isobars (Zaitsev, 1964a).

be seen, for example, from the maps of the distribution of Pontella in the northwestern part of the Black Sea in July 1960 (Fig. 54). Anomalocera patersoni behaves in similar fashion.

A third representative of the Black Sea pontellids - Labidocera brunescens - differs from the previous two in this respect (Fig. 53). In the first place the absolute abundance of the species is strikingly low: Labidocera is the least common pontellid representative in the open part of the Black Sea. Secondly, there is a distinct drop in numbers of the crustaceans in the direction of the open sea. A number of data show that L. brunescens is among the inshore pontellids to have adapted themselves to life in various shallow bays, lagoons and coastal salt lakes. Accordingly, Labidocera is less attached to the 0-5 cm layer than Pontella or Anomalocera, though it still shows a distinct preference for it (Table 38). Such a feature of the vertical distribution is obviously useful in inshore waters and close to the shore. As a result, L. brunescens is the only representative of the family to have mastered the nearsurface biotope of the Sea of Azov (where its numbers reach several hundred specimens per m^3) and a number of salt lakes adjoining the Black Sea. This is also confirmed by the eurythermicity of the species.

The average absolute abundance of I. stephensi (Fig. 53) is also low, but in some cases not to be examined here it reaches 3-500 spec./ m^3 in the 0-5 cm layer. The character of the curve shows that the highest abundance of Idothea corresponds to the pelagic zone. As early as 1933, B.S. Il'in assigned it to the

"halistatic biocenosis", while S.E. Kleinenberg, as already noted, reported dolphin stomachs filled with this crustacean.

Decapod larvae, which have a fairly high abundance away from the coast, reach their peak 10-30 miles off shore, after which their numbers decline abruptly. Such a picture agrees on the whole with the distribution of the parent individuals, which lead a demersal mode of life. Generally speaking decapod larvae are situated somewhat further seaward compared with the position of the main benthic biocenoses, in which the adult decapods are fairly numerous (Nikitin, 1964). An analysis of the depths above which the larvae of Black Sea decapods are discovered shows that they are sharply predominant numerically over the 20-50 m isobaths. Over depths greater than 100 m their density drops to 2-2.5%, which corresponds to depths of 20-50 m. Nevertheless, the absolute number of decapod larvae in the hyponeuston layer over the hydrogen sulphide region is very considerable due to the predominance of great depths in the Black Sea. Thus, whereas /166/ in the Black Sea the area occupied by the benthos is roughly 23% of the area of the entire basin (Zenkevich, 1963), the ratio of the total absolute abundance of decapod larvae in the hyponeuston layer over this region to the number over greater depths is approximately 1.1:1.

The mass removal of the larvae of demersal decapods from the shelf area obviously affects both their numbers and the length of the hyponeustonic phase of their development. In the opinion of M.A. Dolgopol'skaya (oral communication), young Macropipus

holsatus individuals from collections of hyponeuston made in the halistatic regions of the Black Sea are "backward" specimens whose settlement was delayed as the result of removal to biologically "bottomless" regions of the sea. How the life of such backward creatures ends if they find their way back to the shallows again is not clear. It may be that they die or are eaten. It is quite probable that the crab Nautilograpsus minutus Edw. from the "halistatic biocenosis" of the Black Sea, which is cited by B.S. Il'in (1933), referring to the earlier identification made by I. Markuzen and expressing doubts as to its accuracy, was also "backward" like M. holsatus. Since then this warm-water oceanic species has never been discovered again by anyone in the Black Sea and does not figure in the latest list of M. Bacescu (1967), who made a full systematic revision of the Decapoda of the Black Sea.

The fact that the megalopa stages tend to settle further out towards the open sea than the zoea stages may be due to their longer stay in the 0-5 cm layer. On the whole, however, the maximum density of the megalopa stages also corresponds to the shelf area.

The distribution of amphipods (Fig. 53) is distinctly inshore in character. These crustaceans, which dwell in the hyponeuston only at night, are less likely to be resettled by currents than decapod larvae, which remain under the surface tension film for twenty-four hours a day. Therefore the horizontal distribution of the amphipods in the 0-5 cm layer reflects chiefly the places where they stay during the daytime, although they may occur over the

hydrogen sulphide region.

Anchovy eggs are the most numerous component of the summer ichthyoneuston of the Black Sea and they are found all over it. The highest density of the eggs, however, corresponds to areas situated 10-20 miles from the coast (Fig. 53). On either side of this zone the number of eggs is markedly smaller, but in the central waters they are still three times more numerous on average than in the 10 mile inshore zone. According to the data of fish surveys made from the air, most of the aggregations of adult anchovy in the Black Sea in summer are to be found roughly 30 km (about /167/ 16 miles) from the coast (Krotov, 1938), which coincides on the whole with the area of maximum density of anchovy eggs in the hyponeuston. The same region is the place of maximum density of horsemackerel eggs (Fig. 53), and 30-50 miles away from the coast the numbers are still several times greater than near the shore.

Black Sea mullet in the early stages of ontogenesis display a very marked tendency to increase in density with distance from the shore and greater depth. Before the onset of spawning sexually mature mullet migrate to the open sea and deposit their eggs tens of miles from the shore. The only case of mass spawning (hundreds of individuals) by grey mullet (Mugil cephalus) was recorded in the Gulf of Mexico 50 miles from the shore over a depth of some 1400 m (Arnold and Thompson, 1958). In the Black Sea spawning mullet behave in the same way, as can be judged from the distribution of their eggs and larvae (Fig. 55). From the

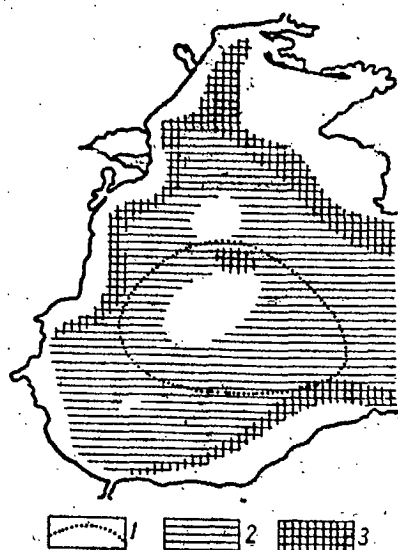


Fig. 55 - Distribution of eggs (1), larvae and fry of *Mugil salines* up to 10 mm long (2) and over 10 mm long (3) in the western half of the Black Sea in July-August 1961 (Zaitsev, 1964b).

Figure it can be seen that the eggs are found mainly in the halistatic region, whereas the larvae and fry approach the shore as they grow. The closer the fry are to the shore, the longer their body length. Fig. 55 does not show the sizes of the fry caught right near the shore since the expedition concerned did not explore the territorial waters of all the countries bordering the Black Sea. Nevertheless, it is known from numerous literary sources (Zambruborsht, 1949, 1962; Savchuk, 1965-1968) that the length of the fry of *Mugil saliens* caught in August and September in the surf zone in the western half of the Black Sea is 15-25 mm.

Thus, in view of the hyponeustonic character of their eggs, larvae and fry, mullet exhibit pronounced "shore phobia" before spawning, i.e. they execute catadromous spawning migrations within the sea. This explains too why, in small closed basins such as lagoons, coastal salt lakes, etc., and also when kept in artificial conditions, the mullet does not breed (Zaitsev, 1960a, 1964a, 1964b), even when given injections of hypophysis hormone (Krotov and Starushenko, 1963). This reflects the characteristic of adult Black Sea mullet - consolidated by natural selection - of depositing hyponeustonic eggs at a distance from the shore sufficient to ensure that they will not be tossed on land by waves, which would inevitably be the case if the mullet spawned in small basins. That distance from the shore and not depth is the chief prerequisite for the breeding of Black Sea mullet is shown by the discovery of eggs of Mugil saliens and Mugil cephalus in the central area of the shallow Sea of Azov (Zaitsev, 1964a). The impression is created that Black Sea mullet can be induced to spawn in artificial conditions (very desirable for the purposes of mullet culture) only as the result of substantial modification of the nature of these fishes through artificial selection. /168/

The examples examined in Fig. 53 show that the neustonic species or their developmental stages generally avoid the 5-10 mile nearshore zone and attain their maximum density in the waters beyond this zone. The density maximum may occur in the region of the shelf in the case of the merohyponeuston, which is

associated with the shelf biocenoses, or in the oceanic region in the case of the euhyponeuston and nektogenic merohyponeuston. But in either case it will be in waters more or less remote from dry land. The exceptions are Labidocera, with a high abundance in the inshore waters, and the benthohyponeuston, whose scope for diffusing horizontally is relatively limited owing to the brevity of its stay in the nearsurface biotope.

Such is the scheme reflecting the averaged data. For each actual case deviations from this scheme are possible, and there are reasons for them. Here are some examples.

Stations 729-733 (Table 44) belong to the same section i.e. Dnestrliman - sea, and they were executed during the day-time on July 13 th, 1960, in settled weather conditions. The composition and numbers of the various organisms at three stations generally reflect the overall pattern referred to above, but under the influence of a number of factors certain deviations from the pattern occur. In this particular instance Labidocera was actually encountered closer to the shore, but its maximum density was not at the shallowest point because station 729 was taken in the immediate vicinity of the mouth of the Dnestrliman, where the salinity of the water at the surface was only 8.22%.

The distribution of Anomalocera and Pontella conforms well to the scheme. The decapod larvae showed a maximum at the station closest to the shore because a hydrological front passed near by, with its characteristic concentration of hyponeuston. This may

also have been the reason for the increase in numbers of anchovy larvae at station 729.

Thus, the local hydrological conditions manifestly influence the distribution of hyponeustonic organisms, but the overall pattern is quite clearly marked even where the difference in salinity between the first and last points of the profile exceeded $9^{\circ}/\text{oo}$. /169/

Another example relates to a region of the Black Sea with a relatively stable salt regime. This is the section Cape Anapskii-Cape Inebolu, extending for 270 miles, which was executed in the

Table 44

Composition and density (spec./m³) of hyponeustonic organisms in the 0-5 cm layer in relation to distance from the shore and depth (Zaitsev, 1964a).

1 Номер станции	729	730	733
2 Расстояние до берега, мили	1	8	31
3 Глубина, м	9,5	16	28
<i>Labidocera brunescens</i>	0,6	1,4	—
<i>Anomalocera patersoni</i>	—	1,74	19,65
<i>Pontella mediterranea</i>	—	—	30,30
Decapoda, larvae	884,5	2,17	0,41
<i>Engraulis encrasicolus</i>	0,6	4,20	18,45
<i>ponticus</i> , ova	—	—	—
<i>Trachurus mediterraneus</i>	0,38	0,14	42,70
<i>ponticus</i> , ova	—	—	—
<i>E. encrasicolus ponticus</i> , larvae	41,20	0,29	—

Key: 1. number of station; 2. distance from shore, in miles; 3. depth, in metres.

course of 59 hours in the middle of August 1962. The weather was stable, the sea state no more than 2. The first station lay three miles from Cape Anapskii, the last 20 miles from Cape Inebolu. In all, eleven neustonological stations were taken in this section, the surface water temperature being $23.4-25.1^{\circ}\text{C}$ and the salinity $18.01-18.40^{\circ}/\text{oo}$.

Three abundant representatives of the hyponeuston, i.e. Pontella, anchovy eggs and surmullet, which do not leave the 0-5 cm layer at any time during the 24-hour period, were found at all or most of the stations on the section, their numbers, as shown in Fig. 56, increasing from the shore towards the open sea. Concerning this section across the Black Sea, it should be said that the regular circadian fluctuations in the abundance of anchovy eggs, caused by the nocturnal spawning of the species, does not upset the overall distributional pattern of the neustonic organisms in relation to "distance from the shore" and the associated "depth" factor.

Individual instances of a sharper deviation from the norm are known. According to the author's calculations, in the 0-5 cm layer over depths of more than 1500 m there are approximately /170/ 0.002 amphipods per m^3 and 0.04 cumaceans. Over a depth of some 2200 metres at a point 52 miles from the shore the seahorse Hippocampus guttulatus microstephanus it to be found, while over 2240 metres 63 miles from the coast L.N. Polishchuk discovered a comparatively large number of Calanipeda aquae-dulcis - a dozen of freshened shallow areas of the sea. These finds of neuston-

-ic and non-neustonic organisms, which are of definite zoogeographical interest though currents are said to have a considerable influence on the distribution of hydrobionts, are rare and cannot obscure the recurring elements of the relationship between neuston and depth. These are: confinement of the benthohyponeuston to the shallow inshore zone, a weaker but still evident association between the benthogenic merohyponeuston and the shelf, and the association of the euhyponeuston with great depths, and also with those larval forms which, on completion of the hyponeustonic phase, join the plankton or nekton. The composition of the neuston of a given water basin depends on the pattern of depths. The greater the preponderance of deep-water areas, the greater will be the percentage of euhyponeuston, the planktonogenic and nektogenic parts of the merohyponeuston, and bathyplanktohyponeuston. As the depths decrease the proportion of benthohyponeuston and the remaining (benthogenic) part of the merohyponeuston increases.

An example of a water basin with preponderance of benthohyponeuston and benthogenic merohyponeuston is the Sea of Azov, while one of a basin with a predominance of euhyponeuston, bathyplanktohyponeuston and plankto-nektogenic merohyponeuston would be the deep-water portion of the Black Sea, or, better still, the deep-water parts of open seas and oceans.

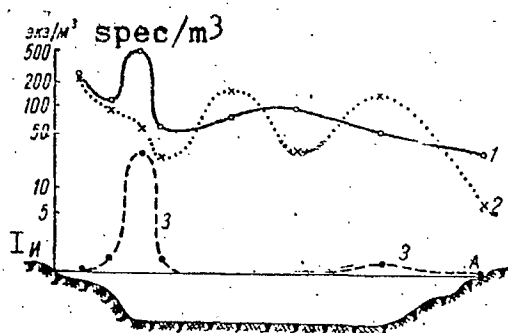


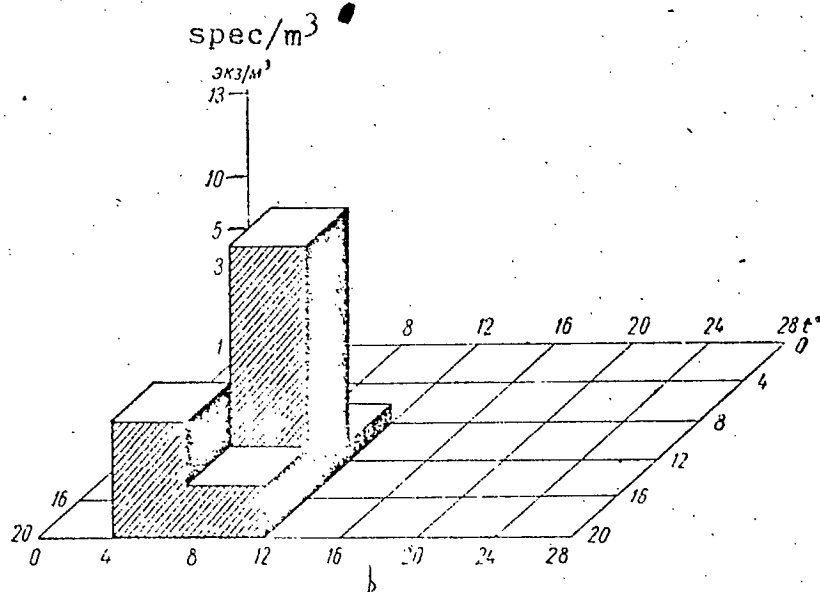
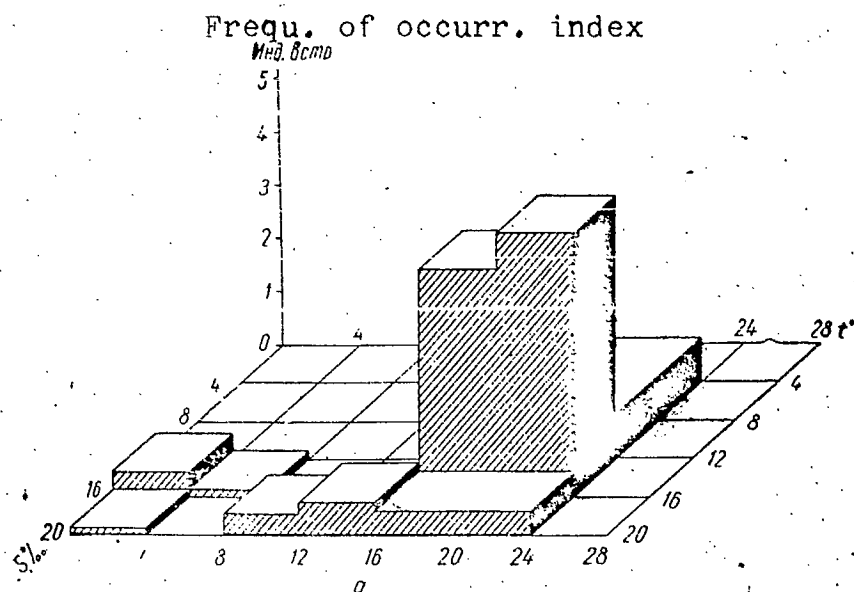
Fig. 56 - Density (spec./m³) of Pontella mediterranea (1), eggs of Engraulis encrasicolus ponticus (2) and larvae of Mullus barbatus ponticus (3) in the 0-5 cm layer on the section Cape Anapskii (A) - Cape Inebolu (I) in August 1962 (Zaitsev, 1964a).

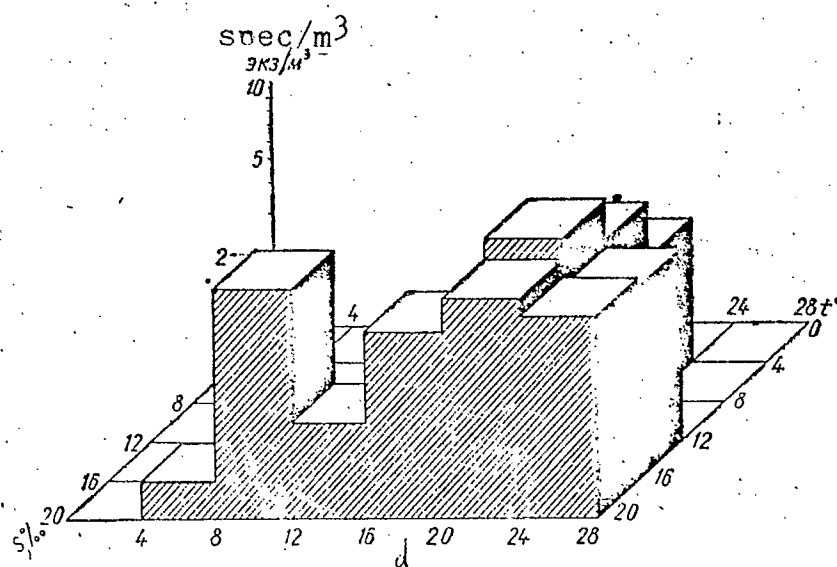
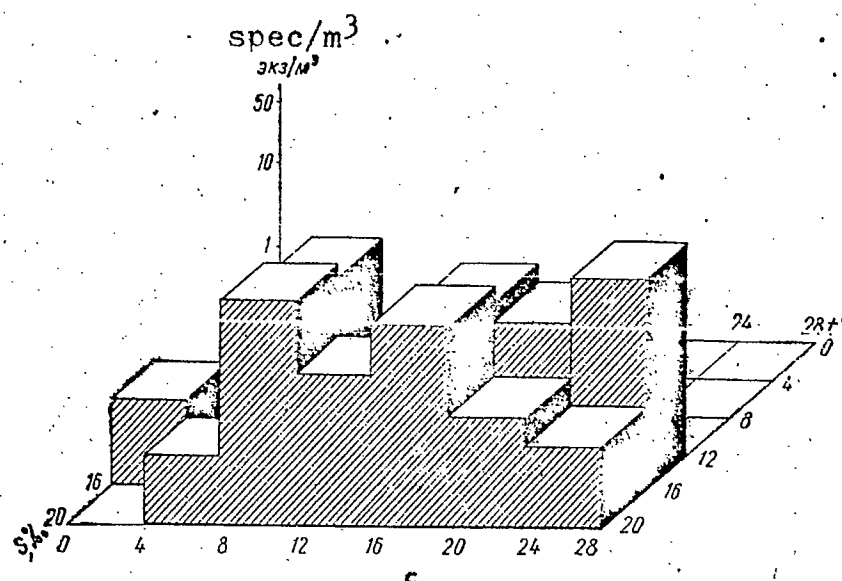
Water temperature and salinity

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As hydrobionts, hyponeustonic organisms depend on the temperature and salinity of the water, and this affects their distribution within a given water body and within the ocean as a whole. Owing to the large number of neuston collections made it is now possible to give the thermohaline characteristics of certain abundant components of the hyponeuston. To depict these characteristics a rectangular system of three coordinates was adopted. This method was first proposed for use in hydrobiology by A.V. Tsyban' to illustrate the corresponding properties of bacterioneustonic organisms. On the Ox axis he plotted the values of the surface water temperature, on the Oz axis the salinity values, and on the Oy axis the numbers of organisms of a particular species discovered at each value of water temperature and salinity. This method of depicting the temperature and salinity characteristics of a species gives more complete information than the method of TS diagrams proposed ear-

lier (Zaitsev, 1956). Fig. 57 (a-f) shows the relations of certain abundant species of hyponeustonic organisms to the temperature and salinity of the waters of the Black Sea and Sea of Azov, plotted from collections made in 1960-1965.





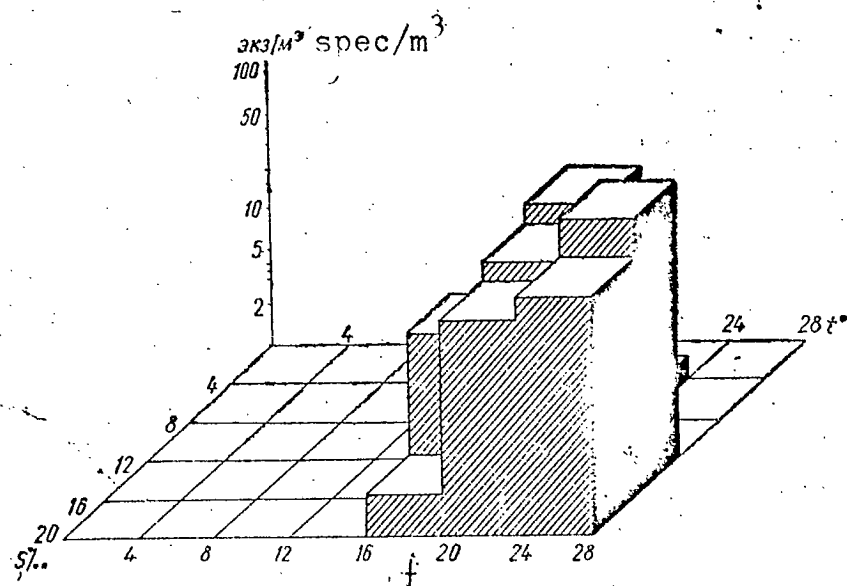
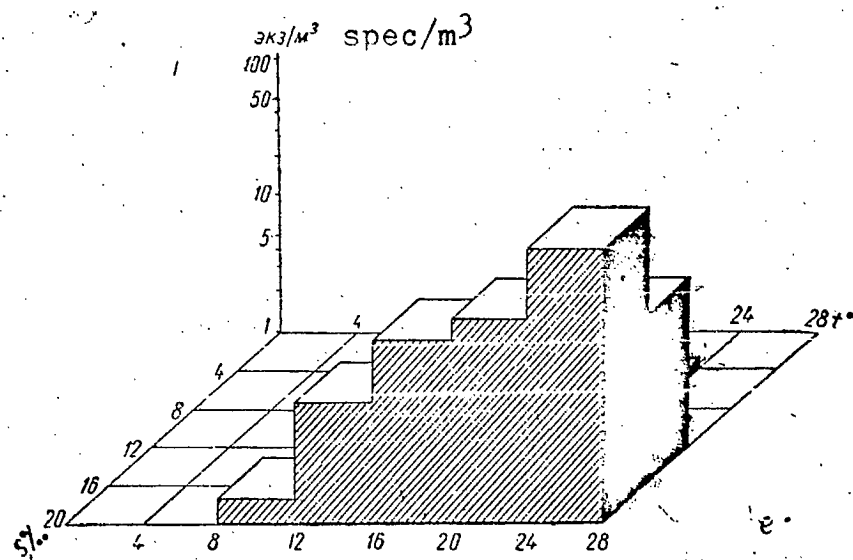


Fig. 57 - Prismatic echograms of certain neustonic organisms in the Black Sea:

a - Bacterium agile. On the ordinate axis are plotted the frequency of occurrence indices, i.e. the probability of discovering a species at a particular value of temperature and salinity of the water (Tsyban', 1968); b- eggs of Platichthys flesus luscus - a representative of the stenothermic (thermophobic) and euryhaline neustonts; c-Anomalocera patersoni and d- Idothea stephenseni - representatives of neustonts which are eurythermic and euryhaline in differing degrees; e - Pontella mediterranea and f - eggs of Engraulis encrasicolus ponticus - representatives of neustonts which are stenothermic (thermophilic) and halophilic in differing degrees.

The relationship of neustonts to water salinity and temperature can also be illustrated by the following example.

Stations 33 and 34 (Table 45) were taken on July 20th, 1961, in Zhebriyansk Bay of the Black Sea, less than 0.5 miles apart. Between these two points lay a clearly defined hydrological front, the presence of which was signalled at the surface by a narrow strip of foam and floating material less than 1 metre wide. As determined by V.S. Bol'shakov (1962), the chief hydrological characteristics at stations 33 and 34 respectively were as follows: depth 15.1 and 15.3 m, transparency 0.9 and 4.6, colour XVII- XIX and XIII on the colour scale, temperature at the surface 21.6°C and 20.0°C, salinity at the surface 6.87 and 13.53‰.

According to the "Atlas of Hydrological Characteristics of the Northwestern Part of the Black Sea" (Vinogradov, Rozengurt, Tolmazin, 1966), there are three distinct water masses in this area: river water (with a salinity rising to 6-7‰), surface water (10-18.5‰) and bottom water (19.5‰). Thus, station 34 was situated - as regards the 0-5 cm layer - in the river water mass,

and station 33 in the surface water mass. These two stations were worked between 08.00 hrs and 11.00 hrs.

At station 34 marine species were represented by solitary specimens only. The deficiency was made good by fry of the small southern stickleback and "chekhon" (Pelecus cultratus), which are not characteristic of saltier waters. The stomachs of these fry contained land insects mainly, which indicates that they stay and feed in the 0-5 cm layer for a lengthy period. At station 33 no sticklebacks or "chekhon" were found, but seahorse, pipefish, Black Sea mullet, horsemackerel and Pontella made an appearance, and the numbers of other marine species increased sharply.

Table 45

Composition and density (spec./m³) of organisms in the 0-5 cm layer at two closely situated stations corresponding to different water masses (Zaitsev, 1964)

1 Организм	2 Номер станции	
	33	34
Decapoda, zoëa	6,30	49,6
Brachyura, megalopa	1,0	17,0
<u>Pontella mediterranea</u>	0	0,5
Amphipoda	2,0	15,0
<u>Engraulis encrasicholus ponticus</u> , ova	8,9	29,1
<u>E. encrasicholus ponticus</u> , larvae	0,18	0,9
<u>Trachurus mediterraneus ponticus</u> , larvae	0	1,0
Blenniidae g. sp., larvae	1,48	5,8
Gobiidae g. sp., larvae	1,0	4,0
<u>Mugil saliens</u> , juv.	0	1,0
<u>Syngnathus</u> sp., juv.	0	1,0
<u>Hippocampus guttulatus microstephanus</u> , juv.	0	2,0
<u>Pungitius platygaster platygaster</u> , juv.	0	1,0
<u>Pelecus cultratus</u> , juv.	1,0	0
	3,0	0

Key: 1 - organism; 2 - number of station.

In this particular case the main factor responsible for the differences in the composition of the population of the 0-5 cm layer at the two closely situated stations was probably the salinity of the water, since the temperature difference was only 1.6^oC. In other cases/^{the} same species exhibit a clearly defined tendency to favour certain temperature conditions (Fig. 57). The influence of water temperature on the species composition of hyponeuston is graphically illustrated by representatives of the family Pontellidae. For the north (tropical) region of the Indian Ocean for example, 23 species of pontellids were described (Voronina, 1962). For the Mediterranean, ten species and subspecies are known (Trégouboff, Rose, 1957; Crisafi, 1960), for the Black Sea - three species, and for the Sea of Azov - one. The transition from the Mediterranean to the Black Sea - Azov region entails not only a drop in temperature from 17-13^oC to 10-0^oC, but also a more than twofold drop in salinity. Elimination of euhyponeustonic species may occur under the combined influence of these factors. In respect of salinity the difference between /176 the northern part of the Indian Ocean and the Mediterranean is small, amounting to a mere 2-3^o/oo, yet the difference in winter temperatures is more than 10^oC, since the surface water temperature in the northern part of the Indian Ocean does not drop below 25^oC. Thus, one of the main reasons for the sharp drop in the number of species of pontellids in the Mediterranean compared with the Indian Ocean is the temperature factor, or more precisely the limiting influence of the winter temperature minimum on the species

composition of the warm-water euhyponoestonic crustaceans.

In the tropical and subtropical regions of the Pacific, according to the data of a number of authors (Brodskii, 1950; Sherman, 1963; Geinrikh, 1960, 1964; Voronina, 1964), there are 23 species of pontellids. In Posyet Bay in the Sea of Japan, four species have been discovered (Brodskii, 1957), while in the Bering Sea only one has come to light - Epilabidocera amphitrites (Brodskii, 1957; Zaitsev, 1964a). Hence, at similar salinity values the number of pontellid species suffers a sharp decline meridionally as the temperature of the nearsurface layer of the pelagic zone drops.

On the whole the aquatic part of the marine neuston consists chiefly of thermophilic and halophilous species and is therefore most diverse in the tropics, whereas in the temperate zone it becomes most varied during the warm part of the year and in water areas subject to mild freshening only. The species poverty of the hyponeuston in freshened areas of the sea is clearly illustrated by Taganrog Bay in the Sea of Azov, the Gulf of Odessa and some other regions. The same thing was found by Specchi (1966) when studying the hyponeuston in the Gulf of Trieste in the Adriatic. On examining four samples taken in May 1966 Specchi discovered neither Pontellidae, nor Sapphirinidae, nor Isopoda, nor any other abundant representatives of the Adriatic hyponeuston, and only an abundance of decapod zoea and metazoea larvae distinguished the nearsurface layer from the underlying ones. This case calls to mind the examples already

examined (see Tables 44 and 47) in which the larvae of higher crustaceans exhibited greater abundance in the nearsurface layer of an area of the sea with low salinity.

The poverty of neuston in the inshore zone of a sea may also be caused by water mass removal effects, but an example from the Gulf of Trieste, which is the the freshened northern corner of the Adriatic, most likely reflects the response of neustonts to low salinity. Collections of Adriatic neuston made in October-November 1967 by L.G. Kulebakina and examined by L.M. Zelezinskaya, reveal marked impoverishment of the species composition and numbers of pontellids and other species north of the 45° parallel compared with the central and southern regions (Fig. 58).

Currents

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The distribution of neuston is greatly influenced by surface currents and, directly, by the wind, which is capable of shifting epineustonic forms about the surface of the water. Because of its topography the film of neustonic organisms can be detached by currents and carried off elsewhere, where it once again forms a high concentration of neustonts. In terms of lability neuston ranks between pleuston and plankton. It differs from pleuston (in this regard) in that its distribution is influenced mainly by currents, and not by winds. On the other hand, it differs from plankton in that it may be removed entirely by the surface currents to another area of the sea.

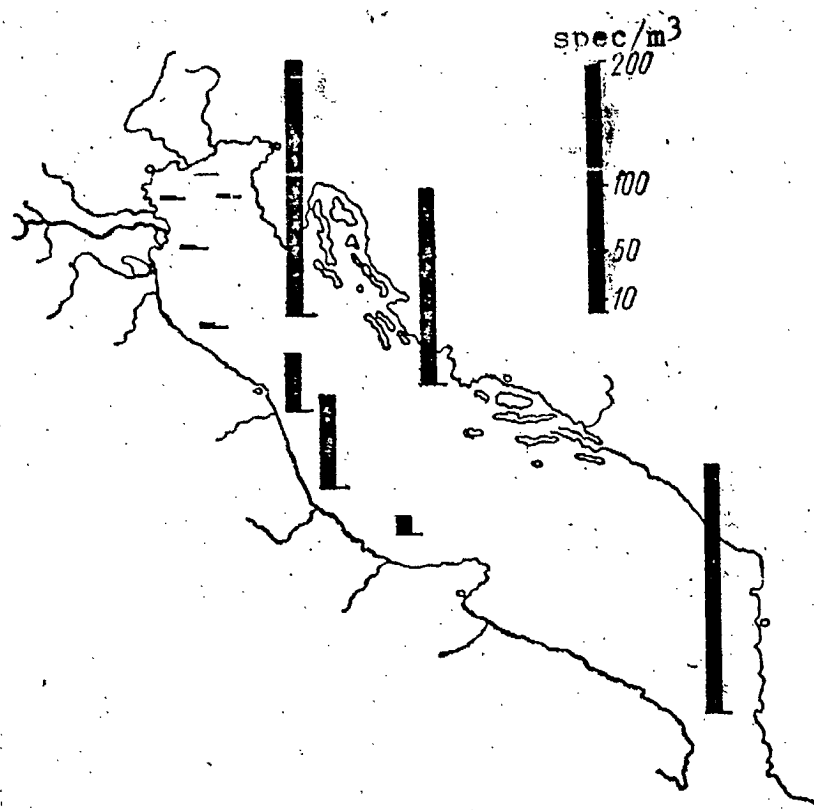


Fig. 58 - Density of *Pontella mediterranea* in different regions of the Adriatic in October-November 1967.

If we represent the surface of the sea as a pair of zones of cyclonic and anticyclonic circulation, divergence and convergence, upwelling and sinking of water, etc., the general rule for the distribution of neuston would be that its areas of maximum development correspond to the second half of each pair of zones, i.e. to the regions of anticyclonic circulation, convergence and sinking of water. This water, called "old water" by V.G. Bogorov (1967), is distinguished by low phytoplankton productivity. In the block diagram (Fig. 59) constructed by M.E. Vinogradov and N.M. Voronina (1964), the zone of maximum

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neuston development corresponds to the nearsurface layer of the macroplankton zone. This feature of the distribution of neuston in the sea is due to the effect of surface currents and the fact that the nearsurface assemblage of organisms has little or no direct dependence on the producers.

The mechanism of the concentration of neustonts in regions of convergence is basically identical to that of the formation of concentrations of phyto-, phytophagous and predatory plankton referred to in the papers of M.E. Vinogradov and N.M. Voronina (1964), V.G. Bogorov and N.M. Voronina (1967), and V.G. Bogorov (1967). In simplified form it can be described as follows.

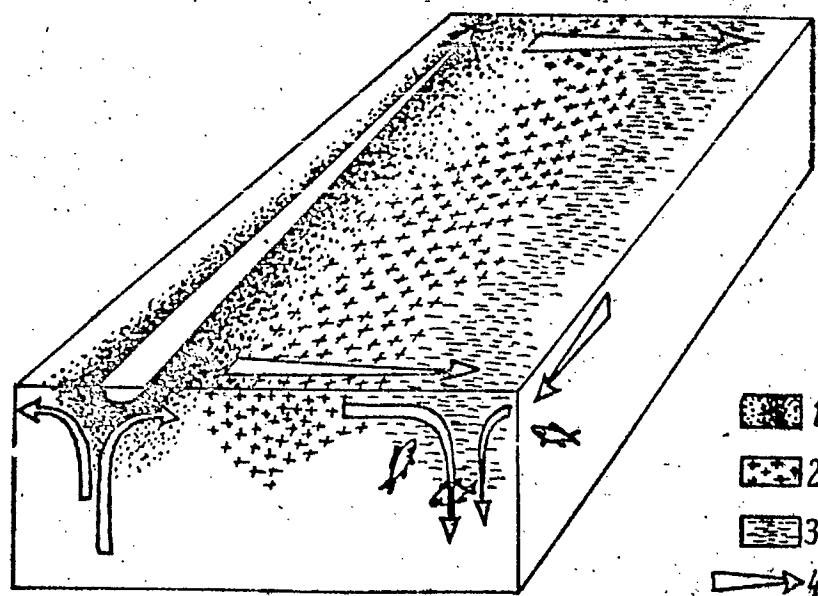


Fig. 59 - Block-diagram of distribution of maxima of various organisms in tropical waters in connection with circulation: 1- phytoplankton, 2 - small phytophages, 3 - predators, large phytophages and aggregations of fish, 4 - direction of currents (Vinogradov and Voronina, 1964).

In regions of divergence there is an upwelling of deep water rich in nutritive substances and abundant phytoplankton /179/ develops. As the water spreads, it "ages", its plant population becomes impoverished, and the quantity of phytophagous organisms increases. This is then followed by an increase in the numbers of carnivorous invertebrates and fish. In regions of convergence, where the now finally "aged" water descends, the animal population concentrates, together with various types^{of}/autochthonous and allochthonous floating material. Later, hydrobionts carried by currents into regions of sinking water suffer various fates, determined largely by the specific gravity of the bodies of the organisms, or their buoyancy. Organisms with neutral buoyancy or an insignificant reserve of positive buoyancy (planktonts) are quite easily dragged down by the descending waters. Organisms with a greater reserve of positive buoyancy (neustonts) easily resist submergence and remain in the nearsurface biotope, to which they are adapted by a whole complex^{of}/morphological and physiological characters and behavioural characteristics (Fig. 60).

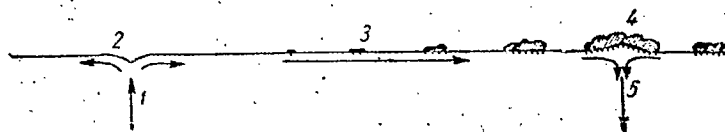


Fig. 60 - Schematic diagram of the formation of concentrations of neuston in regions of converging currents.

1.-ascent of subsurface waters rich in biogenic materials;
2 - region of divergence, abundance of phytoplankton and dearth of neuston; 3 - transport of water in direction of regions of convergence, abundance of neuston and dearth of phytoplankton, accumulation of foam and floating material; 5 - descent of water containing mainly macrozooplankton,

Because of the continuity of this process in regions of convergence high concentrations of neuston, floating material and persistent clumps of foam form. The abundance of nonliving organic material in the form of the foam provides a basis for the development of a rich bacterioneuston. This in turn forms the basis of the subsequent links of the neustonic assemblage of organisms. As a result the water, which is "old" as far as the producers are concerned, proves to be "young" for the reducers and consumers, while regions which have been unfavourable for phytoplankton and phytophagous zooplankton become highly favourable for the existence of all links in the neuston chain - from bacteria to fish. This is why, for instance, there are far fewer species of hyponeustonic pontellids in the highly productive equatorial region of the Pacific (Bogorov, 1967) than $10-20^{\circ}$ to the south or north (Geinrikh, 1960; Voronina, 1964). The abrupt minimum of the nearsurface species at the equator is ascribed by Voronina to the equatorial divergence and its consequence, i.e. to the action of the meridional component currents in carrying /180/ pontellids and other denizens of the nearsurface biotope away from the equator. Therefore the distribution of the biomass in the 0-5 cm layer is inversely proportional to that revealed by vertical hauls, which in fact do not take account of neuston. However, the absolute biomass of neuston is so small compared with that of the plankton of the entire water mass that the overall distributional pattern of the latter on the scale of oceans, when it is a question of estimating the organic resources of the

halosphere and their distribution, as in the papers by V.G. Bogorov (1967), V.G. Bogorov and L.A. Zenkevich (1966) et alia, remains unchanged. Because of the high abundance of bacteria and the early developmental stages of hydrobionts the secondary production of the neuston must be higher than that of the plankton, but its chief value in the water basin is measured not by indices of biomass and production but by the role it plays in the development of ecological processes and the cycle of substances in the ocean.

Because the position of the regions of diverging and converging currents materially affects the distribution of the nearsurface assemblage of organisms, it is essential for neustonological purposes to compile special maps based on the dynamic surface of the ocean. The first experiments in this direction were conducted in the Black Sea. They revealed that in the most clearly defined and stable regions of convergence, such as to the south of Capes Kaliakra and Sarych, high concentrations of hyponeuston, floating material and foam are encountered from year to year. It is interesting to note that the regions of converging currents on the ocean surface are attracting more and more attention from hydrobiologists and ichthyologists (Ozawa and Matsuike, 1966; Ozawa and Nakamura, 1966). Of course it cannot be said that neuston develops only in regions of convergence. Those of its components which develop most rapidly (bacteria and protozoans) also occur in regions of divergence, but as we get closer to the area of sinking water the composition of the neuston gradually "matures" and the oldest hyponeustonic stages of

invertebrate larvae and fish fry are commonest among the accumulations of floating material generally characteristic of regions of convergence. This is the scheme of the formation of persistent concentrations of neuston, but in nature there are also ephemeral regions of converging currents, the life of which is measured in hours or days. Here also high concentrations of neustons are formed, but they break up as soon as the forces which brought them together cease to operate. Examples of such temporary regions are storm belts. At wind speeds exceeding 5-6 m/sec. the development of a wind current is accompanied by the formation of storm belts extending in parallel lines along the path of the wind (Ozmilov, 1960). The distance between the striae is proportional to the depth and diminishes over shoals. In /181/ striae the same phenomena occur as in other regions of convergence, only in this case the accumulations of neuston form narrow (less than 1 m), long strips extending in the direction of the wind. They are easily visible to the naked eye - largely because of the foam and floating material arranged in long parallel lines. Particularly striking against the blue background of the sea are the strips formed by concentrations of contrastively coloured neustons, such as the carmine-red Gymnodinium breve or ochre Sargassum. Special investigations revealed that because of their high buoyancy hyponeustonic sargasses find it easy to remain at the surface, forming characteristic wind-rows in stormy weather. Only strong winds can drag down the least buoyant thalluses in a storm (convergence) stria (Woodcock, 1950; Faller and Woodcock, 1964).

Planktonic organisms with neutral buoyancy are easily dragged down, and this is one of the most important reasons for the abundance of macroplankton in the downflow of regions of convergence. In the southern part of the Atlantic K.V. Beklemishev (1958) observed storm striae up to 3 km long and over 1 m wide forming in winds of strength 5-6. In these striae salps (Thalia longicaudata) predominated in quantities of at least 2500 specimens per cubic metre of water. The salps were situated not only near the surface, as is characteristic of neustonts, but also at a depth of at least 6 m and in such numbers as to clog the screens of mechanical filters, although the Kingston valves were placed 5-5.6 m from the surface of the water. After the wind abates the storm striae become eroded and the neustonic organisms are redistributed by the surface currents.

Small-scale regions of convergence may form on the surface of the sea in calm weather also, as the result of thermohaline circulation. Owen (1967) observed striae in the Pacific which were made up mainly of Oikopleura longicaudata. The width of these striae was 2-8 cm, the length up to 30 m. The accumulation of organisms extended vertically to a depth of 5 cm. Similar striae formed by certain hyponeustonic organisms can also be observed in calm weather on the surface of the Black Sea.

Yet another type of short-lived and small-scale concentration of neustonts occurs under the influence of turbulence currents like those that form on the surface of a river beyond the buttresses of a bridge. One such case off Cape Rybach's in the

Crimea was reported by A.N. Bulavinov (1963). Sixty metres from the shore at this point there is a solitary rock jutting out above the surface. Between the rock and the shore there flowed a strong easterly current. On passing the rock the right /182/ branch of the current diverged and formed a vortex (Fig. 61), in the centre of which there was a circular patch of neuston measuring $3-4 \text{ m}^2$. From ten to twelve pontellids were counted in 1 dm^2 of water surface at this point. T.S. Rass informed the author that in the Pacific, on the lee side of buoys rigged by the "Vityaz'", such large concentrations of organisms formed in the nearsurface layer that they attracted albatrosses.

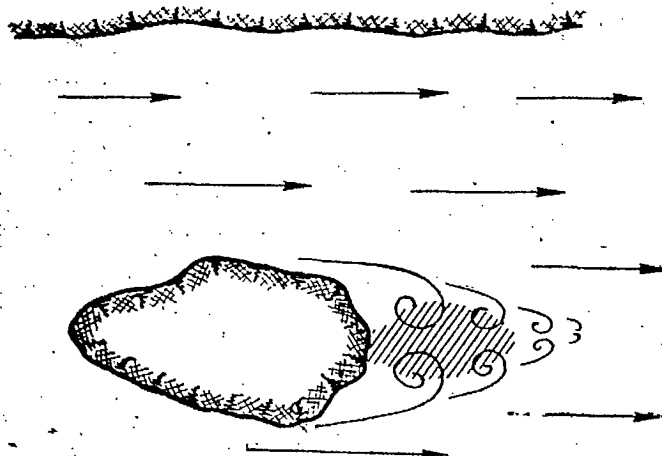


Fig. 61 - Example of the formation of a patch of neuston (hatched) in the zone of turbulence under the lee of a rock (schematic diagram) (Zaitsev, 1964a).

The examples given show that neuston reacts sensitively to permanent and temporary, large-scale and small-scale surface currents, being distributed and redistributed under the influence of the water mass prevailing in the sea in that place and at that time. Near the shore this relationship is rendered more complex by the piling up and removal of water.

Piling up and removal effects

Pure wind surface currents can be observed only in the open sea, far from the shore. In the inshore zone wind currents inevitably lead either to a lowering or raising of the sea level, causing the removal or piling up of water (Zhukovskii, 1953). The removal and piling up of water, being hydrological effects, have gradations reflecting the velocity at which the surface water is carried away from the shore or accumulated in the inshore zone, and produce biological consequences of corresponding strength in the form of changes in the composition of the population within their sphere of action (Koval', Rozengurt, Tolmazin, 1968). /183/

As in the case of surface currents in the open sea, the most sensitive biological indicator of removal and piling up effects is neuston. Neuston is the first of the pelagic assemblages of organisms to be carried away to the open sea by slope currents, and the surface of the sea near the shore is then left without neuston. In such cases deep water rich in nutrients ("young" water) rises to the surface and pelagic microphytes develop in it, though not neuston because the surface layers are constantly being removed from the shore. Depending on the force of removal,

the first signs of neuston can be detected in such situations 10 miles or more from the coast. The circadian migrations of the benthohyponeuston continue even when removal of water occurs, but at such times the migrants obviously do not find the food and other conditions in the nearsurface biotope which are observed when neuston is present. This point requires further special research, but it has already been established in particular that the breeding of benthonic and benthohyponeustonic organisms is inhibited in the event of persistent removal, especially in summer, but that after removal has ceased oviposition and hatching of larvae occur rapidly, as though to compensate for the enforced delay in this process during the period of removal.

The cause of the cessation and resumption of breeding can be seen not only in the removal or return of neuston with its food resources and biologically active foam, but also in other factors characterizing a particular water mass, above all the water temperature. The breeding of many organisms, and especially invertebrates, continues during both the warm and the cold parts of the year, but the removal of water, which in this context means the removal of neuston, invariably causes the retardation or inhibition of this process, both in winter and in summer. As far as the distribution of the neuston is concerned, even the weakest incipient removal effect, which has not yet led to a change in the water temperature at the surface or to transport of water masses, can chase neuston away from the shore, together with driftwood, foam, oil slicks and other floating material.

Piling up affects the distribution of neuston in the opposite way. If it is weak and the waves are small, there is an increase in the quantity of neuston in the inshore zone and typical open-water forms appear, such as pontellids, mullet eggs, etc. Accumulation of neuston is especially marked in gulfs and bays, into which it is "herded" from adjacent water areas situated further seaward. If the prevailing onshore wind strengthens and the waves grow bigger, the returning neuston becomes intermingled, dies and is cast up in large quantities on the shore. At such times the process of foam formation is /184/ intensified due to the increase in the amount of organic matter entering the water (as a result of the injury and death of the organisms) and the abundance of air bubbles produced by the waves.

Thus, removal and piling up effects have a considerable influence on the distribution of neuston close to the shore, and this must be taken into account when studying neuston in this part of the sea.

Neuston in the "contact" zones of the sea

The concept of "contact" zones in the sea expounded in the recent papers by K.A. Vinogradov (1966-1968) embraces copious and comprehensive factual material indicating the necessity for a deeper and more specialized study of the natural boundaries of the sea. Vinogradov includes among these the "sea/air", "sea/shore" and "sea/bottom" systems, and the boundary zones of the various water masses within the pelagic division. One need merely recall the abundance of life at the polar and hydrological fronts, in

the density discontinuity zones of the water, in the nearsurface biotope of the pelagic zone, on the shelf etc. to become convinced that Vinogradov is right about the existence of specific contact zones in the sea and that these boundary biotopes between water and land represent promising areas of biological research. The magnitude of the contact zones of the sea differs depending on the criterion used. For example, Vinogradov includes in the zone of "oceans and continents" even the area of the supralittoral, littoral and upper sublittoral right next to the water's edge, lagoons and limans, and also vast tracts of seas of the mediterranean type. If the boundaries between the contact zones are viewed on a scale commensurate with the scale of the neuston biotope, it is easy to see that these areas must play an important role in the biology and distribution of neustons and other classes of communities associated with the neuston.

It is impossible to place the "sea/bottom", "sea/shore" or "sea/river" contact zones within boundaries equally as precise as those of the "sea/air" zone. This is the most distinct and contrastive boundary surface of the sea, and it is no accident that only a few pleustonic species cross it, and even then only with the part of their body adapted for this purpose. Other boundaries are freely "violated", but often these crossings cannot be classed as violations because they represent phases of biological cycles and ecological processes occurring in certain biotopes and environments. For example, migratory fish easily cross the boundary between sea and river and penetrate far upstream, the organisms of the benthonic infauna burrow deep into the bottom, /185/

others settle on rocks above the waterline, being satisfied merely with a periodic wetting, and so on. All this goes to show that the boundaries of the contact zones are to some extent or other relative. Nevertheless, the pattern of the occurrence and distribution of neuston in these zones leads us to conclude that the data of neustonology constitute a convincing argument in favour of the concept developed by K.A. Vinogradov.

The main dwelling place of neuston is the sea/air contact zone, but being subject to the action of currents it is easily swept away and as a result "stumbles across" other contact zones. The consequences of such "collisions" affect both the neuston and the life of the biological structure with which it has come into contact. Thus, willy-nilly, the neuston is forced into new associations when it enters other contact zones owing to circumstances beyond its control. In addition, many neustonts themselves seek different contact zones when taking part in the appropriate ecological processes. Finally, situations exist where it is difficult to distinguish between coercive and non-coercive factors and to explain which of them is more responsible for the creation of a given situation. And so it is with the superconcentrations of neuston at the hydrologic fronts of rivers.

The area of contact between river and sea water is termed a river hydrologic front. River hydrologic fronts are distinguished by the clearly marked colour boundary of the contiguous water masses, an overfall and converging currents (Bol'shakov, 1967, 1968). Like other regions of convergence, the river hydrologic front is marked on top by an accumulation of persistent

foam and driftwood and an abundance of neuston. The width of the hydrological front, according to measurements made in the Black Sea, is very small, being about 1 m (Bol'shakov, 1962), and sometimes only 0.5 m (Zaitsev, 1964a). At the same time, the narrower the front the higher the density of hyponeustonic organisms. Visual underwater observations at ^{the} hydrologic front provide valuable information on the hyponeuston, and particularly on its distribution. One such set of observations was conducted by the author in August 1963 in the Gulf of Odessa, into which extend the long branches of the Dniepr hydrologic front. Some 200 m from the shore a strip of foam 30-60 cm wide formed, so to speak, a boundary face between the comparatively turbid water situated to seaward and the transparent water closer to the shore. The surface of the water beneath the patches of foam and in the gaps between them literally teemed with hyponeuston. Amid fragments of algae and empty shells of freshwater gastropod mollusks, lumps of wood and land insects, seeds and all sorts of debris swam fry of grey mullet and frogfish, larvae of blenny, sole, anchovy, zoea of decapods and megalopa of crabs, isopods, /186/ pontellids, and also a host of smaller creatures indiscernible to the naked eye. Most numerous were the sporting pontellids. They were constantly jumping and falling, now plunging to a depth of 1-2 cm, now rising to the surface again to leap out of the water once more. Possibly the word "sporting" in this case is not very apt, since the leaps became markedly more frequent when the hand of the observer holding a white notepad approached the surface of the water. In spite of the high concentration of organisms at the hydrologic front, they occupied a layer of water

no more than 3-5 mm thick and only the occasional surge of a wave plunged them temporarily 2-3 cm below the surface. On the one side - that of the overfall (in the turbid water) - no hyponeuston was observed, on the other (in the transparent water) the solitary pontellids and isopods merely served to emphasize the large numbers concentrating at the front.

It was noted that well away from the river, where the water masses meeting at ^{the} hydrological front differ less than they do closer to the mouth, the density of neustonts in the overfall is also less. This is especially true of the Chernomorka area, through which pass the boundaries of the Dniest hydrological front at its greatest extent in spring and summer (Vinogradov et alia, 1966). Here, during the passage of the above-described front in August 1963, some 8-10 pontellid specimens per dm^2 of sea surface were discovered in the overfall.

Another case dates back to July 1961. Observations and measurements were conducted off Chernomorka pier. At 11.00 hours the number of pontellids was no more than 1 per $5-6 \text{ m}^2$ of sea surface. By 12.00 hours the south current had brought clearer water to the pier preceded by a strip of foam not much wider than $\frac{1}{2}$ metre. A neuston net towed in the strip brought a rich haul. Calculations showed that there were up to 15 Anomalocera per dm^2 of sea surface. Within another hour (at 13.00 hours) the strip marking the position of hydrologic front was a long way off and the haul in the new sample taken was the same as at 11.00 hours.

Distinct accumulations of neuston form at the hydrologic

fronts of rivers in the Caucasus, such as the Kodori, the Inguri, the Rioni etc. According to the observations of V.P. Zakutskii, the hydrologic front near the mouth of the river Kodori on August 13 th, 1963 had a width of about 0.5 m. Along it extended a long line of birds - shearwaters, gulls, terns - pecking hyponeuston and land insects. Samples obtained at this station (unfortunately the net could only be towed at an angle to the overfall) revealed that the water here contained a very large concentration of pontellids and larvae of Black Sea mullet, anchovy, decapods and other neustonts.

Another observation and measurement was made by Zakutskii /187/ on September 11th, 1963, at the hydrologic front of the Danube. The width of the strip of foam was approximately 25 cm. Making a 2-metre sweep with a half-submerged drop net having a collar diameter of 25 cm, Zakutskii fished a portion of the hydrologic front 2 metres long. Laboratory examination of the sample revealed 2 striped mullet fry, 61 grey mullet, 3 pipefish, 117,760 Pontella, 36 isopods, 39 shrimp larvae and 4 megalopa of crabs. It is not difficult to calculate that in this particular case there were over 2000 large neustonts per dm^2 of sea surface.

Since river hydrologic fronts in the Black Sea cover a distance of hundreds of kilometres, it will be readily understood that they play an important role in the distribution of neuston in the water basin. They have also become places where masses of neuston are sampled for various laboratory purposes.

The fact that neuston concentrates at river hydrologic

fronts can also be proved by visual observations, but it is far more difficult to explain the reasons for this phenomenon. There is no doubt that one of the reasons is current convergence, whose mechanism was examined earlier. However, this does little to explain the formation of such high concentrations of organisms, the more so as the streams of water bringing the neuston to the hydrologic front can only be of marine origin and not from the river. Another factor leading to the concentration of neustons may be the advancing river water mass. Being lighter, river water, on entering ^{the} sea, spreads over the surface of the sea water, and the mobile neustonic organisms gradually retire before its advancing front, thereby creating an elevated concentration at the hydrologic front. Both these factors are coercive and operate without the collaboration of the neustons, but the organisms themselves cannot be ignored. It is quite obvious that such rapidly moving animals as fish fry, isopods and pontellids could quite easily flee from the immediate vicinity of the river water and stop at a safer distance from the hydrologic front. However, they do not, and even in calm weather they stay right in the overfall area. It is probable that something attracts them here, such as an abundance of food for example. Owing to the high concentration of dead organic matter in the form of ~~dam~~ and the bodies of hydrobionts (Zelezinskaya, 1966c), the overfall area becomes a focus for the development of a very rich bacterioneuston (Tsyban', 1966) and other initial links of the neuston serving as food for large invertebrates and fish. The trophic factor

appears to be one of the important reasons why the neustonic forms are in no hurry to leave the area of the hydrological front.

At the present time the only direct proof of the abundance of life in the contact zone of sea and river on the scale described above is the data of neustonological investigations. /188/ However, as the boundary between river and sea water lies not at the surface but beneath it, it may be hoped that similar visual and instrumental observations of plankton will provide equally interesting information. The neustonological data also indicate a direct connection between neuston and the contact zone of sea and land.

In the first place, there is a natural movement towards the surf zone on the part of such neustonts as Black Sea mullet fry, which in all seas of the tropical and temperate zones begin feeding in the shallowest gulfs, bays, lagoons, limans, and estuaries after completing the hyponeustonic phase of their lives (which may last up to 7-8 months). Here the "sea/shore" zone, as it were, receives the "baton"* from the "sea/air" zone. But there is also a forcible encounter between neuston and the sea/land boundary. This occurs during piling up effects, when the waves pound and toss up on the shore the suspensoids contained in the water masses, most of which are hydrobionts, and primarily neustonts, since the latter are most vulnerable to wave action and stranding. At present there are no data on the quantitative aspect of this phenomenon. There

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By analogy with the relay race in athletics - Translator's note.

is no doubt however that a vast quantity of neustonts are cast up on the shore and that the foam which wets the rocks and permeates unsolidated soils consists largely of the bodies of forms from the nearsurface assemblage of organisms and their fragments. This time there is a "baton-change" of a different kind, involving the transfer from the "sea/air" contact zone to the "sea/shore" zone not of live organisms which are to continue their existence in the new environment, but of the matter and energy contained in the dead neustonts, which then undergo further transformation. There are grounds for stating that the enrichment of the shore by foam replete with organic substances is directly connected with the development of the fauna in the midlittoral zone, which is amazingly abundant on the apparently lifeless wave-washed sandy beaches. For instance, on the bar of Donuzlav Bay in the Crimea O.B. Mokievskii (1949) counted up to 3100 specimens of the mollusk Mesodesma corneum (Poli) per square metre at depths down to 7 cm.

In the midlittoral zone of the Rumanian coast of the Black Sea, on a narrow strip a few metres wide demarcated by the boundaries of the advancing and receding waves, M. Bacescu and his co-authors (Bacescu et alia, 1966) counted beneath 1 m² over 2000 specimens of M. corneum, up to 5000 specimens of the polychaete Ophelia bicornis Savigny and roughly 35,000 specimens of the amphipod Pontogammarus maeoticus (Sov.). In the same strip, in the Danube-Dnestr interfluvium, V.A. Sal'skii (1959) discovered 776 specimens of M. Corneum at depths down to 60 cm under 1 m². Naturally, such an abundance of large organisms can dev-

dev-/
elop only where there is a good food supply. In fact, the interstitial fauna includes such diverse systematic groups as Protozoa, Coelenterata, Turbellaria, Nematoda, Archianellida, Polychaeta, Oligochaeta, Copepoda, Isopoda, Gastrotricha, Kinorhyncha and others (Govindankuttu and Balakrishnan, 1966). As was convincingly demonstrated by the famous specialist L. Laubier (1967) for polychaetes, the interstitial species possess special adaptations for life and nutrition in their specific environment. The establishment of a connection between the quantity of organic matter and microfauna in sandy beaches, especially bacteria and ciliates (Fenchel, Jansson, 1966), provides further confirmation of our hypothesis that a link exists between the neuston and psammon in the "sea/shore" contact zone.

The "sea/bottom" contact zone is also directly connected with the distribution of neuston. This is demonstrated mainly by the existence of a large group of benthohyponeustonic organisms, the lives of which are divided equally between two contact zones- "sea/bottom" and "sea/air". Hence, the disposition of the former also determines the distribution of the benthohyponeuston in the sea. In addition, the boundary zone of the sea and bottom receives that part of the merohyponeuston which becomes benthos (benthogenic merohyponeuston) after completing the neustonic phase of its life. This is yet another form of "baton- change" from zone to zone, from biotope to biotope, along the "track" of ecological processes. The contact zone of the sea and bottom also represents the finishing post for the dead neustonts joining the "rain" of dead bodies. Whereas this "rain" is

extinguished before reaching the bottom in the deep-water regions of the ocean (Bogorov, 1967), in shallow waters it is an objective reality (Zelezinskaya, 1966a) which probably plays a fairly important part in the transformation and exchange of energy and substances in this part of the sea.

Thus, on the one hand an examination of the contact, or boundary, zones of the sea reveals important features of the distribution of neuston and raises a number of new questions of interest to neustonology and related fields. On the other hand, the neustonological data indicate the fruitfulness of investigations in contact zones and the obvious possibilities of a study of the benthonic, planktonic, nektonic benthos, plankton, and interstitial fauna organisms in them.

After our brief look at certain general characteristics of the distribution and diffusion of neuston in the sea let us examine the composition, abundance and disposition of the organisms of the nearsurface assemblage in different types of marine basins. The main examples chosen are areas which have been relatively /190/ thoroughly studied by the same method. These proved to be primarily the southern seas of the USSR, and to a lesser extent the Far Eastern seas and the American Mediterranean.

Chapter XVI. Characteristic features of the neuston in the temperate zones of the ocean as exemplified by the southern seas of the USSR

From the structure and composition of neuston and its ecology and distribution it is clear that the temperate zones of the ocean will be distinguished primarily by a qualitatively

poorer nearsurface assemblage of organisms. This is inevitable because of the elimination of a whole number of thermophilic species due to the drop in the water temperature minimum, shortening of the warm season and formation of ice (in the cold season). In the preceding chapters it was noted that it is the epineuston and euhyponeuston which react most sensitively to the temperature factor. The pontellids were used to illustrate this point. If, however, the pertinent water area in the temperate zone is also subject to freshening, leading to a twofold reduction in salinity compared with the normal figure for the ocean, neustonic forms will also disappear on account of the salt regime. The forms more likely to vanish from the neuston will therefore be the stenohaline halophilous ones, whereas the euryhaline forms will remain. As the southern seas of the USSR are freshened water basins situated in the temperate zone of the ocean, the composition of the neuston and other classes of communities in them will reflect this general characteristic.

In its topographical, hydrological and biological indices the Black Sea is closer to an ocean, whereas the other seas of this group- the Azov and Caspian - are examples of later stages of freshening and isolation from the ocean, as is confirmed by the composition of their neuston.

There has been a vast amount of literature written on the geological past and contemporary physical-geographical features of the Black Sea and other southern seas of the USSR. This literature includes such major works as "The Geological Structure and History of the Evolution of the Black Sea" by A.D. Arkhan-

gel'skii and N.M. Strakhov (1938), the appropriate sections of "Regional Oceanography" by A.K. Leonov (1960), "The Biology of the Seas of the USSR" by L.A. Zenkevich (1963) and others, so there is no need to describe in detail once again the ecological background against which the life of the above sea basins develops. In order to understand certain peculiarities of the neuston of these seas we need only recall certain periods in their past /191/ and features of the present, and more specifically the fact that the most recent phase in the history of the Black Sea - Azov region began after the last subsidence of the earth's crust in the vicinity of the straits, which, as stressed by biologists, occurred in historical times (Puzanov, 1953).

Most researchers consider that in the semi-freshwater neoeuxinic* lake-sea the marine fauna of the preceding saline Sea of Karangat became extinct and that now organisms are again arriving from the Sea of Marmora, the Aegean and the Mediterranean, forcing the relict fauna back into the estuaries and limans (Zenkevich, 1963). In recent years this process has intensified, and this led I.I. Puzanov (1967a, 1967b) to conclude that the Black Sea and Sea of Azov were gradually becoming "mediterraneanized". This natural process has not extended to the landlocked Caspian Sea, but recently the anthropogenic factor has been operating strongly there. The Caspian has become the site of large-scale and successful experiments in altering the natural life of marine basins, and the effects have been felt by its neuston.

*The Euxine is the ancient 'Pontus Euxinus' or Black Sea .-

Translator's note.

The Black Sea

The structure and composition of the neuston of the Black Sea bear the stamp of its physical-geographical characteristics. It contains no epineustonic oceanic water striders, as their range extends no further eastward than the Red Sea (Benko, cited by Vallo, 1948), while in the west the range boundary is to be found in the Atlantic near the coast of Morocco (Herring, 1961). The penetration of water striders into more northerly waters is influenced largely by the water temperature, and in the seas of the Soviet Union they are never encountered. Their nearest kin - Gerris, Hydrometra and others, forming part of the epineuston of fresh waters - occur much further north. This is due to the fact that they lead an epineustonic mode of life only during the warm part of the year, and spend winter on the shore, under leaves, stones and other places of concealment. The oceanic water striders, on the other hand, remain in the epineuston all year round, and as a result the area of their range in the ocean is sharply reduced. Another group of epineustonic organisms in the Black Sea and, probably, much further from the equator, is formed by the creatures inhabiting persistent agglomerations of foam, but at present only certain data are available, and these are given in Chapter XII.

The Black Sea hyponeuston is fairly rich and includes representatives of most classes of animals forming the aquatic part of the nearsurface assemblage. Relatively speaking, the poorest category is the euhyponeuston, with three species of pontellids,

one of Idothea and one of Syngnathus. These species, or forms /192/ closely related to them, are widely distributed in the tropical and temperate zones and do not flee from areas heavily diluted with fresh water.

The merohyponeuston of the Black Sea is far richer than the euhyponeuston. Its numerical superiority is characteristic of all sea basins, but it is particularly great in the temperate zone and high latitudes. This is due to the fact that the merohyponeuston develops in the course of one, usually warm, season and can stay entirely within flying range of regions remote from the equator. The benthohyponeuston makes its circadian vertical migrations all year, and its development in the Black Sea depends chiefly on the area covered by the shelf. Therefore, it attains its greatest abundance in the northwestern shallows. The bathyplanktohyponeuston of the Black Sea is poor in respect of species because, on account of the existence of the hydrogen sulphide region, rising to within 150 metres of the surface in the central waters, and the low salinity, many species of deep-water plankton which lead a hyponeustonic mode of life at night are absent here. Recently V.P. Zakutskii (Kir'yanova and Zakutskii, 1967) showed that this group probably also includes the marine hairworm (Nectonema agile). Hourly collections made in the middle of August 1965 near the coast of the Caucasus revealed that the hairworms appear in the 0-5 cm layer at the beginning of the night and then disappear. These organisms were observed only once (although in large quantities), and as this was the first time they had been found in the seas of the USSR a final verdict

on their relationship to the neuston will be possible only after further research. A live worm about 50 mm long and closely resembling Nectonema in its outer appearance was caught by the author (Zaitsev, 1964a) in August 1962 near Anapa during the daytime. A.R. Prendel suggested that it should be classed under the genus Gordius.

Other abundant representatives of the Black Sea bathyp plankton, i.e. Calanus helgolandicus and Sagitta euxina, have not yet been adequately studied by neustonologists, and so far few cases have been recorded of high concentrations at night in the 0-5 cm layer. Therefore the circadian rhythms of neuston in the Black Sea are governed chiefly by the existence of a fairly numerous group of benthohyponeustonic species and by nocturnal spawning of masses of pelagophilous fish. As it is situated in the temperate zone the Black Sea is characterized by seasonal changes in the composition and numbers of the neuston. The wide range of fluctuation in the temperature of the surface layer of water (from -1.4° when frozen to 29° in summer (Zenkevich, 1963) imparts a pronounced seasonal rhythm to the development of life in the 0-5 cm layer. The dates for the beginning and culmination of each biological season are variable and depend on hydro- /193/ meteorological conditions in the year in question. However, using certain average indices the following picture emerges.

The seasonal changes in neuston composition are most clearly marked near the shore, where the range of fluctuation in water temperature is greatest. Therefore, it is better to take the

northwestern part of the Black Sea, from which the greatest number of neustonological collections have come. Thus, in spring (March-April) the 0-5 cm layer of this area is marked by a predominance of cold-water forms and a small number of eurythermal forms (Table 46). Data on Calanus, cumaceans and shrimps are given for the night stations.

Table 46

Composition and average density (spec./m³) of organisms near the surface in the northwestern part of the Black Sea in April 1960 (Zaitsev, 1962b)

1 Организм	2 Микрогоризонт, см				
	0-5	5-25	25-45	45-65	65-85
<i>Anomalocera patersoni</i>	0,41	0	0	0	0,08
<i>Calanus helgolandicus</i>	2,93	1,62	1,70	1,70	1,60
<i>Idothea</i> sp. sp.	0,62	0,01	0,02	0	0
<i>Cumacea</i> g. sp.	0,13	0,07	0,07	0,01	0
<i>Palaemon adspersus</i>	7,84	0,73	0,16	0,16	0,08
<i>Sagitta</i> sp.	1,74	0,41	0,55	0,71	0,52
<i>Pleurobrachia pileus</i>	0,72	0,37	0,49	0,71	0,56
<i>Platichthys flesus luscus</i> , ova	11,40	4,10	5,20	3,80	2,50
<i>P. flesus luscus</i> , larvae	15,0	6,10	4,10	5,20	3,10
<i>Scophthalmus maeoticus</i>	16,40	4,80	3,70	3,70	0,40
<i>maeoticus</i> , ova					
<i>Sprattus sprattus phalericus</i> , ova	13,80	9,10	7,40	6,50	7,10

Key: 1. Organism; 2 - microlayer, cm.

The table shows that in April the hyponeuston layer was populated predominantly by cold-water representatives of invertebrates and fishes that are common in the Black Sea in autumn, winter and spring, but absent (e.g. flounder eggs) or sink into the deep layers of the pelagic zone (sprat eggs) in summer. In April they are still found near the surface and even form more

or less distinct concentrations in the 0-5 cm layer. Apart from the organisms listed in the table, the spring hyponeuston also contains the eggs and larvae of Gaidropsarus mediterraneus, Odontogadus merlangus euxinus and many other small multicellular organisms, protozoans and bacteria. It is striking that the cosmopolitan cold-water ctenophore species Pleurobrachia pileus, like many medusae, does not concentrate in the 0-5 cm layer.

The spring season is marked by a low abundance of pontell- /194/
ids. Solitary specimens of A. patersoni were encountered on the voyage only at the three southernmost stations situated near Zmeinyi island. The biological summer arrives earlier in this region than in the others, and this coincides on the whole with the intrusion of warm water from the more southerly regions of the sea (Vinogradov et alia, 1966). It is from here that, according to the "Atlas", the mackerel advances on the northwestern shallow-water feeding grounds.

The summer neuston develops gradually, depending on the weather conditions. If the appearance of anchovy eggs (spawning of anchovy in the Black Sea begins at a water temperature of 17-18^o C) and decapod larvae is taken as a sign of the start of the biological summer, the transition of neuston from the ~~spring~~ state to the summer state in the northwestern part of the sea can be said to occur in May, usually in the last ten days of the month. As in the rest of the Black Sea, so also in this region, the summer neuston is in full flourish in July and August (Table 47).

Table 47

Composition and average density (spec./m³) of organisms near the surface of the northwestern part of the Black Sea in July 1960 (Zaitsev, 1962b)

Организм	2 Микрогоризонт, см				
	0—5	5—25	25—45	45—65	65—85
<i>Anomalocera patersoni</i>	15,10	0,54	0,06	0,28	0,02
<i>Pontella mediterranea</i>	18,20	0,21	0,14	0,10	0,04
<i>Labidocera brunescens</i>	4,0	2,01	0,23	0,06	0
Decapoda, zoea	62,28	15,10	15,10	13,60	12,75
Bracyura, megalopa	3,60	0,10	0,22	0	0
<i>Idothea stephensi</i>	13,10	0,30	0,54	0,12	0
Amphipoda g. sp. sp.	11,60	1,50	1,0	0,85	0,84
Cumacea g. sp. sp.	10,51	0,90	0,91	1,17	0,75
<i>Palaemon adspersus</i>	12,50	1,48	0	0,16	0
<i>Sagitta</i> sp.	10,42	9,40	5,24	6,73	5,77
<i>Engraulis encrasicolus ponticus</i> , ova	17,60	9,25	6,36	6,42	6,21
<i>E. encrasicolus ponticus</i> , larvae	11,0	2,50	1,11	2,40	1,20
<i>Trachurus mediterraneus ponticus</i> , ova	15,71	4,31	3,69	2,68	2,17
<i>T. mediterraneus ponticus</i> , larvae	6,58	1,0	1,22	1,50	0,96
<i>Blennius</i> sp.	3,04	0,45	0,08	0,18	0,23

Key: 1. Organism; 2. microlayer, cm.

Data on amphipods, cumaceans and shrimps are given for night stations. The voyage lasted from July 4th to July 13th. Collections of samples at the 28 stations were made all over the water area to the north of the parallel of Zmeinyi island, and in the western part - southward as far as the parallel of the Giurgiu branch of the Danube. The water temperature at this time fluctuated between 18.1 and 23.9°. /195/

The data in Table 47 show that the summer neuston is considerably richer than the spring neuston. During the summer the eggs and larvae of many fishes (the table gives the most

abundant of them - anchovy and horse-mackerel), decapods etc. appear. Compared with spring there is a sharp rise in the numbers of pontellids and isopods. However, among the zooneustons the greatest quantitative development in summer-time is achieved by small crustaceans, their eggs, nauplius and copepodite stages, larvae of mollusks and polychaetes, protozoans and so on. Figures for the most abundant small multicellular organisms and protozoans among the summer neuston of the Black Sea were given earlier (see Tables 13, 37).

Thus the Black Sea summer neuston is distinguished by great diversity and high quantitative indices. The confinement of the development of the maximum number of organisms to the warm part of the year creates optimum feeding conditions in the 0-5 cm layer for young invertebrates and fish, and it is no accident that spawning of the overwhelming majority of the Black Sea pelagophilous fishes studied takes place at the end of spring or in summer.

At the end of summer and beginning of autumn new quantitative and qualitative changes takes place in the Black Sea neuston, due to seasonal variations in environmental conditions and the development of ecological processes. Particularly marked during this period is the change in the merohyponeuston, reflecting the end of the breeding and development of larvae of many Black Sea species of invertebrates and fish (Table 48). Of the abundant organisms in the summer neuston, the eggs of anchovy and horse-mackerel disappear and the numbers of decapod ~~zoa~~ drop

Table 48

Composition and average abundance (spec./m³) of organisms near the surface of the northwestern part of the Black Sea in September-October 1960 (Zaitsev, 1962b).

1 Организм	2 Микрогоризонт, см				
	0-5	5-25	25-45	45-65	65-85
<i>Anomalocera patersoni</i>	20,94	0,74	0,09	0	0
<i>Pontella mediterranea</i>	4,23	0,07	0,02	0	0
<i>Labidocera brunescens</i>	0,34	0	0	0	0
Decapoda, zoëa	4,15	4,31	1,40	0,70	0,65
Brachyura, megalopa	6,61	0,25	0,19	0,11	0
<i>Gaidropsarus mediterraneus</i> , ova	0,43	0,17	0,14	0,10	0,11
<i>Sprattus sprattus phalericus</i> , ova	0	0,10	0	0	0
<i>Engraulis encrasicolus pon-</i> <i>ticus</i> , larvae	0,60	0,06	0,20	0,05	0,05
<i>Blennius</i> sp. larvae	2,34	0,60	0,10	0	0,02

Key: 1 - organism; 2. microlayer, cm.

sharply. On the other hand the numbers of megalopa increase. This is due to the transition of the crab zoea to the final stage of development, which culminates within a short time in the settling of the young crabs on the bottom. There is also a distinct drop in the numbers of pontellids. The appearance in the hyponeuston of hake eggs and sometimes sprat eggs may mark the beginning of the biological autumn, just as the appearance of anchovy eggs signalled the beginning of summer. Autumn spawning is also characteristic of the golden-grey mullet, but it is confined in the main to the open waters of the central and southern regions of the sea. There, in the 0-5 cm layer, are found the bulk of its eggs, larvae and fry.

Owing to differences in the hydrologic conditions, and particularly temperature, the neustonts in the various regions of

the Black Sea acquire their autumn appearance at different times. Signs of the biological autumn appear first in the neuston of the northern regions and gradually spread south.

From September 29th to October 7th 1960 neuston was collected along the western shores of the Black Sea, between the northernmost point, near Sychavka, and the southernmost at the Bosphorus (Fig. 62). Examination of the material revealed that the richest collections of pontellids, isopods, decapod larvae and golden-grey mullet were made at stations 15-21, i.e. in the southwest region of the sea. For example, larvae and the early (hypo-neustonic) fry of golden-grey mullet were found only at stations 4, 10 and 15-21, and their numbers at stations 15-21 were 7 times higher than at stations 4 and 10. /196/

The transition to the biological winter occurs gradually and also at different times in different areas. In places where the winter water temperature at the surface normally does not drop below $10-8^{\circ}\text{C}$ (e.g. in the south-west and south-east deep-water regions), the composition and abundance of neustonts in the cold season differs only slightly from the composition and abundance in autumn.

In the northwestern part of the sea, where the winter water temperatures may drop to zero (and sometimes even further), and the surface is covered with ice, the picture is quite different. On the basis of winter collections made in the Chernomorka region it may be concluded that the warm-water element is lacking in the neuston of the shallowest parts of the northwestern region in the period from December to March inclusive. Pontellids,

decapod larvae and most species of fish eggs and larvae are missing, and Idothea and others are very few in numbers. In December sprat and hake eggs can still be found in the Chernomorka region, but in January and February spawning of these fishes ceases in the shallows and shifts to deeper parts of the sea. At the end of February or in March the eggs of sprat and a new fish - the flounder, which in warm winters begins to breed as early as /197/ the end of January (Tables 49,50), reappear.

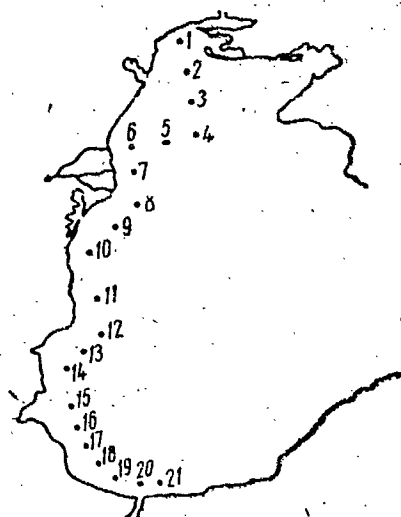


Fig. 62 - Position of neustonological stations (1-21) during the voyage of RV "Miklukho-Maklai" in the western half of the Black Sea from 29.IX to 7.X. 1960.

Table 49

Composition and average density (spec./m³) of organisms near the surface of the northwestern part of the Black Sea in February-March 1961.

Организм	Микрогоризонт, ² см		
	0-5	5-25	25-45
<i>Pleurobrachia puleus</i>	7,10	1,80	16,20
<i>Sagitta</i> sp.	0	1,10	0
<i>Calanus helgolandicus</i>	0	0,10	0
<i>Acartia clausi</i>	52,60	12,80	32,0
<i>Balanus</i> , nauplii	4,30	0	0
<i>Platichthys flesus</i>	26,70	9,10	7,80
<i>P. flesus</i> , ova			
<i>P. flesus</i> , larvae	4,0	3,10	0

Key: 1 - organism; 2 - microlayer, in cm

Table 50

Average weight (mg) of different sizes of eggs of Encraulis encrasicholus ponticus.

Большой диаметр, мм	Начало развития зародыша	Конец развития зародыша
1	2	3
1,0	0,2578432	0,2583552
1,1	0,3374120	0,3380720
1,2	0,4048944	0,4056984
1,3	0,5066216	0,5072276
1,4	0,6395720	0,6408420
1,5	0,7906520	0,7922220
1,6	0,9497896	0,9516756

Key: 1 - large diameter; 2 - beginning of development of embryo; 3 - end of development of embryo

Collections of winter neuston in the Chernomarka region were taken at a surface water temperature of 1.2-2.6°C. On the 28th of March 1962, PNS-2 and MNT* hauls taken in the Dnestr bank area, 7-8 miles off shore, at a water temperature of 3.05°C, revealed only Sagitta, medusae, ctenophores, some Calanus specimens, and flounder and whiting eggs. Thus, even at the end of March the composition of the population of the 0-5 cm layer is typical of the winter season.

*PNS = plankton - neuston net, MNT = fry - neuston trawl - Translator's note.

It is interesting that P. mediterranea, as V.N. Nikitin also notes (1926), is considerably more thermophilic than A. patersoni, which is regarded more correctly as eurythermic. In the winter months, in the Chernomorka region, Pontella was generally not to be found and Anomalocera was caught very rarely. For example, on February 16th 1961 solitary specimens of the latter species were discovered in the 0-5 cm layer 1 km from the shore at a surface water temperature of 1.2°C . These were large females weighing up to 1.4 mg. The length of the cephalothorax was 2.7 - 3 mm. The eurythermicity of Anomalocera is apparent from its geographical distribution also, as it penetrates far to the north. C.B. Wilson (1942) encountered Anomalocera near Iceland, at a point with the coordinates $62^{\circ}45'$ northern latitude and $25^{\circ}52'$ western longitude.

As regards Pontella, as an obvious thermophile it reacts sensitively to a drop in the water temperature. This can clearly be seen in the Black Sea. Whereas Pontella is absent in the northwestern shallows in the winter months, in the Novorossiiskaya Bay area it occurs all year round. Even in the severe winter of 1962-1963 Pontella was found in the bay on February 1st and 27th, i.e. in the month with the lowest water temperatures in the Black Sea*. Crustaceans occurred in ones and twos, and compared with the great abundance in summer, seasonal variations in the neuston were also very marked. However, because the water

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* The author expresses thanks to his scientific colleague at the Novorossiisk Biological Station, E.G. Kryshtyn, who has made collections of neuston in Novorossiiskaya Bay and neighbouring waters for a number of years.

temperatures do not drop below $6-7^{\circ}\text{C}$ in the winter months the warm-water element does not completely disappear in the Novorossiskaya Bay area as it does near Odessa. As regards the state of its winter neuston Novorossiskaya Bay appears to rank between the northwestern and northeastern shallows on the one hand and the warmest regions of the sea - in the south-east and south-west - on the other. In these latter areas winter the bulk of the warm-water (Mediterranean) forms, comprising the nucleus of the summer neuston in the Black Sea.

Using ichthyological criteria to indicate the beginning of a particular season of the year in the neuston, it can be concluded that the onset of the biological spring coincides with the appearance of turbot eggs in the 0-5 cm layer. In Zernov's phyllophore area this occurs at the end of March and the beginning of April, and in Gulf of Odessa - no earlier than the middle of April. The spring neuston appears in the northwestern part of the sea with the warm waters intruding at this time into the area containing the most extensive shallows in the sea.

Realizing how complex a matter it is to make a quantitative estimate of the pelagic population only a few authors, making many assumptions and important qualifications, venture to give approximate figures for the stocks of plankton in a particular sea. The Black Sea is no exception in this regard. According to V.N. Nikitin (1950), the total biomass of Black Sea plankton, excluding nanoplankton and part of the microplankton, is roughly 7,000,000 metric tons. According to V.A. Vodyanitskii (1941), the total biomass of Black Sea plankton fluctuates /199/

between 12 and 18 million metric tons.

At present, estimation of the total neuston biomass in the Black Sea is difficult for two reasons: the first is the short duration of quantitative neustonological investigations, and the second, the fact that many neustonts, and especially the larval stages, have not yet had their average weights calculated. To compute the latter the appropriate measurements were made on two pontellid species (Zaitsev and coauthors, 1961), the eggs of anchovy, frogfish, sole, surmullet, horse mackerel, hake, flounder, sprat, Black Sea mullet, and the larvae and fry of surmullet and Black Sea mullet (Zaitsev, 1964a).

Until recently the pelagic eggs and larvae of fish were not included in the biomass of zooplankton at the various depths. They were usually viewed as potential recruitment to the fish stock, as raw material for comparing fishery forecasts, as future nekton, and so on, but not as food for other organisms. This was in spite of the fact that fish eggs and larvae were firmly believed to be consumed in vast quantities by various predatory invertebrates and vertebrates, and no doubt was entertained that the survival rate of each year-class depended on this factor to a large degree.

It has long been known that fish larvae are consumed in large quantities by A. patersoni, decapod larvae, the medusae Obelia and Rathkea, the Scyphomedusa Aurelia aurita, the ctenophore Pleurobrachia pileus, and Sagitta (Lebour, 1925). In the Black Sea great harm is caused to fish larvae by Balanus larvae (Dolgopol'skaya, 1946). The greatest enemy of the Azov anchovy larvae is considered by T.F. Dement'eva (1954) to be the adult

anchovy, while R.M. Pavlovskaya (1958) found anchovy larvae 4-5 mm long in the stomachs of pelamid larvae 6.2 mm long.

Analysis of hyponeuston samples has revealed eggs and larvae of fish inside medusae, ctenophores, Sagitta and other invertebrates.

All these examples indicate that fish eggs and larvae should be regarded not only as potential fishery stock but also as food for many marine invertebrate fishes, and also certain aerobionts. In this connection a calculation was made of the average weights of the most numerous eggs of Black Sea fish species.

For determination of the volume of anchovy eggs use was made of the formula for the volume of the closest geometrical figure - the ellipsoid:

$$V = \frac{4}{3} \pi a^2 b,$$

where a and b are, respectively, the large and small semiaxes.

The volume of the spherical eggs of all the other species was /200 determined using the formula for the volume of a sphere:

$$V = \frac{4}{3} \pi r^3 .$$

The volume (of the ellipsoid or sphere) thus obtained was multiplied by the specific weight of the relevant species and developmental stage (Zaitsev, 1954, 1955, 1959 c) (Table 51).

Table 51

Average weight (mg) of eggs of different species of fishes
(Zaitsev, 1964a)

Диаметр икринок, мм 1	Начало раз- вития заро- дыша 2	Конец разви- тия заро- дыша 3	Диаметр икринок, мм 1	Начало раз- вития заро- дыша 2	Конец разви- тия заро- дыша 3
<i>Callionymus belenus</i>			<i>Trachurus mediterraneus ponticus</i>		
0,60	0,11392563	0,114231	0,90	0,385056	0,38582
0,65	0,14484901	0,145137	0,95	0,452592	0,45349
0,70	0,18081035	0,181295	1,0	0,528192	0,52924
0,75	0,21213738	0,212706	<i>Gaidropsarus mediterraneus</i>		
0,80	0,26995640	0,270680	0,70	0,18156425	0,18192325
0,85	0,32435060	0,325220	0,75	0,2130219	0,2134431
<i>Solea lascaris nasuta</i>			0,80	0,271082	0,271614
1,0	0,5289256	0,5299736	0,85	0,325703	0,326345
1,05	0,6116964	0,6129084	<i>Platichthys flesus luscus</i>		
1,10	0,7045612	0,7059571	1,05	0,6130296	0,6143628
1,15	0,8034824	0,8050744	1,10	0,7060868	0,7076324
1,20	0,9135070	0,9153170	1,15	0,8052336	0,8069848
1,25	1,0326162	1,0346622	1,20	0,915498	0,917489
1,30	1,16081	1,16311	1,25	1,0348668	1,0371174
1,35	1,302126	1,304706	1,30	1,16334	1,16587
<i>Mullus barbatus ponticus</i>			<i>Sprattus sprattus pahlericus</i>		
0,65	0,145137	0,14545314	1,0	0,530288	0,531598
0,70	0,181295	0,1816899	1,05	0,613272	0,614787
0,75	0,212706	0,2136932	1,10	0,706376	0,708121
0,80	0,27068	0,2712696	1,15	0,805552	0,807542
0,85	0,32522	0,3259284	1,20	0,91586	0,9181225
<i>Trachurus mediterraneus ponticus</i>			<i>Mugil auratus</i> и <i>M. saliens</i>		
0,75	0,2122848	0,212706	0,75	0,2120742	0,2122848
0,80	0,270144	0,27068	0,80	0,269876	0,270144
0,85	0,324576	0,32522	0,85	0,324254	0,324576
			0,90	0,384674	0,385056

Key: 1 - diameter of eggs, mm; 2 - beginning of development of embryo; 3 - end of development of embryo.

The relation between body weight and body length in larvae and fry of Black Sea mullet and surmullet is shown in Fig. 63. The average weight of the pelagic larvae of certain fish species was computed by L.A. Duka (1965). By using the average weights /201/ of plankters determined by T.S. Petipa (1957) it is possible to calculate the biomass of other components of the Black Sea neuston,

but for most of them the weight characteristics are not yet known. Therefore the author made his first attempt to calculate the total biomass of the summer neuston in the Black Sea using the wet weight of samples obtained with neuston nets of No. 23 mesh, which let through protozoans and the eggs and larval stages of many invertebrates. The biomass of the summer hyponeuston in the Black Sea, judging by these samples, fluctuates between 50 and 3500 mg/m³. The average biomass of the summer neuston in the northwestern part of the sea is approximately 610 mg/m³, and in the sea as a whole approximately 320 mg/m³. Assuming the surface area of the Black Sea to be 423,000 km² (Stepanov, 1961), the volume of the upper 5-cm layer will work out at:

$$423\ 000 \times 0.00005 = 21.15 \text{ km}^3, \text{ or } 21.15 \times 10^9 \text{ m}^3.$$

In this event the total biomass of the Black Sea summer hyponeuston (judging by hauls made with a No. 23 mesh net) will be $21.15 \times 10^9 \times 320 = 6768 \times 10^9$ mg, or 6768 metric tons. /202/

The following comparison is an interesting one. The total biomass of the Black Sea plankton from the 0-25 m layer; according to V.N. Nikitin (1950), comprises approximately 2,161,000 metric

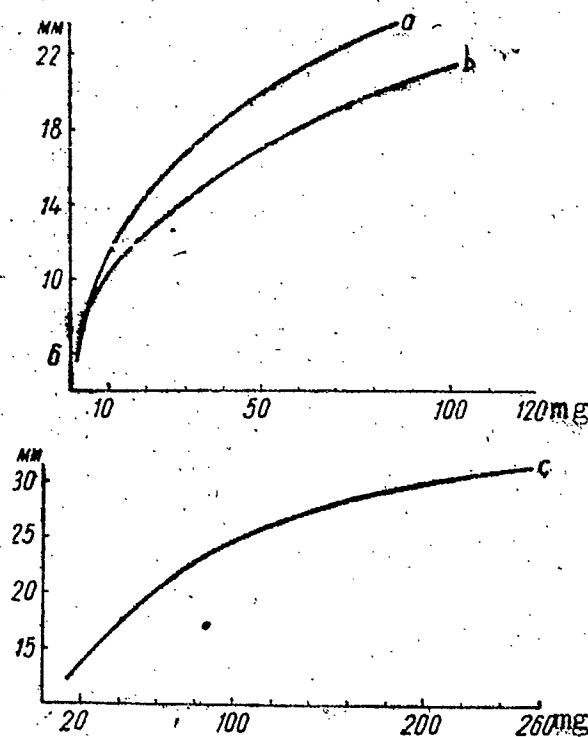


Fig. 63 - Relation between body length (mm) and body weight (mg) in larvae and fry of surmullet (a), golden-grey mullet (b) and grey mullet (c) from the pelagic hyponeuston of the Black Sea (Zaitsev, 1964a).

tons. Assuming that the biomass of the plankton is distributed evenly throughout the entire 25-metre layer, the 0-5 cm layer will contain 1/500, or 4320 metric tons, of the plankton, which is equal to approximately 2/3 of the hyponeuston biomass computed earlier. We must qualify this by saying that these data are not exactly comparable. V.N. Nikitin apparently failed to take into account the eggs and larvae of fish. On the other hand he did allow for the microzooplankton passing through the No. 23 mesh net, and those inhabitants of the lower part of the 0-25 m layer of high individual weight, such as Calanus, medusae, ctenophores and others, which are not found near the surface in summer. Taking into account the small invertebrates and bacterioneuston,

the total biomass of summer hyponeuston would come to 10-12,000 tons. This figure does not include fish fry. If the total abundance of mullet (grey mullet, striped mullet, golden-grey mullet) fry in the Black Sea amounts to 2×10^9 specimens during the summer (Zaitsev, 1963a), at an average weight of 30 mg they will weight 60 metric tons.

In the 0-5 cm layer of the western half of the sea, according to the calculations of V.V. Krakatitsa (1963), there are approximately 5×10^8 surmullet fry in summer. If their numbers are the same in the eastern half of the sea, at an average weight of the fry of 40 mg they will total approximately 40 metric tons. Taking into account the fry of all other species of fishes, and also live cells of microphytes, the total biomass of the population of the 0-5 cm layer in the Black Sea will probably be increased to 15-20,000 metric tons.

For all the roughness of these estimates, at least two facts are established beyond doubt: firstly, the highest density of organisms in the entire pelagic zone is concentrated in the 0-5 cm layer, and secondly, the biomass of total neuston represents an insignificant percentage of the biomass of total plankton in the water basin. If the latter is taken to be 7,000,000 metric tons, the biomass of the 0-5 cm layer will be only about 0.3% of the former. As regards these figures it needs to be emphasized once again that the biomass indices do not reflect the quantitative characteristics of the neuston, which is characterized by a high "turnover" of its components due to the breeding habits of the invertebrates and fishes. Every twenty-four hours a new generation of merohyponeuston enters the 0-5 cm

layer and just as frequently organisms that have completed the neustonic phase of their existence abandon it for different biotopes. Neuston, which consists predominantly of larvae and young, is characterized by a rapid rate of increment of the biomass. All these features are bound to be reflected in the magnitude of neuston production which not only leads to an upward change in the quantitative indices of neuston compared with /204/ the static characteristics of the biomass, but also sheds more light on its role in the life of the sea. However, this is a matter for the future and for the present we must be satisfied with approximate values for the biomass.

In conclusion some charts have been included to illustrate the quantitative distribution of neustonic organisms in the Black Sea (Fig. 64). It is interesting to note that the highest concentrations of neustonts are confined to those same areas which mark the positions of the regions of converging currents.

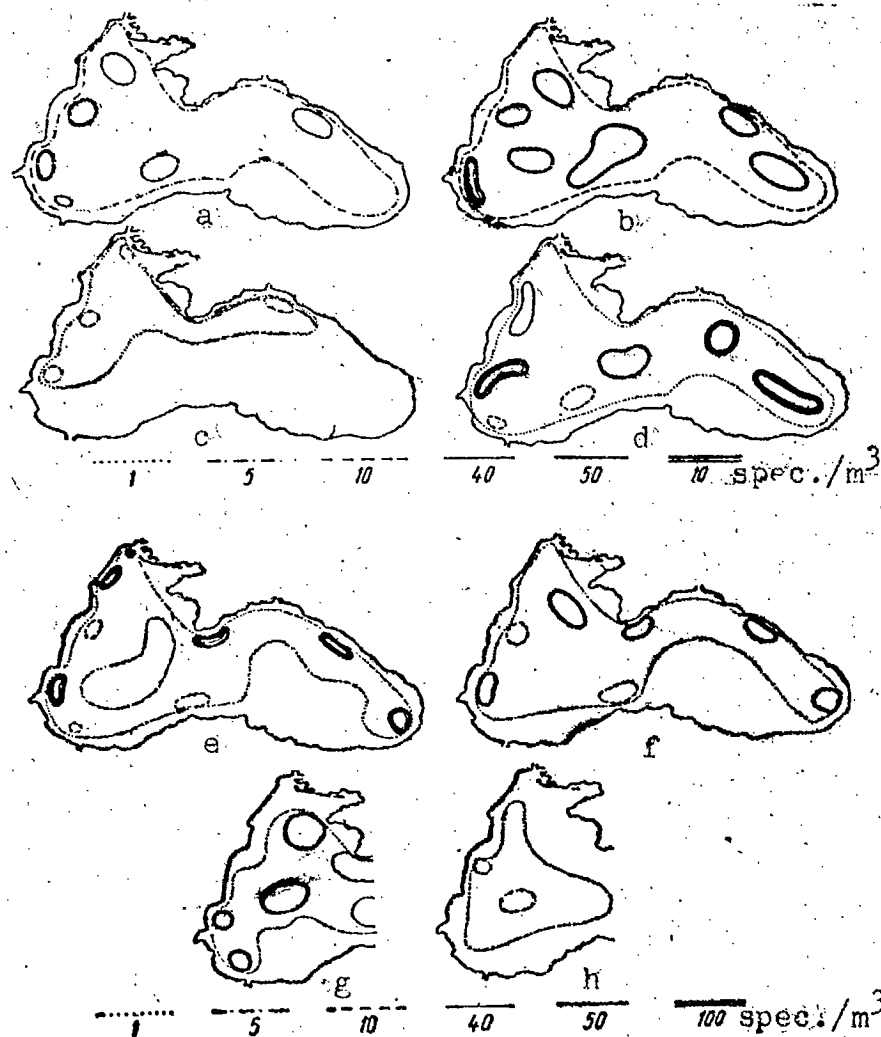


Fig. 64 - Distribution of some hyponeustonic organisms in the Black Sea in the summer of 1961 (Zaitsev, 1964a):
 a - Anomalocera patersoni, b - Pontella mediterranea, c - Labidocera brunescens, d - Idothea stephensi, e - Decapoda, zoea, f - Brachyura, megalopa, g - Mullus barbatus ponticus, larvae, h - Pomatomus saltatrix, ova.

The Sea of Azov

In the Sea of Azov those features of neuston which characterize freshened areas in the temperate zone of the ocean undergo further development (Zaitsev, 1964a, 1964c).

The results of neustonological surveys conducted all over the Sea of Azov in the 0-5 cm layer from August 2nd to August 9th 1962 are shown in Table 52. The wave height during collection was between 0.2 and 1.5 m, the water temperature at the surface 22-24.8⁰ C, and the salinity from 10.93-12.83‰.

As can be seen, the difference compared with the Black Sea is fairly considerable, although these two bodies of water are linked by Kerch strait, which is 2.2-7 miles in width and roughly 23 miles long (Stepanov, 1961).

Table 52

Composition and average abundance (spec./m³) of organisms near the surface of the Sea of Azov in August 1962 (Zaitsev, 1964a)

1. Организм	2. Микрогоризонт, см		
	0-5	5-25	25-45
<i>Labidocera brunescens</i>	94,20	4,53	2,66
<i>Palaemon</i> sp., larvae	87,82	20,56	16,15
<i>Mysidacea</i> g. sp. sp.	126,50	48,80	35,80
<i>Brachyura</i> , megalopa	38,80	4,20	0,70
<i>Engraulis encrasicolus</i>	1,22	1,47	0,98
<i>maeoticus</i> , ova			
<i>Mugil saliens</i> , larvae	0,32	0	0
Gobiidae g. sp. sp., larvae	2,90	1,20	1,50

Key: 1 - organism; 2 - microlayer, cm.

Even before laboratory examination of the samples a salient point emerges, i.e. instead of the typical blue-green samples of hyponeuston normal for the Black Sea and other seas, in the Sea of Azov the semi-submerged net yields a pale-yellow sediment. This is due to the absence of the intensely pigmented P. mediterranea and A. patersoni in the Sea of Azov. They do not figure /205/ in the list of free-living invertebrates of the Azov compiled by

F.D. Mordukhai-Boltavskoi (1960) on the basis of material published earlier. Nor are they to be found in the collections of plankton (171 samples) obtained in the period from June to November 1931 (Dolgopol'skaya and Pauli, 1964). Such a difference in the composition of the neuston in two communicating seas is all the more surprising because Pontella and Anomalocera are quite common in similar conditions of temperature and salinity in the northwestern part of the Black Sea. They do not form large concentrations here, but are included among the common hyponeustonic forms in the freshened areas of the Black Sea.

The samples of neuston obtained in September-October 1963 and in May 1968 did not contain these two species either. This is most unlikely to be due to the chemical composition of the water, the more so as abundant development of phyto-, zoo- and ichthyoplankton occurs in the Sea of Azov. Table 52 shows that, in addition to other species, Labidocera - a representative of the same family - is also abundant in the 0-5 cm layer of the Sea of Azov.

From what has been said it follows that only the failure of Black Sea surface waters to pass through Kerch strait can explain why there are two areas of hyponeuston of different composition 23 miles apart : in the south an area of Pontella, Anomalocera and to a lesser degree Labidocera, and in the north an area of Labidocera, with^a/density here amounting to several hundred specimens per cubic metre in the 0-5 cm layer. The blossoming of Labidocera in the Sea of Azov is made possible by

its eurythermicity. Anomalocera and especially Pontella are far more thermophilic, and it would be impossible for them to stay in the Sea of Azov all year round on account of the low water temperature in winter and the ice cover. In the warm seasons it would in theory be quite possible for them to exist here, and it is only the peculiarities of water exchange through the strait that prevent this. It may be, however, that in individual cases, when the wind is blowing hard from the south, Black Sea surface water containing pontellids may be swept into the part of the Sea of Azov just beyond the strait, but the next current in the opposite direction returns them to the Black Sea.

Observations of the changes in composition and numbers of pontellids in this region may obviously be of indirect interest for studying the nature of water exchange through Kerch strait.

Quantitatively the merohyponeuston of the Sea of Azov is very rich. Among invertebrates decapod zoea are especially numerous, particularly the crabs Rhitropanopeus harrisii tridentatus (Maitland) and Brachynotus sexdentatus Risso (syn. B. lucasi H.M. Edwards). On August 5th 1962, at one of the stations situated in the centre of the sea, an examination of one cubic metre of water in the 0-5 cm layer disclosed 18,603 crab larvae belonging, according to O.G. Reznichenko*, mainly to B. sexdentatus. /206/

*The author expresses his gratitude to O.G. Reznichenko for determining the species composition of the early developmental stages of the crabs from the neuston collections made in the Sea of Azov.

These large larvae were so numerous (the haul was repeated twice at an interval of 2 hours and the result was the same) that they were a nuisance to bathers. The 5-25 cm layer contained only 63.3 spec./m³ of the larvae of the two crabs species referred to above, whereas there were 30.4 spec./m³ in the 25-45 cm layer. Hence, of all the crab zoea encountered in the 0-45 cm layer at wave heights up to 1 m about 99.5% were in the 0-5 cm layer. It is revealing that collections of plankton made at the same time at the same station with vertical sweeps of a Juday net did not contain a single crab larva. This is yet another proof that the vertically operated gear used for collecting plankton from various depths is not suitable for the collection of neuston, and, as in the present case, may fail to record major hydro-biological phenomena. Such concentrations of hyponeustonic crab larvae were not observed in the Black Sea. No less interesting and novel for the biology of the Sea of Azov were neustonological materials illustrating the breeding of the Black Sea mullet. Prior to the first neustonological survey (August 1962) the literature contained no convincing data on the spawning here of golden-grey mullet, grey mullet and striped mullet. Only in S.K. Troitskii's paper do we find a reference to the unpublished materials of V.P. Kornilova, who in July 1953 discovered 13 Mugil sp. eggs and several fry measuring 12-14 mm in length which, according to Troitskii, could not have come from the Black Sea. There was no further confirmation of these data and the Black

Sea mullet fry found in the Sea of Azov were viewed as arrivals from the Black Sea, particularly as abundant concentrations had been observed more than once while passing northward through Kerch strait.

During a voyage in August 1962 in the central regions of the sea, eggs, larvae and fry of grey and striped mullet were found in the 0-5 cm layer in an area of some 12,000 km². The abundance of eggs was low and averaged 0.15 spec./m³, whereas there were some 75,000,000 hyponeustonic fry, belonging chiefly to the species M. saliens. There was no doubt that grey and striped mullet spawned here. This is proved, in the first place, by the fact that Black Sea surface waters, in which the eggs, larvae and fry of Black Sea mullet concentrate, do not penetrate into the Sea of Azov. Otherwise Pontella and Anomalocera, which are the constant companions of the earlier ontogenetic stages of the mullet, would also have penetrated into the Azov. In the second place, the eggs and larvae of these fishes were found in the central regions of the Sea of Azov, and not close to Kerch strait. The previously referred to "shore phobia" of the Black Sea mullet spawning stock during the breeding season became the main cause of a split in the spawning area of grey and striped mullet of the Black Sea - Azov area in the vicinity of Kerch strait and the formation of a separate spawning ground in the middle of the Sea of Azov. It is still not known whether an separate population forms there, but the conditions apparently exist for it. /207/

Hence, among the marine basins studied, the Sea of Azov probably ranks last in area among those in which mass spawning of Black Sea mullet occurs.

Spawning of the golden-grey mullet (M. auratus) has not yet been recorded in the Sea of Azov. From the neustonological materials obtained in the Black Sea (Zaitsev, 1963a, 1964a, 1964b; Babayan and Zaitsev, 1964), it is known that the chief spawning grounds of the golden-grey mullet - a species that spawns in autumn - are situated in the southern part of the water basin, where conditions exist for normal wintering of the fry. The Sea of Azov, like the northwestern part of the Black Sea, lies far to the north of these waters and breeding here would mean that the fry have far less chance of reaching their wintering grounds before the cold weather sets in. Therefore, there appears to be little likelihood of discovering larvae and fry of golden-grey mullet in the Sea of Azov.

Garfish fry and adult three-spined stickleback may be regarded as abundant components of the hyponeuston in the Sea of Azov. In the Black Sea this stickleback is encountered chiefly in inshore waters, whereas in the Sea of Azov it occurs at most stations, including those in the middle of the sea, 35 miles from the shore. In August 1962 anchovy eggs were also found. This was at the end of spawning and the eggs numbered no more than 6.4 spec/m^3 . Characteristically, during the entire voyage we observed hardly any accumulations of anchovy eggs in the 0-5 cm layer. At roughly half of the stations they concentrate in the

nearsurface layer, but the difference in egg distribution density compared with the underlying layer is so insignificant that the averaged data do not reflect it. One of the reasons for this is probably the low water density in the Sea of Azov, which is insufficient for the eggs to be pushed against the surface tension film. The eggs of Black Sea mullet, being more buoyant and having an impermeable membrane, can float up against the surface tension film and stay there, whereas the eggs of other fishes are not capable of this. There are serious grounds for thinking that it is the low water density in the Sea of Azov that is the main obstacle in the way of the spawning migrations of those Black Sea fishes whose eggs develop primarily in the hyponeuston. Therefore the ichthyoneuston of the Sea of Azov is far poorer than that of the Black Sea (Fig. 65), and that of the Black Sea far poorer than the ichthyoneuston of the Mediterranean.

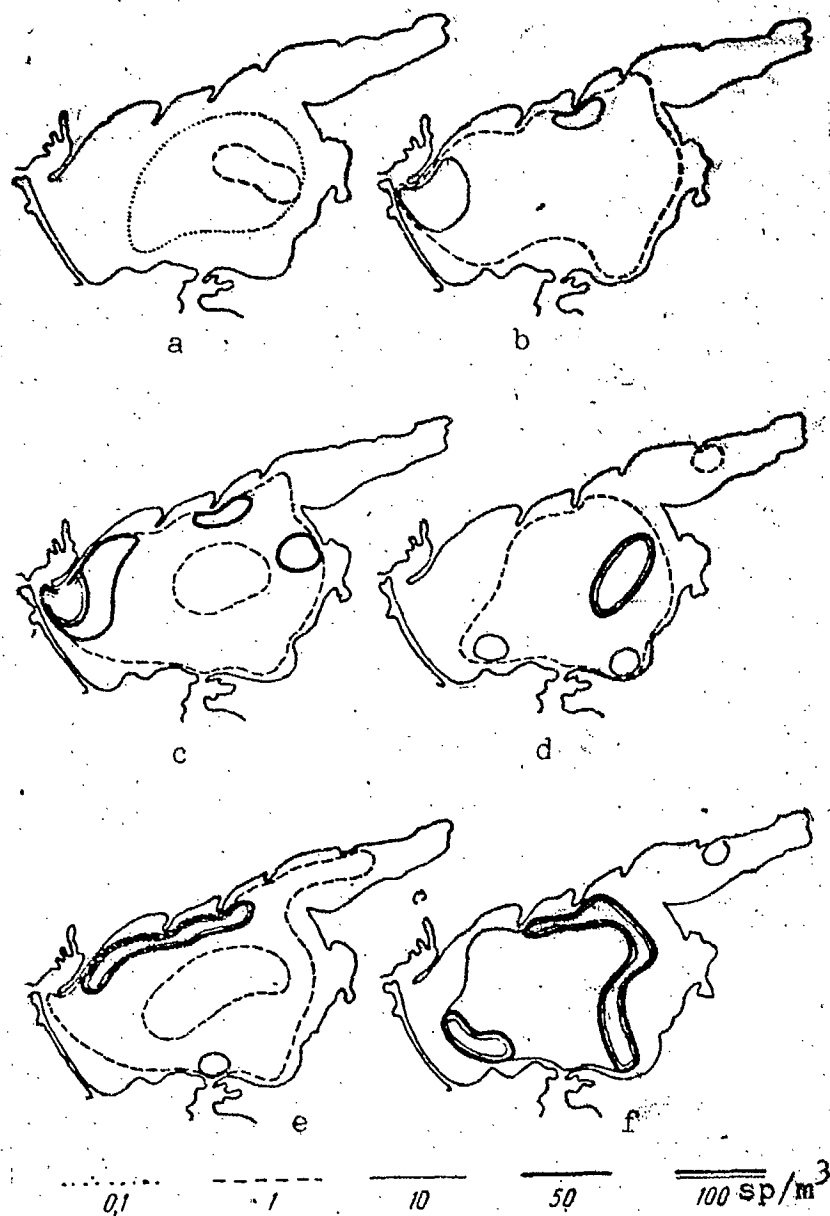


Fig. 65 - Distribution of certain hyponeustonic organisms in the Sea of Azov in August 1962 (Zaitsev, 1964a):
 a - *Mugil saliens*, ova, b - *Engraulis encrasicolus maeoticus*, ova,
 c - *Labidocera brunescens*, d - *Brachyura*, larvae, e - *Palaemon* sp.,
 larvae, f - Mysidacea.

The Caspian Sea

A neustonological survey of the Caspian Sea was made in the period from July 5th to July 23 1962. Material was collected at 40 stations situated in the north, central and southern parts of the water basin. At the collection sites the wave heights ranged from 0.2-3 metres, the salinity at the surface from 6.96 to 13.10‰, and the water temperature from 17.4 to 29.0°C. The relation of the various hydrobionts to the near-surface layer of water is shown in Table 53. The fry of grey mullet, which were caught mainly with a fry - neuston trawl, cannot be included in the table, but their dorsal fins were seen cutting through the surface of the water just as in the Black Sea and Sea of Azov.

Table 53

Composition and average abundance (spec./m³) of organisms near the surface of the Caspian Sea in July 1962 (Zaitsev, 1964a)

1. Организм	2. Микрогоризонт, см		
	0—5	5—25	25—45
<i>Palaeomon</i> sp. larvae	7,60	1,14	1,12
Cumacea	3,90	0,40	1,10
Amphipoda	1,68	0,06	0,03
<i>Mugil saliens</i> , ova	0,48	0,12	0,10
<i>Atherina mochon pontica</i>	0,30	0,08	0,12
<i>n. caspia</i> , larvae			
<i>Syngnathus nigrolineatus</i>	0,24	0	0
<i>caspius</i> , juv.			
<i>Clupeonella</i> sp., ova	4,11	0,21	0,22

Key: 1. - organism; 2 - microlayer, cm.

It can be seen from the table that the 0-5 cm layer contains a concentration of organisms already familiar from the neuston of the Black Sea and Sea of Azov, i.e. shrimp larvae, cumaceans, amphipods and grey mullet eggs. The caspian pipefish, S. nigro-lineatus caspius, behaves just like the Black Sea pipefish, S. schmidtii. At the same time, however, the Caspian neuston has its own specific features.

It is striking that there are no widely distributed components in the euhyponuston. In the Caspian there are no pontellids or I. stephenseni. As regards local isopods, in 233 samples (from the various microlayers of the 0-80 cm stratum) not one specimen was discovered. The merohyponuston of the Caspian contains shrimp larvae which appeared in this water basin in the thirties. An even later arrival - the Dutch crab (Nebol'sina, 1959) - was also discovered in the hyponuston at the mouth of the Volga delta. This suggests that conditions for breeding are just as favourable in the Caspian as in the Black Sea and Sea of Azov. /210

The nauplius larvae of Balanus and of the latest arrival in the Caspian (Zevina, 1959; Logvinenko, 1959) are found in the northern and middle parts of the sea, where, according to the data of L.N. Polishchuk (1966), obtained on the same voyage with the aid of a PNS-4 plankton-neuston net, they form a distinct concentration in the hyponuston layer (Fig. 66). The accumulation of cumaceans and amphipods in the 0-5 cm layer of the Caspian at night occurs with the same regularity as in the Black Sea - Azov region, the more so as a considerable number of the species of benthohyponustonic organisms are common to all the

southern seas of the USSR (Zenkevich, 1963).

The eggs of the "kilka" are one of the distinguishing features of the Caspian merohyponeuston. In the collections made on the voyage in question the eggs of the anchovy-like "kilka" Clupeonella engrauliformis predominated. "Kilka" larvae were encountered singly and mainly at a distance of more than 5 cm from the surface of the sea.

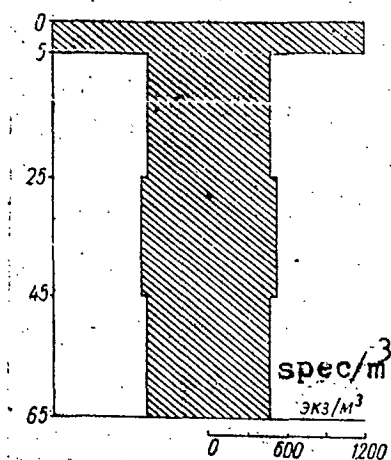


Fig. 66 - Vertical microdistribution of Balanus larvae near the surface of the Caspian Sea (Polishchuk, 1966).

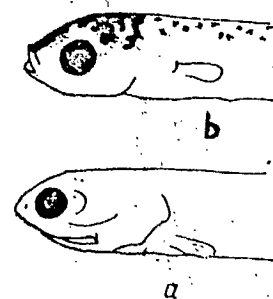


Fig. 67 - Pigmentation of dorsal side of cephalic part of body of (a) Black Sea anchovy larvae, (b) Atherina larvae (Zaitsev, 1964a).

The wide distribution of the larvae of the Caspian Atherina is characteristic. It was found both in inshore waters and in the deep-water parts of the sea, and clearly predominated in the 0-5 cm layer. Larvae of the Black Sea species Atherina moch-on pontica occur only in the narrow inshore zone and abound in shallow bays, gulfs and limans. It is possible that the "pelagization" of the larvae of the Caspian Atherina is the result

of the poverty of the Caspian hyponeuston, which allows neritic organisms to occupy a free niche in the nearsurface biotope of the open part of the pelagic zone. In the Black Sea the 0-5 cm layer, occupied by pontellids, decapod larvae, isopods and other predators and devourers of young fish, was populated by the most highly adapted fish larvae. In this connection it is interesting that the Atherina larvae, which stand closest to the group of transparent forms in their type of camouflage, are not nearly as "glassy" as anchovy larvae (Fig. 67). The latter have large dark spots betraying their presence at the surface in clear water. This may be why, in the Black Sea, they kept close to the shore, where the abundance of floating material and other places of refuge makes concealment easier. In the Caspian on the other hand, where there are fewer predators in the hyponeuston layer and shearwaters no longer represent a threat, Atherina larvae abandon the inshore zone for the open sea, utilizing the food resources in the 0-5 cm layer.

This hypothesis still requires verification. In particular we need to know how the larvae (less than 10 mm long) which hatch out from demersal eggs near the shore reach the central regions, some 70-80 miles from the coast. What currents exist to transport the Atherina larvae such a distance?

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Thus, the mere- and benthohyponeuston of the Caspian Sea consist mainly of Black Sea (Mediterranean) organisms serving a "spell" in the Caspian. It may be said that the hyponeuston of the Caspian was created and continues to be created by man,

who has acclimatized new species of invertebrates and fishes here and is creating conditions for their subsequent penetration into the Caspian from the Black Sea - Azov region (via the Volga-Don ship-canal). If it were not for these recent arrivals (shrimps, Balanus, Dutch crabs, golden-grey mullet, grey mullet and others) the net hyponeuston would be extremely impoverished, even allowing for the ancient Black Sea forms such as Atherina and pipefish.

It is also highly characteristic that the abundant forms of zooplankton in the Caspian, such as cercopagids, Calanipeda, Limnocalanus and mysids, do not form concentrations in the 0-5 cm layer, although many of them complete distinct vertical migrations similar to those described by V.A. Yashnov (1938), V.G. Bogorov (1939), L.A. Zenkevich (1963), F.G. Badalov (1963) and other authors. However, when they ascend at night into the upper layers of the pelagic zone the organisms are not heading for the 0-5 cm layer: instead they distribute themselves more or less evenly within a stratum many metres thick. V.G. Bogorov (1939) discovered that Eurytemora grimmi rises from the deep layers at 20.00-24.00 hours and forms its largest concentrations not in the 0-10 m layer but lower down, in the 10-25 m layer. It is still too early to draw final conclusions, but it does seem that these traits are important for an understanding of the genesis of marine neuston in general and the Caspian neuston in particular.

The indigenous species of the Caspian - formerly freshwater and brackish-water organisms - do not belong to the original

biological material from which the oceanic assemblage of neustonic organisms was formed. For inhabitants of brackish or fresh waters, populating fairly large areas of water (major lakes, rivers, estuaries), concentration near the surface tension film is attended by the danger of stranding. This danger is diminished in extremely small inland water bodies shielded from the wind, or in large sea and oceanic basins. In either event there is a rich and varied assemblage of neustonic organisms present. The Caspian in this sense ranks between a sea in area and volume and a lake in salinity. Populated in the main by immigrants from fresh and brackish waters, the Caspian failed to acquire that collection of forms which constitutes marine neuston, and only the subsequent interference of man led to the creation of a nearsurface assemblage of organisms, which, however, is highly unusual and lacks that important constituent part known as euhyponuston. As regards the abundant representatives of the autochthonous fauna, i.e. copepods, cercopagids and others, notwithstanding the large surface area of the sea permitting the formation of concentrations in the nearsurface biotope, they behave just the same as in shallow fresh-water and brackish-water bodies, where neuston, if it exists, does not achieve such development and significance as in the sea or a pond. A special study of the neuston of the Caspian and major fresh-water bodies on the same scale as in the seas will make for a better discussion of this problem, but at this stage we can merely suggest the explanation given above for the origin and structure of its neuston. The possibility that it will be enriched with Black Sea and Azov forms, including euhyponestonic organisms,

appears very real.

In conclusion, some data on the eggs and fry of Black Sea mullet to supplement the description of the Caspian neuston. As seen from Table 53, the eggs of grey mullet accumulating in the 0-5 cm layer are fairly numerous in the underlying layer also, whereas in the Black Sea they have a more obvious tendency to congregate near the surface film (Zaitsev, 1964a). This is due to the fact that the density of the water in the Caspian is $1\frac{1}{2}$ times less than in the Black Sea as the result of substantial freshening and high summer temperatures. Therefore Black Sea mullet eggs are also fairly common at subsurface depths in the Caspian and hence more numerous in hauls by completely submerged nets operating horizontally. That is why the collections of ichthyoplankton made in the Caspian always included more Black Sea mullet eggs than those taken in the Black Sea, and the authors describing them came to the conclusion after comparing hauls from various parts of the water basin that grey mullet and golden-grey mullet spawn predominantly in the open sea (Pertseva-Ostroumova, 1951; Probatov, 1955; Babayan, 1957). A similar conclusion and analogous results arrived at by certain foreign specialists were not generally recognized at first, as there was no explanation for this peculiarity of breeding biology. Now, because of the discovery of the hyponeustonic nature of the early developmental stages of Black Sea mullet, the reasons for the catadromous spawning migrations of these fishes are becoming understood. It is also becoming clear why the conclus-

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ion - based on egg collections - that they breed far from the shore was first reached by authors who had previously worked in the Caspian and not in the Black or Mediterranean seas.

Hyponeustonic larvae and fry of grey mullet, 4.0-19.3 mm long, were encountered over a large area - from the southernmost stations to the Volga prodelta, but their average body length increased from south to north. Whereas the average length of the fry is 6.61 mm at the latitude of Ogurchinskii Island and 9.24 mm at the latitude of Kara-Bogaz-Gola, north of the 44° parallel it rises to 13.61 mm. This situation can be ascribed to an earlier beginning to spawning in the North Caspian and also to migration from south to north as the fry grow.

The total abundance of grey mullet fry in the 0-5 cm layer in an area of roughly 120,000 km² was about 190,000,000. Spawning of golden-grey mullet had not yet begun while the cruise was in progress. The distribution of some of the representatives of the neuston in the Caspian Sea is shown in Fig. 68.

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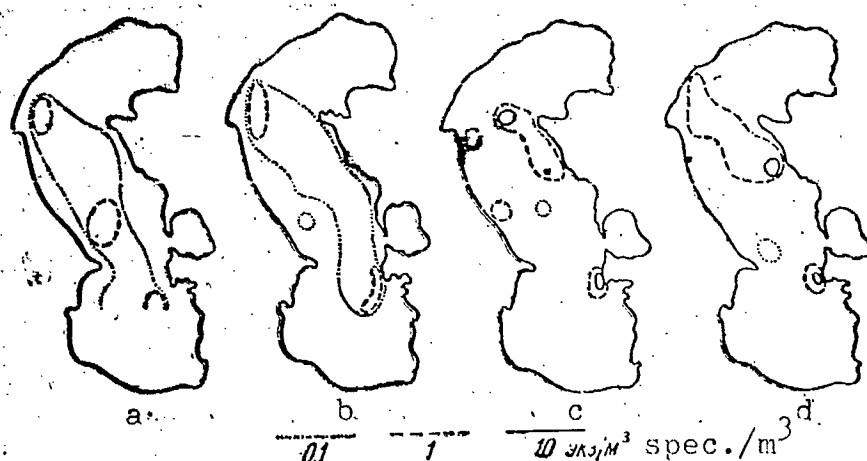


Fig. 68 - Distribution of certain hyponeustonic organisms in the Caspian Sea in July 1962 (Zaitsev, 1964a):

a - *Mugil saliens*, larvae, b - *Atherina mochon pontica n. caspia*, larvae, c - *Palaemon* sp., larvae, d - Amphipoda.

Chapter XVII. Features of the neuston in the high-latitude regions of the ocean

The volume of factual data on the neuston of the high-latitude regions of the ocean is at present much smaller than the amount of information available on the southern seas of the USSR. Collections exist which were made in 1962-1963 in waters situated to the east and south-east of Kamchatka and in the Mare australis. More representative are the materials from the Pacific, and the results of analysing these samples provide the basis of the following preliminary description of the neuston in water areas situated in the region of latitude 50°.

During the period from June 24th to September 4th 1962, in the southern part of the Bering Sea and the adjoining waters of the Pacific (Fig. 69), samples of neuston were collected by S.M. Chebanov (1965) with the aid of a PNS-2 plankton-neuston net. He operated from a medium-sized trawler type SRTR-4347, belonging to TINRO, and the MV "Gribanov" belonging to the Kamchatka division of TINRO.

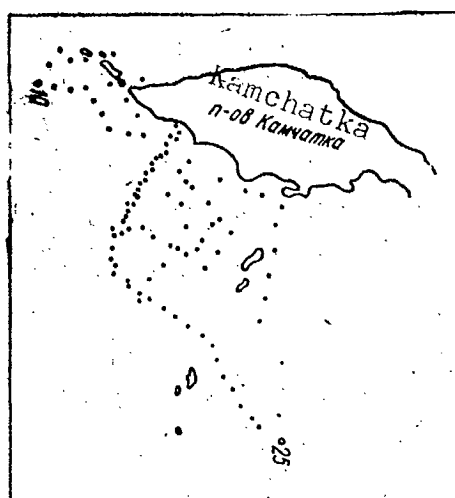


Fig. 69 - The positions of the neustonological stations executed in the northwestern part of the Pacific Ocean between June 24th and August 18th 1962. The circles indicate the stations whose materials are shown in Figs. 39 and 40 (Zaitsev, 1964a).

The water area embraced by the network of stations measures approximately 1,800,000 km². The stations are distributed as follows: Bering Sea - 17 stations, northwestern part of the Pacific - 79, Sea of Okhotsk - 2. Besides this another 12 stations were taken in the inshore zone (Avachinskiy Bay, Utashud

Island region). At each station one sample was taken with the aid of a PNS-2 net, and at some of them samples were taken round the clock at intervals of 1, 2 or 3 hours.

All in all, 346 samples were obtained at 110 stations. For characterization of the plankton at various depths in the pelagic zone 42 samples were taken with a Kidd trawl and 81 with a Juday net equipped with a closing device.

The water temperature at the surface during collection did not exceed 10-11^o C and only in Avachinskii Bay did it rise to 14^o. However, the species composition of the organisms in the PNS-2 collections was much richer than in the summer collections made in the southern seas. Part of the reason for this is the oceanic nature of the region in question, where freshening never becomes so strong that it restricts the spread of stenohaline species. Most numerous in the hauls were representatives of chaetognaths, pteropods, copepods, hyperiids and euphausiaceans. The remainder, including coelenterates, polychaetes, young squids, megalopa stages of crabs and larvae of other decapods, fish larvae and fry, were found in far smaller quantities, and pontellids were even less numerous (Table 54). The numerical data in the table were computed from all finds of each kind of organism by day and by night. During collection of the material the surface of the sea was rarely calm. Usually the waves were from 1-2 m high, and some samples were taken in waves up to 5 m high. This afforded an opportunity to test the reliability of the plankton-neuston gear and at the same time

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to study the reaction of the neustonts to hydrometeorological conditions typical of the region.

Table 54

Composition and average density (spec./m³) of organisms near the surface of the Bering Sea and adjacent waters of the Pacific in June-August 1962 (Zaitsev, 1964a).

Организм	Микрогоризонт, 2 см	
	0—5	5—25
Chaetognatha	7,90	9,20
Pteropoda	3,71	4,57
Cephalopoda, juv.	0,39	0,15
<i>Calanus tonsus</i>	77,30	123,20
<i>C. cristatus</i>	13,90	19,10
<i>Eucalanus bungii</i>	4,50	6,90
<i>Epilabidocera amphitrites</i>	4,80	0,12
Decapoda, zoëa	2,80	8,20
Brachyura, megalopa	5,60	1,10
Cumacea	9,10	1,20
Amphipoda, без Hyperiidæ	18,60	1,60
Hyperiidæ	362,40	140,50
Isopoda	3,10	0,60
Euphausiacea	3,30	2,10
Piscēs, larvae	7,60	1,40

Key: 1 - organism; 2 - microlayer, cm.

As can be seen from the table, the chaetognaths (especially Sagitta elegans) do not concentrate in the 0-5 cm layer and may even avoid it to some extent. At only 17% of the stations where these organisms occurred was the density of Sagitta in the upper microlayer greater than in the lower. In the main these stations were taken during the dark hours, but among the remaining 83% of the stations, where the density was higher in the second layer, there were also many night collections. On the whole, it can be concluded on the strength of these materials

that the chaetognaths in this region, though they make circadian vertical migrations to the surface, do not form such large concentrations as in the Black Sea (Table 48).

The same may be said of the pteropods, among which Clione limacina and Limacina helicina occurred with particular frequency. In only 12% of the cases did these abundant organisms of the Far Eastern plankton exhibit a slight predominance in the upper layer.

Young squids, and mainly Ommatostrephes sloanei pacificus, 15-20 mm long behave differently than chaetognaths and pteropods, being clearly predominant in the hyponeuston layer. According to the visual observations of S.M. Chebanov, these predatory cephalopods swim right near the surface. The stomachs of some dissected individuals were found to contain fish larvae and the remains of crustaceans. In 1965 the author observed a similar vertical distribution of young squids in the Gulf of Mexico, and P.M. David (1965) includes young Teleoteuthis squids, whose skin has a blue sheen, among the components of oceanic hyponeuston.

One of the most abundant species of copepods in our Far Eastern seas - Calanus tonsus (according to averaged data) - shows no sign of being attracted to the 0-5 cm layer. It is probable that this finding was influenced by the fact that the collections were made in daytime, when the number of crustaceans near the surface is minimal. Nocturnal collections, which accounted

for 38% of all samples, revealed 134.1 spec./m³ in the 0-5 cm layer and 74.2 spec./m³ in the 5-25 cm layer. The circadian vertical migrations of C. tonsus can be traced quite clearly, and the fact that it concentrates in the hyponeuston layer during night-time is proved by a large number of observations. Here it comes into contact with hyperiids rising from the depths, as is demonstrated by two actual cases examined in Chapter XIII.

In other basins, as for example the Sea of Japan, C. tonsus /217/ descends to the deep layers as the water warms up according to the data of K.A. Brodskii (1950). The relationship of this species to neuston should be examined in the light of its temperature preferences. It may be that the summer water temperature at the surface of the Sea of Japan is higher than the optimum (as in the Black Sea, for C. helgolandicus), whereas in the higher latitudes this factor fails to prevent the crustacean rising to the surface and concentrating in the hyponeuston layer. Another abundant species, Calanus cristatus, behaves in similar fashion, forming concentrations of up to 1700 spec./m³ in the 0-5 cm layer. In summer this crustacean descends by day to a depth of more than 500 m (Brodskii 1950), and hence it too completes extensive vertical migrations. Yet another copepod, Eucalanus bungii, appears at the surface of the water only during the cold part of the year (Brodskii, 1950). In summer PNS-2 hauls it occurs in quantities of up to 352 spec./m³, with a slight predominance in the 0-5 cm layer during the dark part of the day.

Next in Table 54 comes Epilabidocera amphitrites - the north-

ernmost representative of the pontellid family, with a range extending to the Chukchi Sea (Brodskii, 1950). In PNS-2 collections Epilabidocera was found only at three stations 10-20 miles south of Cape Lopatka. Like other members of this family, Epilabidocera behaves as a typical hyponeustonic species.

Decapod zoea predominated in the 0-5 cm layer in only 20% of the cases. It may be that the result was influenced by an insufficient number of observations (zoea were encountered at only 10 stations), since these larvae lead a hyponeustonic mode of life in all other seas. On the other hand, the number of megalopa stages of crabs was without exception 20 times or more greater than in the deeper-lying layer. Megalopa were found all over the study area, including stations situated 300 miles or more from the coast over depths of 4000-5000 m. In 1964-66 S.M. Chebanov, who studied the Kamchatka crab, discovered the main concentration of larvae of this species in the 0-5 cm layer. Like other typical representatives of the hyponeuston, they had a light-bluish colour.

Specimens of amphipods, cumaceans and isopods were encountered mainly in Avachinskii Bay. Among them, such abundant amphipods as Anonys sp., Parhyale zibellina and Nototrophis guttatus showed a marked numerical predominance in the hyponeuston of the bay, as also in the Black Sea.

Very numerous in the night hauls made with the PNS-2 were hyperiids, especially Parathemisto japonica, which forms distinct concentrations in the hyponeuston, chiefly of deepwater regions. The circadian migrations of these characteristic representatives

of the bathyplanktohyponeuston were examined in Chapter XIII.

Euphausiaceans (it was usually Thysanoessa inermis and T. rashii that were found in the samples) also lead a hyponeustonic mode of life during the dark hours of the day, but unlike hyperiids they have only one density maximum. However, these data require further clarification, as the plankton-neuston net yields understated information on the numbers of such mobile forms as large euphausiids. While it cannot be claimed that they are an accurate reflection of the absolute abundance of euphausiids, the PNS-2 data show that these large crustaceans concentrate in the 0-5 cm layer like the hyperiids. At night they averaged 4.9 spec./m³ in the 0-5 cm layer and 2.3 spec./m³ in the 5-25 cm layer.

Ranking last in the table are fish larvae. These are mainly larvae of the Pacific saury Cololabis saira (Brev.), and to a far lesser extent those of walleye pollock and other species. The saury larvae are hyponeustonic organisms. Their numbers in the 0-5 cm layer are 20-30 times higher than in the 5-25 cm layer. In this respect they are similar to their kin - the needlefish larvae. The stomachs of saury larvae over 20 mm long were found to contain mainly hyperiid remains, which, like their body pigmentation (bluish back and light - coloured abdomen), confirms their hyponeustonic character. The adult saury specimens are also connected with the hyponeuston. Thus, the stomachs of three out of five saury specimens 22-27 cm long, caught at station 11 on August 2nd 1962, were found to contain 4, 2 and 20 saury larvae, respectively, 60 mm long. The stomachs of the other two fish

were filled solely with hyperiids. Hence, the adult saury feeds in the hyponeuston layer, consuming the most typical neustonts, including their own young.

Thus, the collections of neuston disclose important features of the vertical microdistribution of saury larvae and fry and improve the accuracy of the record of their distribution in the northwest part of the Pacific. According to information in the literature, saury does not form commercially useful aggregations north of latitude 44° N, and this reveals that it is relatively thermophilic. As regards saury larvae, they have been assigned to the tropical species (Beklemishev and Parin, 1960). Saury eggs were found south of the 40° parallel by V.A. Mukhachev (1960).

The northernmost find of saury larvae in plankton-neuston net collections was made in latitude 53° . Saury eggs (they attach themselves to floating material and sargassos) were not found in the samples of hyponeuston, and it may be that they were brought here from more southerly latitudes. Yet the nature of the major currents in this region and the presence here of adult specimens suggest that spawning occurred in situ. A more accurate answer will be provided by subsequent studies, but the very fact of the discovery of larvae $11-13^{\circ}$ higher than the northern limit of the reproductive part of the range of the species in these waters (Parin, 1968) merits attention, as it indicates considerable eurythermicity of the saury in the early developmental stages. /219/

Thus, neustonological investigations show that the 0-5 cm layer is very richly populated in the northwestern part of the Pacific, including the adjacent areas of the Bering Sea and Sea

of Okhotsk. However, the temperature regime and other conditions affect the structure and composition of the hyponeuston in this region. Of all the pontellids only one species occurs here, and even then it is found solely in the inshore zone where the water temperature at the surface is $2-3^{\circ}$ higher than away from the shore. Hence, the study area is one of the outposts of the range of pontellids, which are represented here only by a neritic species. It is not yet known whether the isopods encountered in the PNS samples and found only in the shelf zone belong to the euhyponeuston.

The large drop in the mean annual water temperature and the severe conditions during the lengthy cold season do not encourage neuston to stay in these parts all year round. For the same reason peak development of the nearsurface assemblage of organisms occurs in the summer months. As has been shown, this is clearly seen from the example of the Black Sea.

The merohyponeuston, judging by the collections obtained, is represented by crab larvae, young squids and saury larvae. It may be that the larvae of other higher crustaceans should also be included here, but the data available do not confirm this.

The benthohyponeuston, as in the southern seas, includes representatives of cumaceans and amphipods, and this major point of similarity is emphasized by the presence of a benthohyponeustonic species which is also found in the Black Sea - Nototrophis guttatus (Costa).

Of most significance in the life of the 0-5 cm layer of the study area are the bathyplanktohyponeustonic species of hyperiids, euphausiaceans and calanids. The scale of the diel vertical migrations of pelagic organisms in the northwestern part

of the Pacific is truly grandiose and encompasses a huge stratum of water (Vinogradov, 1954, 1955 and others). PNS collections reveal that these phenomena have a direct bearing on neuston. The 0-5 cm layer is the upper terminal point of the migration paths of these species, which, concentrating and maintaining their position beneath the surface tension film, have a considerable influence on the life of the nearsurface biotope. Further study of the smaller forms of neuston will shed more light on the trophic links between the various inhabitants of this highly important microlayer of the pelagic zone.

It might be noted incidentally that genuine deep-water fishes also take part in the vertical migrations. Thus, at a point with the coordinates $53^{\circ} 45'$ northern latitude and $172^{\circ} 00'$ eastern longitude S.M. Chebanov, using a Kidd trawl, caught two specimens of Chauliodus maccouni during the night at a depth of only 35 m. T.S. Rass, who identified the fish, thinks that this is one of the shallowest depths at which this fish has ever been caught. /220

The general pattern of neuston characteristic of the northwestern part of the Pacific is repeated with a few small changes in the Antarctic Ocean. Here, in the fishing regions frequented by Soviet whaling flotillas, qualitative collections were made with a neuston net from November 1962 to March 1963 by A.I. Ivanov, who studied the phytoplankton of the Atlantic, Indian and Pacific Ocean sectors of the Antarctic. As made evident by his observations and by an examination of the samples

forwarded by him to the author, the hyponeuston of the Antarctic Ocean is poorer in respect of species than the northwestern part of the Pacific, and this is due to the temperature conditions. There are no pontellids and the euhyponeuston, merohyponeuston and benthohyponeuston also look very poor, consisting of a few larvae of decapod crustaceans and amphipods. The bulk of the population of the 0-5 cm layer consists of bathyplanktohyponeuston - those same hyperiids and euphausiaceans performing circadian vertical migrations equally distinct as those in the northwestern part of the Pacific. A.I. Ivanov reports that their density during these migrations is very high.

Thus, the neuston of the high latitudes is marked by a pronounced circadian rhythm in its composition and numbers owing to vertical migrations of such abundant and large crustaceans as hyperiids and euphausiids. From the data available it follows that the lower the water temperature in a particular part of the ocean, the smaller the percentage of euhyponeuston and the greater the proportion of bathyplanktohyponeuston. It is in the high latitudes, where the bathyplanktohyponeuston attains its maximum quantitative development, that we find concentrated the main feeding grounds of the principal consumers of euphausiids, hyperiids and large calanids, i.e. the baleen whales. It is quite evident that because of differences of scale between the consumers and the 0-5 cm layer it cannot be said that whales feed only on inhabitants of the hyponeuston layer. The discovery in their stomachs of a whole range of floating objects such as pumice, slag, wood etc. (Sleptsov, 1952, 1955) shows, however, that

baleen whales often swallow food at the very surface of the ocean, including the hyponeuston layer.

When the water temperature rises the composition of the oceanic neuston changes abruptly. Six qualitative samples were taken with a PNS-3 net by G.N. Nefedov (AzChernIRO) on September 10th 1961 at a point 7-8 miles from the coast in the Walvis Bay region. The water temperature at the surface was 16⁰ C. In terms of geographical latitude the points of the stations lie in the Tropic of Capricorn, but the temperature conditions, because of the passage through here of the cold Bengal current, correspond to those of the temperate zone. However, regardless of the inhibitory effect of the temperature factor, the structure of the neuston in the Walvis Bay region is far different from that characteristic of the high latitudes. A wide variety of organisms was discovered in the samples, and especially noticeable were the warm-water forms - mainly in the euhyponeuston and merohyponeuston. Pontellids made an appearance. There were only a few of them (Pontellina sp.), but the very fact that they proved to be in these sparse collections indicates the nature of their distribution. /221/

The merohyponeuston was represented by numerous decapod larvae, including crab megalopa stages and larvae of Engraulis, Sardinella and Callionymus. The benthohyponeuston was represented by amphipods, and the bathyplanktohyponeuston by Rhincalanus nasutus and pelagic polychaetes of the family Tomopteridae. Hyperiid and euphausiaceans, which are common forms in these

waters, were not found in the PNS samples. It may be that the water temperature at the surface in this region is higher than the optimum and that on ascending during the night they halt some distance from the surface. On the other hand it is possible that the continual presence of rich merohyponeuston and euhyponeuston in the 0-5 cm layer, and also the appearance here at night of benthohyponeustonic organisms, intensifies competition for food and renders concentration of a large number of hyperiids and euphausiaceans in the same biotope biologically inexpedient. Something similar was observed in the region of Avachinskii Bay on Kamchatka. There the 0-5 cm layer contained Epilabidocera, amphipods and cumaceans, but no hyperiids or euphausiaceans. In the open waters, where the benthohyponeuston and euhyponeuston were many times less abundant, the number of hyperiids and euphausiids in the 0-5 cm layer increased sharply.

Since one of the crucial conditions determining the concentration of particular organisms in the thin 0-5 cm layer of water is the trophic factor, it may be assumed that the presence of masses of hyperiids and euphausiaceans is of biological significance only where there is a paucity of other neuston consumers. Such conditions obtain over great depths and in the high latitudes, and it is there that bathyplanktohyponeuston, including euphausiaceans and hyperiids, flourishes most. On the other hand, the higher the water temperature the greater the percentage of round-the-clock components of neuston among invertebrates and fishes, and the smaller the amount of bathyplanktohyponeuston in the area.

Chapter XVIII. Characteristics of neuston in the tropics

All the components of marine neuston are most completely represented in the tropics. This can be seen from the collections made by V.V. Krakatitsa fishing with NS* and NT-3 nets and trawls in the Indian Ocean from trawler SRTR-9036 in August-September 1962, and from those made by the author with PNS-3 and MNT nets and trawls in the Gulf of Mexico, Florida Strait and Old-Bahamas Channel in April-August 1965. In addition to this the Hyponeuston Division has in its possession various collections from other regions amounting altogether to over 200 neustonological samples. On the basis of these collections, laboratory tests, and also numerous visual observations (both above and below the surface) by the author in the waters off Cuba, an initial idea of the characteristics of tropical neuston can be formed.

Along with my own data, obtained by the same methods throughout, certain published sources were also used to characterize the tropical neuston, e.g. Herring's survey of the oceanic water-striders, and also the data yielded by collections obtained with a PT pleuston trawl (according to other authors, a PS net), designed by A.I. Savilov (1963), from aboard the "Vityaz'" in the tropical regions of the Pacific and Indian oceans. This fishing gear is identical in overall design to the pyramidal neuston net (Zaitsev, 1959), but differs from the latter in certain

*

See glossary at end of translation for these various types of gear - Translator.

respects.

For the collection of pleustonic organisms the PT trawl is lowered to a depth of as much 25-30 cm. Since pleustonic animals proper do not leave the surface, the PT trawl has no second or lower levels like the multi-level PNS net. This means that it is impossible to judge what layer of water is populated by the organisms appearing in the haul, i.e. whether they are found more than 25-30 cm below the surface and in what quantities, or whether they are concentrated in a still thinner layer than 0-30 cm. Since true pleustonic organisms are passive, the PT is designed to operate while the vessel is drifting. The towing speed then depends on the speed of drift, but in most cases it is low for collecting those motile organisms for which the MNT is employed, operating while the vessel is under way. Thus, while the PT trawl is entirely adequate for collecting pleuston, because of its design and mode of operation it does not meet the requirements for collecting and counting neuston. However, since the PT trawl also fishes the 0-5 cm layer, its samples contain a large quantity of neustonic organisms. The PT catches enabled A.K. Geinrikh (1960, 1964) and N.M. Voronina (1962) to compile a list of pontellids inhabiting the tropical region of the Pacific and Indian oceans, while A.I. Savilov (1967) was able to make a similar list of oceanic waterstriders in the Pacific. Some use has already been made of these data in preceding chapters to illustrate one point or another. Several other published works can also be cited whose material could be used to characterize the neuston of the tropics, but factual

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data are still very limited.

One of the most important structural features of the tropical neuston is the epineuston. Whereas in other climatic zones the epineuston is the entirely unstudied world of micro-organisms in the foam, in the tropics it also includes comparatively large oceanic water striders of the genus Halobates, the most typical species of which have no link with dry land, no wings, and are confined solely to the aerial side of the surface tension film of the pelagic zone. This also explains the confinement of oceanic water striders to regions with warmer water. Strong winds are apparently able to remove some of these insects to the temperate zone, but the general pattern of distribution is circumtropical, and in the case of such species as H. sericeus it is circumtropical with an incursion into the boreal and notal regions (Fig. 70).

The map clearly illustrates what has been said. In neuston collections from the Arabian Sea and Gulf of Mexico representatives of H. micans are also to be found, but this merely reinforces its description as a circumtropical epineustonic species. Another abundant species, H. sericeus, according to A.I. Savilov's data (1967) for the Pacific Ocean, populates the north and south subtropical current circulations, including the halistatic parts /224/ of their central areas and extending north and south as far as the 40° parallel (Fig. 71). The following five species of water-striders from Savilov's collections in the Pacific - H. princeps, H. flaviventris, H. germanus, H. splendens and

H. sobrinus - spread byond the tropics. In some places water-striders, according to Savilov's observations, form concentrations with a density of several specimens per square metre of sea surface.

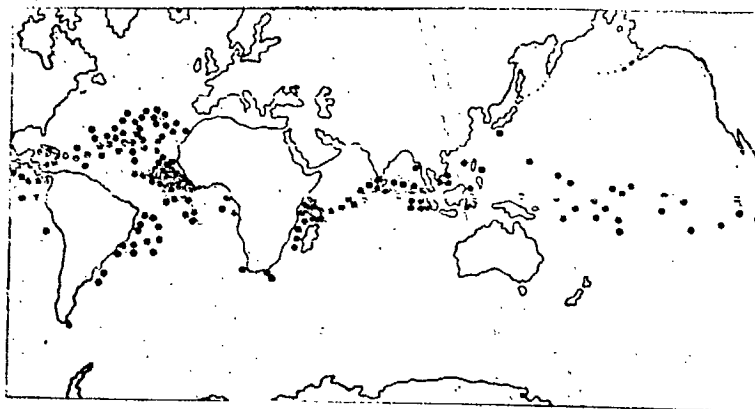


Fig. 70 - Discovery sites of Halobates micans in the ocean (Herring, 1961)

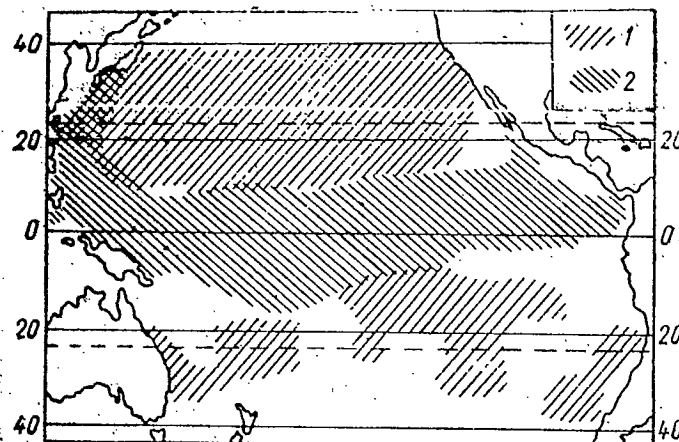


Fig. 71 - Diffusion of Halobates sericeus (1) and H. micans (2) in the Pacific (Savilov, 1967)

The hyponeuston of the tropical region is extremely rich. Favourable temperature conditions throughout the year ensure the development of what is in respect of species the richest euhyponeuston fauna. In the warmest areas of the world ocean there is a genuine flourishing of such organisms as mollusks of the genera Glaucus and Janthina, the shrimps Parapeneus longipes and Leander tenuicornis, the crabs Planes and Portunus portunus, and dozens of species of the family Pontellidae.

In the central and northwestern parts of the Pacific A.K. Geinrikh (1960, 1964) discovered the following pontellid species which do not penetrate further north in this basin than the 40° parallel: Labidocera (L. detruncata (Dana), L. acutifrons (Dana); L. trispinosa Esterly, L. acuta); Pontella (P. tenuiremis Giesbrecht, P. princeps Dana, P. securifer Brady, P. fera Dana, P. agassizi Giesbrecht, P. danae Giesbrecht, P. diagonalis Wilson, P. spinipes Giesbrecht, P. whiteleggei, P. chierchiaie); Pontellopsis (P. villosa Brady, P. strenua (Dana), P. armata (Giesbrecht), P. occidentalis Easterly, P. regalis (Dana); Pontellina (P. plumata Dana).

To this list N.M. Voronina (1964) adds Labidocera minuta Giesbrecht, and K. Sherman (1963) L. madurae. K.A. Brodskii (1950) includes yet another tropical species encountered in the Pacific and Indian Oceans - Labidocera pavo Giesbrecht. The total then is 23 species, of which only one - Pontella plumata - keeps to depths of up to 50-100 metres by day and rises to the surface at night (Wilson, 1942; Voronina, 1964). This explains

its abundance in the "young" water at the equatorial divergence (Vinogradov and Voronina, 1964). Individual specimens of Pontella tenuiremis are found down to a depth of 100 m (Wilson, 1942), but the maximum of this species is clearly confined to the nearsurface layer (Voronina, 1964). The remaining pontellid species lead a typical hyponeustonic mode of life, thereby graphically illustrating the statement concerning the qualitative richness of the euhyponeuston in the warmest waters of the Pacific. Within these waters the region of equatorial divergence is characterized by comparatively poor neuston (the reasons for this are examined in Chapter XV), and to the north and south of it lie the tropics, with the richest composition of neuston.

For 139 stations situated in the tropical region of the Indian Ocean N.M. Voronina (1964) lists 22 species of pontellids: Labidocera (L. acutifrons, L. detruncata, L. minuta, L. acuta, L. kroeyeri, L. nerii, L. sp. (nova?)); Pontella (P. princeps, P. spinipes, P. securifer, P. danae, P. fera, P. novae-zelandiae, P. atlantica (?), P. denticaudata, sp. (nova?); Pontellopsis (P. regalis, P. strenua, P. armata, P. villosa, P. macronyx, P. sp.; Pontellina (P. plumata).

For comparison the list of pontellids for the Mediterranean can be given. There the water temperature in the central regions drops in winter to 17-13°C (Raymont, 1967). According to the data of G. Trégouboff and M. Rose (1957), there are nine species of pontellidsⁱⁿ/these waters: Anomalocera (A. patersoni Templ.); Labidocera (L. wollastoni Lubbock, L. brunescens Czern); Pontella

(P. mediterranea Claus, P. atlantica Dana , P. Lo Biancoi Canu); Pontellopsis (P. regalis Dana, P. villosa Brady); Pontellina (P. plumata Dana); Parapontella (P. brevicornis Lubbock).

As can be seen, the number of pontellid species in the Mediterranean is much lower than in the tropical regions of the Indian and Pacific Oceans, and the two new genera which have appeared - Anomalocera and Parapontella - are common in the boreal region.

Yet another group of organisms characteristic of the euhyponuston of the tropical region of the ocean are the sargassos. They are very widely distributed, but only in the Atlantic Ocean do they form a vast accumulation discovered long ago by Columbus on September 16th, 1492. This region is now called the Sargasso Sea. Situated between 20 and 35° northern latitude and 40 and 75° western longitude, the Sargasso Sea extends beyond the geographical boundaries of the tropics proper, but climatically it is an integral part of them. Because of the influence of the Gulf Stream the water temperature at the surface of the Sargasso Sea does not drop below 20-25°C in February, and in August it fluctuates between 25 and 28°C (Péres, 1961). The sargassos which make up this sea (S. natans L. and S. fluitans Borgensen) breed only vegetatively and are always found in the hyponeustonic position. Their phylloids, air bladders and other parts of the thallus became in the course of evolution objects which could be imitated by a number of neustonts, such as invertebrates and fish, both the larval stages and adult individuals, making up the unique "sargasso fauna" - one of the characteristic groups of tropical

hyponeuston. The abundance of living creatures in the near-surface layer of the Sargasso Sea and of food needed by the numerous fishes and large invertebrates in the hyponeustonic "sargasso fauna" conflicts with the fairly large number of statements made concerning the poverty of these waters. Thus, V.Ya. Yashnov (1962) considers the Sargasso Sea to be an example of an ultraoligotrophic region. In all probability this is yet another case where vertical hauls obtained with plankton nets do not give an objective picture of life in the near-surface layer of the sea.

The merohyponeuston of the tropics is represented by the same groups of hydrobionts as in the temperate zone, but they include many more species than in either temperate or high-latitude waters. In collections of neuston from the Gulf of Mexico are found still unidentified larvae of polychaetes, lamellibranchs and gastropods, young squids, larvae of Balanus and Lepadidae, higher crustaceans (zoea, megalopa, alima, phyllosoma), Enteropneusta (tornaria), lancelet (Branchiostoma lanceolatum), eggs, larvae and fry of fishes, and many others. The abundance of merohyponeuston in the Gulf of Mexico, as in other seas, increases sharply over the shelf zone.

Benthohyponeuston is also associated with the shallow-water region. In the Gulf of Mexico it is represented by many species of adult polychaetes, amphipods, cumaceans, isopods and shrimps. On June 21st 1965, at 23.00 - 24.00 hours, in the Old Bahamas Channel, a very rich benthohyponeuston consisting mainly of isopods (Eurydice) and amphipods was fished over depths of some

30 metres. The biomass of the entire population of the 0-5 cm layer was 2400 mg/m^3 . This was apparently a rare case, as the hyponeuston biomass at night in these waters is usually $300-800 \text{ mg/m}^3$.

The large "palolo" polychaetes (Eunice viridis) are probably one of the most glaring, yet most peculiar, examples of a rich benthohyponeuston in the tropics. For instance, in the region of Fiji and Samoa, heteronereid forms of these worms cause the calm sea surface to "boil" for two to three nights, beginning in the early days of the last lunar quarter in October and November. This occurs in the second half of the night and at dawn, while in the daytime the worms disappear from the surface biotope. Unfortunately, the author does not know how these worms behave in other months, but, judging by analogies with related polychaete species from other seas, it can be concluded that they constantly make circadian vertical migrations which are intensified in the breeding season. /227/

As yet very little is known about the significance of the bathyplanktohyponeuston in the life of the nearsurface microlayer of the pelagic zone in tropical waters, but it is clearly less prominent than in the high latitudes or, probably, than in the temperate zone. This may be due to the high degree of development of round-the-clock components of the hyponeuston, the large forms of which may compete seriously for food with the nocturnal refugees. Nevertheless, this element of the hyponeuston does exist in the tropics and it consists of chaetognathic copepods, euphausiaceans, hyperiids and representatives of other systematic groups.

Likewise, very little is known about the quantitative characteristics of tropical neuston. A common feature is that the abundance of specimens of individual species is usually not as high as in temperate or, especially, cold waters. There are only one or two exceptions, as, for example, the few cases of very high abundance of Eunice viridis and Gymnodinium brevis during the "red tide" outbreaks. Usually species diversity is combined with quantitative sparseness. For example, K. Sherman (1963) gives a figure of 10 spec./m³ as a case of high abundance of the neritic species Labidocera madurae near Neker Island (Hawaii). In the Gulf of Mexico the abundance of the most numerous pontellids (Labidocera acutifrons, L. aestiva, Pontellopsis regalis, Pontellina plumata) in the author's collections did not exceed 20-30 spec./m³. Compared with the hundreds of specimens of pontellids per cubic metre in the Black Sea and Sea of Azov these figures are not very impressive. However, the figures for the biomass of total neuston in the Gulf of Mexico and Black Sea are so close that it is difficult at the present level of knowledge to give clear preference to the Black Sea samples. In the regions of upwelling in the Gulf of Mexico, as for example on Campeche Bank (Bogdanov, 1965), the neuston is poor and its biomass does not exceed 100-200 mg/m³, but in the regions of sinking - north of Campeche Bank - in the middle of the gulf it is 410 mg/m³ (hauls made with a net of No. 23 mesh), which is above the average biomass of net neuston in the Black Sea (see Chapter XVI). The impression is that further special

study of neuston in various parts of the ocean will bring changes /228/ in the currently popular view that life in the upper part of the pelagic zone in tropical waters is extremely poor compared with that in the temperate zone.

A clear idea of the abundance of hyponeuston in the region of Florida Strait was provided by the numerous series of visual observations conducted by the author near the northwest shore of Cuba. A very colourful description of the wealth of life in the nearsurface layer of water off Great Inagua island (Bahamas) was given by the American amateur naturalist G.C. Klingel (1963). Not being specialist, Klingel makes a number of mistakes, but the overall picture painted by him is surprisingly accurate. Here is a small fragment of his description of that underwater world, as seen through a diver's mask.

"For many living creatures the surface of the water is just as impenetrable as metal, yet this film, no matter how opaque it seems from below, lets through light. On top it was covered by a layer of yellow pollen from shrubs along the shoreline, and by winged seeds. In addition I discovered dead beetles on the surface, parts of butterfly wings and insect wing cases. For those living on dry land the ocean surface is a place of death and destruction. Just below the surface however the picture changes completely. Here it is like a nursery for the young animals of the ocean. To the other side of this gleaming ceiling are attached a hoard of newly born creatures: tiny fishes no more than $\frac{1}{4}$ inch in length, transparent as glass and helpless like the current-swept plankton; microscopic crustaceans reflecting all the colours

of the rainbow; the spherical eggs of pelagic organisms, with their long threads and the dark spots of the nuclei; pulsating, gelatinous ctenophores the size of a drop, just detached from their flower-like parents; myriads of other creatures too small to be seen with the naked eye, their presence betrayed by pinpoints of reflected sunlight. This last yard before reaching the surface was indeed a crib for the inhabitants of the ocean" (pp. 259-260).^{*}

G.C. Klingel knew nothing of the features of life at the sea-air interface, but as an attentive and objective observer he described what he saw, and the result was a complete picture of marine neuston - habitat (pollen and insects on the surface of the water), the high abundance of organisms adhering to the gleaming "ceiling", and the abundance of larval stages in this "ocean crib".

The high abundance and biomass of neuston in the warmer parts of the ocean are indicated by the cases of its mass consumption by such large fishes as tuna. For example, Neothunnus albacora in the equatorial region of the Atlantic Ocean sometimes feeds exclusively or predominantly on hyponeustonic larvae of crabs of the families Portunidae and Dromiidae, and of stomatopods (Squilla, Lysiosquilla, Gonodactylus), phyllosoma larvae of Scyllaridea and others (Marchal, 1959). E. Marchal notes that the megalopa stages of crabs formed the major item in the stomach contents of 300 albacores caught opposite the coast of Guinea, over

* The English-language version of this book could not be obtained by the translator - Translator's note.

depths of 200-1000 m. Among the fishes found in the stomachs were the hyponeustonic species Antennarius scaber and Histrio histrio.

Indirect evidence of the abundance of neuston in the neritic zone of the tropics is provided by the presence here of such specialized neustonophages as scissor-bills (Rhynchopidae) and fish-catching bats (Noctilionidae).

down. To the

a hoard of newly born creatures: tiny fishes

in length, transparent as glass and helpless like the current-swept plankton; microscopic crustaceans reflecting all the colours

THE IMPORTANCE OF NEUSTON IN THE LIFE OF THE

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SEA AND THE FUTURE OF MARINE NEUSTONOLOGY

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Chapter XIX. The importance of neuston in the life of the sea

The factual data on the various aspects of the nearsurface assemblage of organisms reveal that there are at least two important facets of life in the sea in which neuston has a special role to play: breeding by hydrobionts and the biogenic cycle of substances in the sea and adjacent biocycles.

Neuston and breeding by marine organisms

In previous chapters it was emphasized several times that neuston consists mainly of the early developmental stages of invertebrates and fishes, and examples were given to illustrate this. Judged by the average age of its component organisms this is the youngest assemblage in the sea. Young individuals are to be found in all the biocenoses of the pelagic and benthic divisions, but they are "diluted" with a considerable number of parent forms. In the neuston, however, entire families and orders are represented solely by eggs, larvae or fry. This significantly reduces the average age of the population of the nearsurface biotope and is one of its important distinguishing features.

Table 55 lists some of the commonest and most abundant genera of fishes and invertebrates in the neuston and indicates the stages of individual development by which they are represented.

out of 63 genera of neustonts 32 are represented solely by the early stages of ontogenesis (eggs, larvae, fry), 26 by both early developmental stages and adult individuals, and only 4 by adult forms alone. In the case of the four genera in the first group and twelve of the twenty-six in the second, the adult specimens appear in the neuston during the night-time only. This table could be added to and amended, but the message is clear: neuston is the realm of the young, and the higher we go up the taxonomic ladder the more obvious this becomes.

Table 55

Age composition of invertebrates and fish in marine neuston

Род	Взрос- лые особи	Взрос- лые осо- би и ранние фазы их разви- тия	Ран- ние фазы разви- тия	Род	Взрос- лые особи	Взрос- лые осо- би и ранние фазы их разви- тия	Ран- ние фазы разви- тия
1	2	3	4	1	2	3	4
<i>Membranipora</i>	—	—	—	<i>Palinurus</i>	—	—	—
<i>Nectonema</i>	+	?	—	<i>Diogenes</i>	—	—	+
<i>Microspio</i>	—	+	—	<i>Pagurus</i>	—	—	+
<i>Nereis</i>	+	?	—	<i>Planes</i>	—	+	—
<i>Eunice</i>	—	+	—	<i>Portunus</i>	—	+	—
<i>Janthina</i>	—	+	—	<i>Brachinotus</i>	—	—	—
<i>Glaucus</i>	—	+	—	<i>Rhithropanopeus</i>	—	—	+
<i>Mytilus</i>	—	—	+	<i>Carcinus</i>	—	—	+
<i>Ostrea</i>	—	—	+	<i>Pachigrapsus</i>	—	—	+
<i>Balanus</i>	—	—	+	<i>Eriphia</i>	—	—	+
<i>Acartia</i>	—	+	—	<i>Paralithodes</i>	—	—	+
<i>Anomalocera</i>	—	+	—	<i>Oikopleura</i>	—	+	—
<i>Calanus</i>	—	+	—	<i>Sprattus</i>	—	—	+
<i>Centropages</i>	—	+	—	<i>Engraulis</i>	—	—	+
<i>Labidocera</i>	—	+	—	<i>Belone</i>	—	—	+
<i>Oithona</i>	—	+	—	<i>Trachurus</i>	—	—	+
<i>Pontella</i>	—	+	—	<i>Pomatomus</i>	—	—	+
<i>Gastrosaccus</i>	—	+	—	<i>Mullus</i>	—	—	+
<i>Mesopodopsis</i>	—	+	—	<i>Trachinus</i>	—	—	+
<i>Bathyporeia</i>	—	+	—	<i>Blennius</i>	—	—	+
<i>Gammarus</i>	—	+	—	<i>Xiphias</i>	—	—	+
<i>Dexamine</i>	—	+	—	<i>Gobius</i>	—	—	+
<i>Idothea</i>	—	+	—	<i>Scophthalmus</i>	—	—	+
<i>Eurydice</i>	+	—	—	<i>Platichthys</i>	—	—	+
<i>Sphaeroma</i>	+	—	—	<i>Solea</i>	—	—	+
<i>Squilla</i>	—	—	+	<i>Syngnathus</i>	—	+	—
<i>Thysanoessa</i>	—	+	—	<i>Mugil</i>	—	—	+
<i>Palaemon</i>	—	+	—	<i>Sphraena</i>	—	—	+
<i>Peneus</i>	—	+	—	<i>Atherina</i>	—	—	+
<i>Crangon</i>	—	+	—	<i>Antennarius</i>	—	+	—
<i>Upogebia</i>	—	—	+	<i>Balistes</i>	—	—	+
<i>Callinassa</i>	—	—	+				

Note: (+) indicates that the forms in question are present in the neuston, (-) that they are absent, (?) that the data have not been verified.

Key: 1. - genus; 2 - adult individuals; 3 - adult individuals and their early developmental stages; 4 - early developmental stages.

Thus, the highly important role of neuston in the sea is connected with the breeding of invertebrates and fish and

the embryonic and postembryonic development of forms of plankton, /231/
nekton and benthos. Neuston contains the early developmental
stages of a large number of animals which are sometimes very
far apart systematically and form concentrations here differing
greatly in density from those of the same species and stages at
greater depths. The probable reasons for such a clearly expressed
preference for the nearsurface biotope of the pelagic zone by the
young of hydrobionts were discussed in earlier chapters. The main
ones were: the abundance of small food items, i.e. bacteria,
protozoans and small multicellular organisms developing on the /232/
nutritive medium of dead organic matter which forms in the area
of the surface tension film; the biologically active properties
of sea foam, which is able to stimulate the development and
growth processes of hydrobionts; and, finally, the optical regime
and especially the presence of medium-and long-wave ultraviolet
and infrared rays, which also have a stimulating effect on the
early developmental stages of organisms. A biotope with such a
combination of favourable ecological factors could not remain
empty. The short-wave radiation from the sun, which a number
of authors saw as the chief factor in the presumed extermination
and elimination of living creatures from the nearsurface layer
of sea, did not prove nearly so deadly as was feared. This is
demonstrated above all by the bacteria, which experience in the
neuston such an outburst of development as is never seen in the
lower layers of water, where there is no "bactericidal" radiation.
Other groups of organisms did not lag behind bacteria, and the
result was the formation of an extremely rich concentration of

living creatures.

For some forms, and mainly the lower invertebrates, the 0-5 cm layer became a biotope accommodating both young and adult individuals; for others it is a place where only eggs and young organisms develop. So that the early ontogenetic stages could successfully develop in the sea-air boundary layer, invertebrates and fish underwent great changes in the course of their evolution, and as a result their eggs, larvae and young attained a high degree of morphological and physiological adaptation to the specific conditions of the nursery biotope. In some cases this adjustment changed the external appearance of merohyponeustonic forms beyond recognition compared with the parent individuals. This is yet another argument supporting the contention that marine neuston plays a tremendous role in breeding by hydrobionts. As a concentration of young organisms, neuston is an important connecting link in the regulation of the complex aggregation of biological processes responsible for the natural reproduction of a large number of marine organisms and for the magnitude and quality of annual recruitment to every population, stock or species.

Neuston and the cycle of substances in nature

The topography (position at the sea-air interface), age composition (predominance of early ontogenetic stages), quantity (high density and biomass of organisms) and scale (surface of the world ocean) of neuston determine its broad and strong links with other classes of communities in the sea and on dry land.

These links are established by the instrumentality of larvae, which, after remaining in the neuston for a certain time, leave /233/ for other biotopes, where they live as adult individuals, and by adult specimens arriving in the nearsurface biotope to breed and feed.

Neuston is linked to the biocenoses of the benthos through three channels: the settling of larvae on the bottom, the ascent of adult individuals to spawn (for example, the palolo and other polychaetes), and nocturnal feeding at the surface of the sea by the organisms of the benthohyponeuston.

Neuston is linked to plankton through the same channels. Hyponeustonic larvae of many species of invertebrates transfer to lower depths and become part of the plankton. Females ascend from the deep layers of the pelagic zone to deposit their eggs or larvae in the nearsurface biotope (Lucifer, Sagitta, calanus, Euphausiacea and others). The same applies to representatives of the bathyplanktohyponeuston (hyperiid, calanoids etc.).

The nature of the links between neuston and nekton is the same as in the previous cases. The eggs, larvae and young of many fish species develop in the hyponeuston. Adult fish sometimes rise into the nearsurface biotope to lay their eggs. Such cases have been recorded for Black Sea mullet, sole and some other species. Nevertheless, spawning fish need not necessarily ascend to the hyponeuston layer, as their eggs are highly buoyant and will rise to the surface anyway (in accordance with Archimedes principle), where they concentrate under the surface tension film. Data exist which indicate that the ability of

eggs to rise to the surface ensures maximum fertilization of the spawn. Yu. G. Aleev (1952) reports that trawling near the coast of the Caucasus in June 1951 revealed that adult horse mackerel were distributed in layers on the spawning grounds roughly according to sex. Ripe males predominated in the 0-10 m layer (75-100% of the catch), and ripe females in the 10-17 m layer (78-86% of the catch). Yu. G. Aleev regarded this as biologically significant because it means that the eggs, in rising to the surface, pass through the entire stratum of milt and are thereby fertilized. This spawning device, Aleev believes, is common to many and perhaps even most fishes with pelagic eggs.

Many nektonic organisms are able to consume hyponeuston in great quantities. A.K. Makarov (1938) observed Pontella mediterranea and the larvae of shrimps and crabs in the stomachs of mackerel. Earlier it was mentioned that tuna consume hyponeuston, that dolphin stomachs are filled with Idothea stephenseni, and that baleen whales feed near the surface of the sea.

No special study has been made of the links between neuston and psammon - the interstitial fauna of sandy beaches, but they are probably effected through the development of psammobiont larvae in the neuston and the intrusion of dead neustonts into the psammon biotope during piling up effects. /23

Likewise no study has been made of the interaction between neuston and the anabiocenosis of pagon. In the Black Sea most of the highly organized forms of neuston winter in the southern regions and do not venture into areas where floating ice occurs.

Nevertheless, since ice forms on the surface of the sea it is neuston which is most likely to occur in pagon. As far as can be judged from the preliminary data, it is the lower forms of neuston such as bacteria, protozoans etc. that are usually frozen into the ice.

Contacts between neuston and aerobionts are one of the important and specific features of the assemblage of organisms situated at the sea-air interface. These contacts involve on the one hand consumption of aerobionts on the surface by neustonts, and on the other consumption of neustonts by aerobionts. In Chapter IV several examples were given of birds and mammals that prey on neuston. These creatures have special adaptations on the beak and talons, in the gullet etc., which make it easier for them to catch neustonts, store them and bring them back for their young to feed on. In this way some neustonic organisms are removed from their marine biotope, transported by air to land, and, after being digested by neustophages, deposited in the guano of birds and bats. Birds not only consume neustonts, they also help to distribute them. On their feet and feathers birds transport the eggs of Artemia, oceanic water striders and other organisms.

Thus, marine neuston, through a whole series of objective circumstances, has become a "communications centre" connecting different elements of the biosphere (Zaitsev, 1964a, 1967a; Zaitsev and Polikarpov, 1967a). Through it pass streams of material and energy flowing towards the most diverse biotopes, both in the sea and on dry land. This important role fulfilled

by neuston in nature has not come about by chance. It is the result of the entry into the nearsurface biotope of the pelagic zone of streams of material and energy from other biotopes.

Viewing the ocean as an arena in which transformational, metabolic and energy-exchange processes take place on a grand scale (Bogorov, 1967), we can say that the links referred to above reflect the mechanism which re-establishes equilibrium and thereby makes it possible for the circulation of material to continue. For example, the flow to the surface of dead organic matter from below, as the result of foam formation, the "anti-rain" of bodies, flotation etc., is balanced by the outflow of live organic matter in the form of planktonic, nektonic and benthonic larvae abandoning the nearsurface biotope, and of organisms from the benthohyponeuston and bathyplanktohyponeuston leaving for their daytime biotopes. The larger flows of ascending dead organic matter in the shelf region are associated with stronger flows of descending live organic matter in the selfsame part of the sea where most of the merohyponeuston settles and the benthohyponeuston resides.

Organic matter is carried from dry land to the sea-surface by the wind. But there is also a flow in the opposite direction - of neustonts being transported ashore. This export of neuston usually takes place in the coastal zone, where the nearsurface biotope of the sea derives its greatest supply of organic sediment. So far no calculations have been made of the material and energy flows to confirm these various links. Nevertheless, they represent real points of contact between neustonts and representatives of

other biotopes and biocycles which have been revealed and substantiated by neustonological methods. Depicting the flow of dead organic matter to the surface of the sea schematically without regard for scale (Fig. 72, I), we find that the flow of live organic matter contained in the bodies of neustons passes through the same channels, but in the opposite direction (Fig. 72, II).

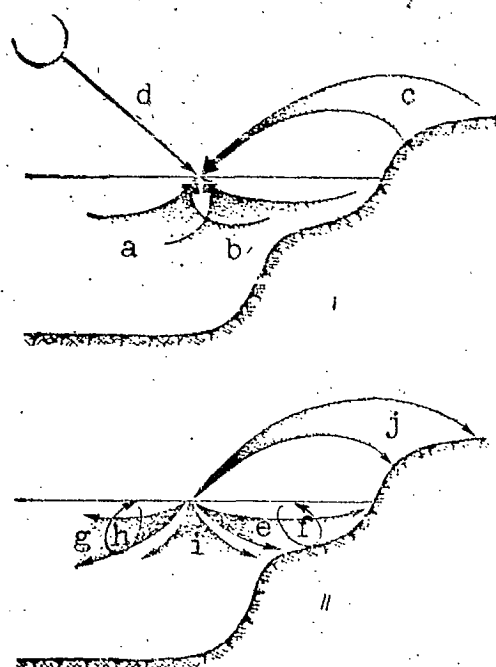


Fig. 72 - Channels linking neuston with other elements of the biosphere (schematic drawing).

I. Inflow of organic matter and energy to the nearsurface microlayer of the pelagic zone: a - foam formation, b - "antirain" of dead hydrobionts, c - eolian deposits, d - solar radiation.

II. Outflow of organic matter and energy from the nearsurface microlayer of the pelagic zone: e - settling of benthogenic merohyponeuston, f - circadian migrations of benthohyponeuston, g - transfer of planktogenic merohyponeuston to plankton, h - circadian migrations of bathyplanktopyneuston, i - transfer of nektogenic merohyponeuston to nekton, j - consumption of neuston and its removal to dry land by neustophagous birds and mammals.

Analysing the probable causes and conditions of the creation of life on earth, J. Bernal (1961) comes to the conclusion that, "like Venus , it was born in the foam of the sea". Bernal holds that the main reason for this was the ability of surface-active substances dissolved in the primeval ocean to accumulate on its surface, where their concentration was hundreds or even thousands of times higher than within the water mass (Bernal, 1969). Life was born on earth and underwent evolution, but the conditions which led to its birth have been preserved: organic substances continue to concentrate on the surface of the sea. This process has been sharply intensified in the course of time, as the mass of living organisms in the halosphere has increased. What outlet remains for this concentration of substances and energy ever present at the sea-air interface now that life can no longer be created de novo ? As far as can be determined on the basis of all the new data obtained, this outlet is the neuston, with its important and controlling role in the development of ecological processes in the sea (Zaitsev, 1967a; Zaitsev and Polikarpov, 1967a). This linking function performed by neuston in nature is making it the focus of attention of an increasing number of scientists working in different fields, and it opens up new vistas of fruitful integrated research.

Chapter XX. The future of marine neustonology

The next task of marine neustonology is the further development of comprehensive and integrated research on neuston and its role in nature. It is a matter of particular importance and

urgency to determine the nature and effect of various artificial influences on neuston and, in particular, its future fate in view of the growing impact of the anthropogenic factor on the seas and /23 oceans. The tasks confronting marine neustonology can be divided into three groups. The first group consists of problems associated with the investigation of specific chemical, physical, radio-ecological and other conditions governing the life of neuston in the sea. In this respect neustonology is primarily the client of a number of other sciences which process this information. The second group of tasks involves investigation of the population of the nearsurface biotope, i.e. neuston itself. This is the hard core of problems whose solution should shed light on all aspects of neuston and its role in nature. The third group of tasks embraces fields in which the interests of neustonology coincide to some extent with those of allied branches of oceanography. As far as can be judged from the research already done, the results of this work will be of great interest to both sides. However, they can be achieved only through the joint efforts of the specialists in both fields. Finally there are various areas of applied science in which it is now obviously impossible to do without neustonological data. The principal ones, which are common to several sciences, are as follows.

Study of the life of the sea as a single ecological process representing a regular alternation of ecological states - or phases - of hydrobionts (Zaitsev and Polikarpov, 1967a) reveals the striking fact that neuston is an ecological phase through which an enormous number of species pass. This point is very

important for anyone studying the ecological processes, phases (phasoecology) and factors governing these species.

In the light of the basic assumptions of radiation and chemical ecology, as elaborated and formulated by G.G. Polikarpov (1964, 1966, 1967a), future research in the field of neuston radioecology acquires great importance. This is because of neuston's, i.e. hyponeuston's, special sensitivity to the radioecological factor in the nuclear age, and the key position neuston occupies in linking together the various classes of hydrobionts and aerobionts, and in the development of ecological processes in the halosphere.

The research done by Z.A. Vinogradova and her colleagues on the ecological biochemistry of marine organisms (Vinogradova, 1967a, 1967b; Kostylev, 1964-1968, and others), dealing chiefly with hyponeustonic organisms, has revealed their biochemistry and in particular the ways and means by which neustonts adapt themselves biochemically to the conditions of their biotope. Vinogradova (1967a) discovered, for example, that hyponeustonic pontellids, unlike planktonic copepods, have no free fatty inclusions. /238/ The lipid compounds, probably in the form of lipoproteins, are localized in a thin continuous layer under the chitinous skeleton, forming what seems to be a waterproof film. The author views this feature as an adaptation to life at the sea-air interface. Further developments in this field promise to be very fruitful and useful both to the ecological biochemistry of marine organisms and neustonology.

The spheres of interest of marine biochemistry, which studies the interrelationships between aquatic organisms mediated by external metabolites (Lucas, 1961; Khailov, 1965), and neustonology meet in the field of research into the nearsurface microlayer of the pelagic zone, which is a biotope with a very high concentration of vital and postmortem excreta of hydrobionts and bodies of organisms. The ecological importance of sea foam as a concentration of external metabolites has been demonstrated experimentally on hydrobionts, and it must be studied more extensively and in greater depth. Foam not only affects hydrobionts, it also stimulates the development and growth of land plants, causes erythema in humans, and acts on terrestrial organisms in other ways. All this tends to suggest that there is some possibility of using sea foam preparations for various practical purposes.

Thus it is clear that neustonology and applied hydrobiology have a common interest in the deeper study of the biological productivity of the nearsurface biotope, which has become the focus of highly intensive transformations that are very important to the entire ocean. Neustonological data are necessary for a correct evaluation of the biological effect of pollutants on the surface of the sea (the field of sanitary hydrobiology) and increased effectiveness of the marine fisheries protection service.

It is quite evident that marine pisciculture - a developing and promising branch of fish husbandry, the task of which is to devise biological techniques for replenishing the stocks

of commercially valuable fishes in artificial conditions - requires a profound knowledge of the conditions in which these species develop in nature.

The main achievements listed in previous chapters and the prospects described here leave no doubt that the future development of marine neustonology will fill many of the gaps in our knowledge of life in the sea and render practical measures for the preservation, augmentation and rational utilization of its riches more effective.

CONCLUSION

The surface of the sea has long attracted the attention of man. There are many ancient myths and legends associated with it which at times come astonishingly close to the truth of phenomena only now being explained.

Science turned its attention to life near the surface of the sea in the nineteenth century, but only incidentally, in connection with other investigations and visual observations. Thus, scientists discovered the leaps made by pontellids, the blue colour of certain organisms living beneath the surface tension film, and the existence of oceanic water striders.

Special biological studies of the surface of the boundary between sea and air were not begun until the 1950s. Research on marine neuston was not merely an extension of similar research in fresh-water bodies, such as was initiated in 1917. True, the ground was already prepared, but after the discovery of the richness of life at the sea-air interface it became clear that this was a phenomenon characteristic of all water bodies, fresh and saline, large and small, and that it was based on common ecological principles operating in the area of contact between the liquid and gaseous envelopes of the Earth.

A detailed explanation of all the chemical and physical factors involved in the outburst of life in the nearsurface biotope of the pelagic zone still lies in the future. At present little is known about them. On the other hand, a good deal is

known about life in the topmost microlayer of water. It has been established that life there is rich and diverse, that the organisms have adapted themselves to the conditions of their biotope, and that neuston is a biological structure which has evolved as the result of the adaptation of a large group of organisms to the specific conditions of the region where the pelagic zone meets the atmosphere. Special (appropriate) methods of probing this region have resulted in the discovery and quantitative evaluation of the importance and significance of neuston in the life of the sea, where it promotes the natural reproduction of marine organisms, the development of ecological processes, and the circulation of substances in nature.

An integrated approach to the study of marine neuston, /240/ yielding a wealth of multifarious scientific information revealed that marine neustonology- a branch of hydrobiology studying the neuston of the world ocean - is one of the more important and promising fields of biological oceanography. This is shown by the fact that it has become possible to shed new light on certain problems and interpret them from the standpoint of neustonology. These problems are now being dealt with by neustonology separately, or else as part of wider studies involving allied fields of pure and applied science.

Notwithstanding the fact that differentiation of fields of knowledge has become one of the characteristic features of the development of modern science, and that we are indebted to the formation of new branches and fields within existing sciences

(with their methods and approaches to the solution of new problems which arise) for all significant contemporary achievements, it is quite possible that some may wonder just how justifiable and necessary it is to create the new science of neustonology. Perhaps the life of the nearsurface layer of the pelagic zone can be studied, or is already being studied, by existing branches of hydrobiology, and especially planktonology, the more so as the population of the nearsurface layer of the pelagic zone, obtained by semi-submerged fishing gear, is sometimes called "nearsurface plankton" in the literature (Kiselev, 1969). And indeed, if neuston is merely a part of plankton, differing from the rest of it in being found at the surface, there is no objective necessity for erecting neustonology as a new discipline. This fundamental problem can only be resolved by getting to the root of it. One method of solution is rather formalistic. According to all the manuals of hydrobiology (Zernov, 1934, 1949; Berezina, 1953, 1963; Konstantinov, 1967), plankton and neuston are different groups - populating water bodies, i.e. different classes of communities. It follows that neuston is not nearsurface plankton, but a new entity. Thus, the necessity for a discipline known as neustonology to study this new entity is already indicated by the facts contained in textbooks. However, the material set out in the present monograph speaks for itself.

The discovery of neuston in the sea was essentially the result of deviating from the methods of conventional planktonology, which views the whole water mass as a largely homogeneous

biotope to be studied by means of vertical hauls. With the aid of special methods the topmost microlayer, to which no special attention had ever been given and for the study of which no special gear had previously existed, was found to contain that new entity made up of organisms ranging from bacteria to fish and given the name of neuston. It was clear that this new entity was not within the purview of planktonology. As regards "nearsurface plankton", this is also neuston obtained with semi-submerged gear, but with a large admixture of sub-surface plankton and pleustonic siphonophores, due to the design of the gear used. /241, Nevertheless, this circumstance does not obscure the novel nature of such samples, and A.K. Geinrikh (1964) is justified to some extent in distinguishing "nearsurface plankton" from the "surface plankton" populating the 0-200 m layer in the Pacific ocean.

In the present book it is shown that the specific qualitative features of the population of the nearsurface microlayer of the sea are so distinctive that these organisms cannot normally exist in the plankton biotope, i.e. in the pelagic zone. Some of them cannot occur there because of their high buoyancy, other lose their adaptive characters and properties in the pelagic zone, yet others pass through the pelagic zone on their way to the surface, where they remain, and so on. Therefore it is methodologically incorrect to reduce neuston to the status of a part of plankton - even the "nearsurface" part - since this ignores the specific features of the population of marine and freshwater basins, which originated as the result of adaptation of the organisms to a particular biotope - the surface of the water-air

interface.

In the first ten years of its existence marine neustonology has proved to be an extremely fruitful field of investigation, operating both within other branches of biological oceanography and in conjunction with them. By making it possible to examine certain established ideas from new angles and revealing new aspects of them, and also by raising a number of new questions, marine neustonology has taken its place as one of the weapons being used by science in its assault on the mysteries of the sea. Like any other new project, neustonology has met with many difficulties, stemming from factors both objective and subjective in nature. It was therefore necessary to summarize the great volume of research already done and direct attention to the topmost region of the waters of the world ocean as a very promising field of study. It was with this aim in mind that the present book was conceived and written, and if the reader finds something new in it to excite his imagination the author will consider his task fulfilled.

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A SHORT GLOSSARY OF SPECIAL TERMS*

(The abbreviations used are transliterations of the Russian)
abbreviations - Translator's note

/* In brackets are given the first, or earliest known, uses of the terms in the literature. The corresponding terms of long-standing from allied fields of hydrobiology are given as analogues/

1. Aggregates - particles of organic matter, dissolved in sea water, which have formed as the result of physico-chemical adsorption on the surface of gas bubbles. (Baylor a. Sutcliffe, 1963).
2. Anemoneuston - organic and mineral particles of terrigenous origin deposited on the surface of bodies of water by the wind. (Beklemishev, 1944).
3. "Antirain" of bodies of dead hydrobionts - the flow of dead organisms and their fragments moving counter to the "rain" of dead bodies. Caused by the buoyancy of the gas bubbles forming in the bodies as they decompose, by flotation etc. (Zaitsev, 1967).
4. Bacterioneuston - the bacterial fraction of the neustonic assemblage of organisms (Tsyban', 1965).
5. Bathylanktohyponeuston - the part of the hyponeuston consisting of organisms staying alternately in the bathylankton (by day) and hyponeuston (by night). Includes many species of hyperiids, euphausiaceans, copepods and others. (Zaitsev, 1964).
6. Benthohyponeuston - part of the hyponeuston consisting of organisms alternately in the benthos (by day) and hyponeuston (by night). Includes many species of amphipods, cumaceans, polychaetes, shrimps and others. (Zaitsev, 1964). In earlier papers this group of organisms was called "tychohyponeuston" (Zaitsev, 1962), formed by analogy with "tychoplankton" (which see).
7. BNS - bacterioneuston collector (Tsyban', 1967). A scooping device for obtaining samples of microorganisms from the 0-2 cm layer.
8. Circadian rhythms - biological processes recurring at intervals of approximately 24 hours (Halberg, 1959).
9. Contact zones of the sea - the boundary zones between the sea and air, the bottom, the shore, rivers etc. (Vinogradov, 1965).
10. Ecological phase (ecological state) - a period of equilibrium in the development of an ecological process (Zaitsev and Polikarpov, 1967).
11. Ecological processes - a regular alternation of ecological

states, or phases, of a species, which consists of ontogenetic and circadian movements and associated internal and external metabolic effects (Zaitsev and Folikarpov, 1967).

12. Epineuston - the upper (aerial) part of the neustonic assemblage of organisms (Geitler, 1942). The marine epineuston includes oceanic bugs and water striders, for example.
13. Euepineuston - part of the epineuston consisting of organisms spending their entire lives on the surface of a water body (Zaitsev, 1968). Analogous to euhyponeuston (which see) and euplankton.
14. Euhyponeuston - part of the hyponeuston consisting of organisms spending their entire lives in the 0-5 cm layer (Zaitsev, 1962). Analogous to euplankton.
15. Haloneuston - neuston in marine basins (Zaitsev, 1964). Analogous to halo plankton, contrasts with limnoneuston (which see).
16. Hyponeuston - lower (aquatic) part of the neustonic assemblage of organisms (Geitler, 1942). The 0-5 cm layer is taken as the biotope of marine hyponeuston (Zaitsev, 1961).
17. Ichthyoneuston - the ichthyological fraction of the neustonic assemblage of organisms (Zaitsev, 1958).
18. Infraneuston - the lower (aquatic) part of the neustonic assemblage of organisms (Welch, 1935). Later the etymologically more correct term "hyponeuston" was proposed for this part of the neuston (see hyponeuston).
19. Meroepineuston - part of the epineuston consisting of organisms (e.g. mosquito eggs) which, after some time, transfer to another biotope (Zaitsev, 1968). Analogous to merohyponeuston (which see).
20. Merohyponeuston - part of the hyponeuston consisting of organisms (usually eggs, larvae, young) which, on completion of the neustonic phase of their life cycle, join the plankton, nekton or benthos (Zaitsev, 1962). Analogue - mero-plankton.
21. Merohyponeuston, benthogenic - those organisms in the merohyponeuston which dwell on the bottom in adulthood. Hyponeustonic larvae of benthic animals (Zaitsev, 1968).
22. Merohyponeuston, nektogenic - those organisms of the merohyponeuston which join the nekton on reaching adulthood. Hyponeustonic eggs, larvae, fish fry and young squids (Zaitsev, 1968).
23. Merohyponeuston, planktogenic - those organisms of the merohyponeuston which dwell in the water mass when adult. Hyponeustonic larvae of planktonic animals (Zaitsev, 1968).

24. MNT - fry-neuston trawl (Zaitsev, 1964). Gear for collecting highly mobile neustonic organisms from a moving ship.
25. Necrogeography, aquatic (thanatogeography) - the geography (distribution) of dead organisms suspended in the water (Zaitsev, 1967), as opposed to biogeography.
26. Neuston - small and medium-sized animal and plant organisms - hydrobionts and aerobionts - populating the aquatic (hypo-neuston) or aerial (epineuston) side of the surface tension film on water bodies. Distribution - world-wide (Naumann, 1917, with subsequent amendments and additions).
27. Neuston-eating birds and mammals (neustophages) - birds and bats feeding on marine neuston with the aid of special adaptations enabling them to detect, seize, retain and store neustonts (Zaitsev, 1964).
28. Neustonology - the field of hydrobiology studying neuston (Zaitsev, 1967).
29. Neustont - a component of the neuston (Zaitsev, 1968). Analogous to planktont.
30. NP - neuston platform (Zaitsev, 1962). Device for rapid approximate estimates of the numbers of neuston in the sea.
31. NS - neuston net (Zaitsev, 1962). A square-mouthed filter net for catching neuston.
32. NT - neuston trawl (Zaitsev, 1962). A trawl for collecting massive quantities of neuston.
33. Phasoecology - division of ecology studying ecological phases, or states, and ecological processes (Polikarpov and Zaitsev, 1968).
34. Phytoneuston - the plant part of the neuston (Naumann, 1917).
35. Pleuston - plant and animal organisms of medium and large size - hydrobionts whose bodies are simultaneously in both the aquatic and aerial media. Free-swimming representatives of pleuston migrate under the influence of the wind and occur in tropical seas and to some extent in temperate regions. Marine pleuston is represented by siphonophores of the genera Physalia and Velella (Schroter u. Kirchner, 1896, with subsequent amendments and additions).
36. PNS - plankton-neuston net (Zaitsev, 1960). Apparatus consisting of two or more NS neuston nets, making possible simultaneous fishing of several microlayers, including the 0-5 cm layer.
37. PO - plankton precipitation gauge (Zelezinskaya, 1966). Instrument for collecting and counting the "rain" of dead bodies.

38. Slicks - calm, or smooth, strips on the surface of the sea, formed by films of organic substances.
39. Supraneuston - upper (aerial) part of the neustonic assemblage of organisms (Welch, 1935). Later the etymologically more correct term "epineuston" (which see) was proposed for this part of the neuston.
40. Tychoplankton - chance plankton. Benthonic organisms found in samples of plankton (Apstein, 1896). After the discovery of the regular character of the vertical migrations of these organisms and of the fact that they concentrate in the 0-5 cm layer to feed and breed, the term "benthohyponeuston" (which see) was proposed for them.
41. Zooneuston - the animal part of the neuston (Naumann, 1917).

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