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Methods of feeding and food groupings of bottom invertebrates of the Northern Caspian

by N.N. Romanova

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METHODS OF FEEDING AND FOOD GROUPINGS OF BOTTOM INVERTEBRATES OF THE NORTHERN CASPIAN

By N.N. Romanova, All-Union Scientific Research Institute of Marine Fisheries and Oceanography, Moscow

As is well-known, the trophic factor is one of the most important environmental factors determining the development and distribution of fauna in a body of water. A number of authors (Chugunov, 1923, Birshtein, 1945; Vinogradov, 1959) have noted that the distribution of detritus transported by the Volga over the expanse of the Northern Caspian determines to a considerable degree the irregularity of the distribution of the bottom fauna in different regions of that part of the sea. The construction of the Volga series of hydroelectric power stations aroused new interest in the food supply of the Caspian Sea, since the influence of runoff regulation on the distribution of biogenic elements and organic substances introduced into the Northern Caspian by the Volga is considerable. To make clear the importance of changes of the food supply to 146*

*Numbers in the right-hand margin indicate the corresponding pages in the original.

the development and distribution of the bottom fauna it was necessary to study the sources of food and the feeding habits of various bottom invertebrates of the Northern Caspian.

The feeding of aqueous invertebrates began to interest domestic and foreign investigators as long ago as the beginning of the 19th century, and much material has now been accumulated on this question. A large number of the Soviet works deal with abyssal and oceanic fauna and fauna of fresh bodies of water. Investigations of the feeding of invertebrates of our inland seas, particularly the Caspian, are not numerous. M.M. Briskina (1952), on the basis of study of the composition of the food of the most widespread molluscs gammarids, corophiids and cumaceans, established the predominance of detritus in the food of the amphipods, whereas in the food of molluscs it plays a smaller role. Analyzing the data, Briskina concluded that the Northern Caspian crustaceans are soil-eaters. The author considers molluscs, the principal food of which is phytoplankton and detritus, to be sestonophages (except Cardium). E. A. Yablonskaya (1955), in an investigation of the bottom invertebrates of the Sea of Azov, describes the composition of the food of some Caspian worms and crustaceans. According to the author's data, of predominant importance in the food of the investigated animals is detritus in the form of an amorphous flocculent mass. L. P. Maksimova (1958) describes on the basis of the composition of the food, the feeding of Caspian crustaceous percarids and worms from the lower course of the Don. The author concludes that Cumacea, Hipania, Hipannola and Mysidacea feed on amorphous detritus of the soil and phytoplankton, and also various residues of plants and animals.

We would like to supplement the available information with data on the methods of acquiring food and its sources for the commonest species of molluscs and crustaceans of the Northern Caspian.

Materials and Procedure 147

The following served as the materials for the present article: 1) the results of experimental investigations to explain the methods of feeding of the commonest species of molluscs and crustaceans of the Northern Caspian and 2) observations of the behavior of animals in aquarium conditions, accompanied by drawings*.

The living material for the experiments was collected in April 1958 and April-May 1959 at different points of the Northern Caspian from the research vessel "Opyt" of the Caspian Scientific Research Institute of Sea Fisheries and Oceanography (KaspNIRO), kindly presented by the director of the institute, I. V. Nikonorov. The fishing apparatus was an "Okean-50" 0.1 m^2 dredge. In some cases a 30-foot otter trawl was used in fishing

*All the drawings were made by artists O. F. Khludova and N. N. Kondakov, to whom the author expresses his gratitude.

the thickets of eel-grass. The captured animals were carefully collected with pincers or by hand and placed in crystallizers with a small quantity of water and soil. The experimental investigations were conducted in the Laboratory of the Nutritive Base of the KaspNIRO and partially (in June-July 1959) in Moscow in the Nutritive Base and Commercial Invertebrates Laboratory of the All-Union Scientific Research Institute of Sea Fisheries and Oceanography (VNIRO). At the start of our work the water temperature in the aquaria was 17-19° and later, in the second stage of our work, it warmed to 25-28°, which unfavorably affected the vital activity of the molluscs. The animals became sluggish and, in some cases, stopped feeding.

The number of specimens of different species of molluscs and crustaceans used for the experiments is shown in Table 1.

The experimental procedure developed under the supervision of Yablonskaya consisted of the following:

Before the experiments were set up, dense cultures of Ankistrodesmus and Scenedesmus were obtained on an artificial Beneke solution by the usual method, and Chlorella vulgaris on Tamiga solution. Five to ten molluscs, depending on the size of the animals, were placed either in crystallizers with a diameter of 16 cm or in Koch dishes and kept in pure water without food for 3-5 days. Then algae in a suspended state were presented to the molluscs in one series of experiments, and in another were placed on the soil after they had been killed by heating. At the expiry of a certain time interval (1-8 hours) one or two mollusc

Table 1 Volume of materials used for experimental work

Таблица 1

Объем материала, использованного для экспериментальных работ

Вид (a)	Число экз. (b)	Число опытов (c)
Mollusca		
Cardium edule	53	24
Didacna trigonoides	45	8
Monodacna edentula	63	36
Adacna plicata minima	78	20
Syndesmya ovata	37	6
Vermes		
Tubificidae sp.	80	26
Hypania invalida	50	8
Hypaniola kowalewskyi	50	8
Manayunkia caspica	30	7
Amphipoda		
Stenogammarus similis	30	3
Stenogammarus compressus	53	4
Pandorites platycheir	73	4
Pandorites podoceroides	71	12
Pontogammarus robustoides	125	5
Pontogammarus maeoticus	Отдельные наблюдения (d)	
Dikerogammarus haemobaphes	191	7
Niphargoides quadrimanus	119	8
Amathillina cristata	193	8
Corophium curvispinum, Corophium mucronatnum, Corophium nobile	Отдельные наблюдения (d)	
Cumacea		
Pterocuma pectinata, Schizorhynchus bilamellatus	Отдельные наблюдения (d)	
	1341	194

Key: a - Species b - Number of specimens c - Number of experiments d - Separate observations

specimens were opened, the presence of algae in the anterior part of the digestive tract was recorded and the algae cells were counted on a counting glass.

When the experiments were set up with amphipods, besides observations and sketches, experiments were conducted with the instrument of N.S. Gaevskaya (the so called "bays") consisting of a crystallizer (40 cm in diameter) divided by radial partitions into four compartments communicating in the center (Gaevskaya, 1939). A small quantity of shelly soil was in the crystallizer containing the water. Before the start of the experiment each compartment was separated from the center with a glass partition, different food was placed in the compartments and 15 – 20 gammarid specimens were placed in the center of the crystallizer. Then the transverse partitions were removed and the gammarids could move freely about the aquarium. After definite time intervals (1-8 hours) the specimens in the bays were counted and the intestine contents of the gammarids from bays with different food were examined.

It was established that the tubificids usually buried their front ends in the soil and grasping silt in the deep layers of soil, pass it through the intestines and carry it out on the surface. 148
This distinctive biological feature of the tubificids was used by us in studying their feeding methods and determining the source from which they scoop nutrient material. The experimental procedure consisted in the following: To determine the depth from which food is accessible to the oligochaetes, layers of <u>Scenedesmus</u> or <u>Ankistrodesmus</u> were arranged at different depths. In aquaria previously prepared in that manner 30-50 tubificids specimens were placed. Then, when the oligochaetes buried themselves, the surface of the ground soil was covered with No. 38 silk bolting.

cloth. After some time the worms thrust the tail parts of their trunks through the silk and the appearance of residue of algae was traced in the excrement of the oligochaetes.

The experimental procedure with Polychaeta was similar to the above-described working procedure with molluscs and consisted in the following: the algae Scenedesmus and Ankistrodesmus were fed to the polychaetes as food in a suspended state and placed on the ground. After a certain time interval the appearance of algae was traced in the excrement of the worms.

Experimental Investigations 149

Mollusca

There is a rather large number of works devoted to the feeding and mode of life of molluscs, and the group Eulamellibranchiata (mussels, oysters, scallops, etc.) has been best studied in this respect. It is known that bivalves are relatively immobile animals; mature forms of some species (oysters, mussels and Dreissena) fasten themselves to underwater objects, whereas others live in a strip of ground. Among the latter are molluscs which bury themselves by means of their feet at a depth of several cm in the ground, and also molluscs remaining in the layer of soil at the surface. But among them there also are such mobile species as Pecten, which can swim great distances thanks to movement of the shell valves.

The mantle cavity of molluscs is connected in two ways with the external environment from which they obtain food. One group of molluscs inhabiting a stratum of the soil has well-developed siphons with different degrees of mobility. Macoma and Syndesmya have long, very mobile, hollow siphons (Jonge, 1952), Joldia -- short united (connate) siphons, but well developed labials lobes by means of which the molluscs collect food particles around themselves. Most Caspian molluscs have united siphons (Figure 1); in some (Monodacna and Adacna) they are capable of considerable extension, while in others (Didacna) the siphons are short and immobile. In the second group of molluscs, immovably attached to a solid substrate, at the rear end of the body the edge of the two halves of the mantle do not fit each other closely and form two slits between them -- analogues of siphons (Mytilaster and Dreissena). According to the classification of E. P. Turpaeva (1949), on the basis of their feeding bivalves can be divided into filtering molluscs, with short or long united siphons, and collecting molluscs, with disconnected, unusually mobile siphons. The experimental investigations presented below showed that most Caspian molluscs belong to the first group, the group of filtering molluscs.

1. Didacna trigonoides leads a relatively immobile life. Adult individuals usually bury themselves at a depth of about half the size of the shell (Figure 2), so that the mollusc as it were rises above the ground. Young individuals can bury themselves completely, displaying on the surface of the ground a small portion of the shell and siphon, which are always directed upward.

Experiments have shown that Didacna trigonoides takes suspended food (Figure 3). Already one hour from the start of

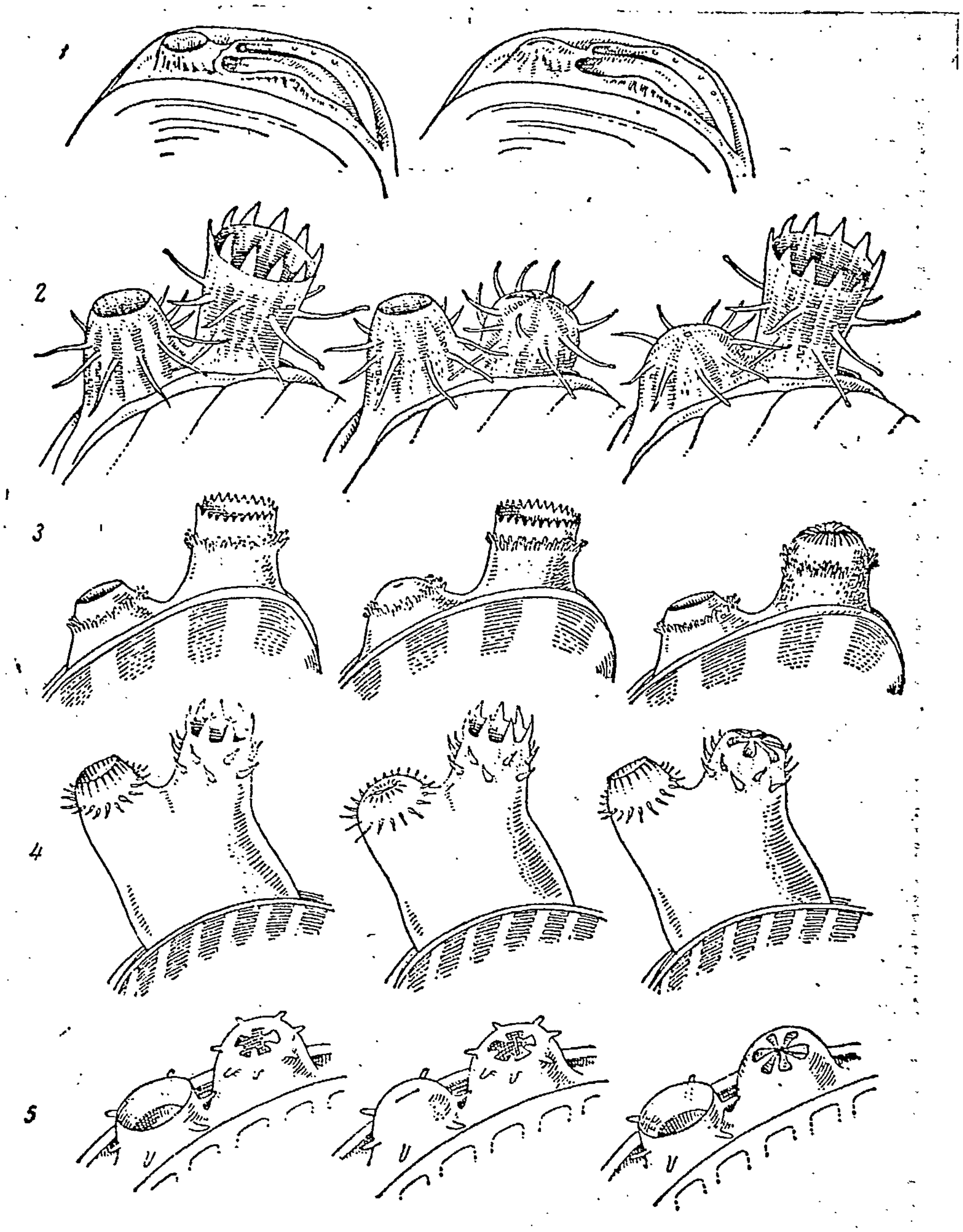

Рис. 1. Строение сифонов у различных видов каспийских моллюсков

1 — Mytilaster lineatus; 2 — Cardium edule; 3 — Didacna trigonoides; 4 — Monodacna edentula; 5 — Adacna plicata minuma

Figure 1. Structure of siphons of different species of Caspian molluscs.

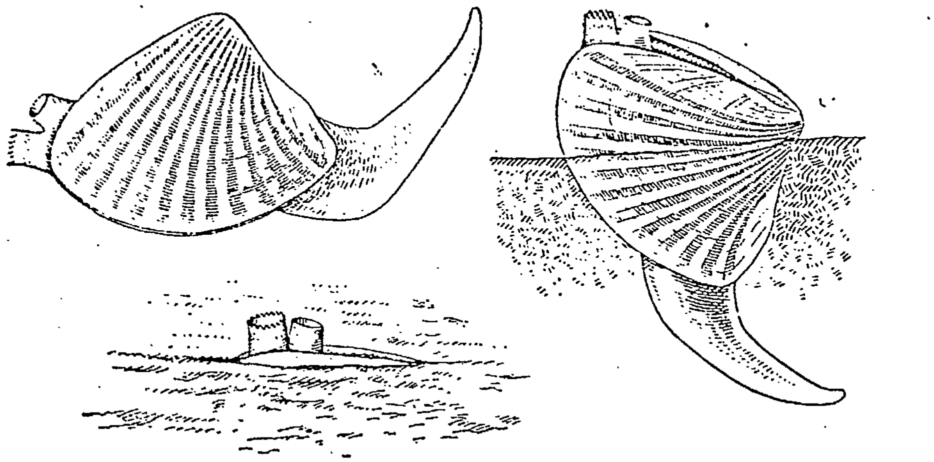

Рис. 2. Didacna trigonoides (положение моллюска в грунте)

Figure 2. Didacna trigonoides (position of the mollusc in the ground).

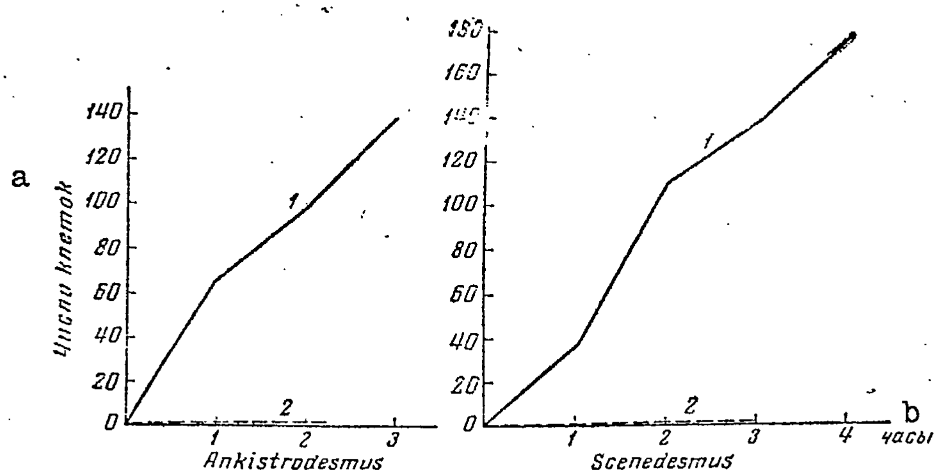

Рис. 3. Изменение количества поглощенных клеток водорослей Ankistrodesmus и Scenedesmus у Didacna trigonoides

1 — взвешенные в воде клетки; 2 — осевшие на грунт клетки

Figure 3. Variation of the number of absorbed cells of the algae Ankistrodesmus and Scenedesmus in Didacna trigonoides.
1 - suspended in water of the cell; 2 - cells which settled on the ground.
a - Number of cells; b - Hrs.

the experiment algae were present in all dissected specimens in the anterior section of the intestines. In the case where the food was placed on the ground, there were no algae at all in the intestines.

2. *Monodacna edentula* according to our observations leads a more mobile life. The molluscs bury themselves either half or completely in the ground, leaving in that case only the siphons above the surface (Figure 4). In comparison with the preceding species, *Monodacna* has more mobile siphons which extend rather considerably. As is clearly visible on the figure, the siphons can assume quite different positions: directed upward, on a slant or parallel to the surface of the ground. Often the siphons are so bent that their openings touch the surface of the ground. However, the siphons of the *Monodacna* usually
are directed upward, and only in some cases (in the absence of 150
suspended nutrients) occupy a different position. Such behavior of molluscs agrees completely with the obtained results of experiments to clarify their method of feeding (Figure 5). The degree of filling of the anterior portion of the intestines is high if the food is in the suspended state, and very low if it lies on the surface of the ground. However, in contrast with
Didacna trigonoides, food on the surface of the ground is ac- 151
cessible to some degree to the *Monodacna*. This becomes understandable if one considers the mobility of the mollusc and its siphons. During the movement of molluscs, naturally, algae present on the surface of the ground are stirred up, and the ability

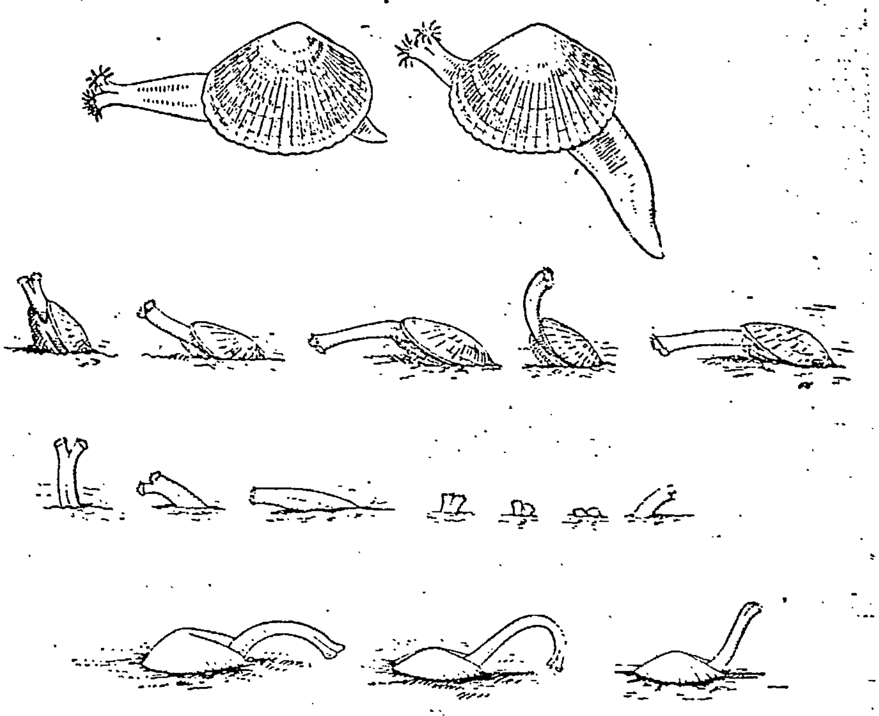

Рис. 4. Monodacna edentula (положение моллюска в грунте)

Figure 4. Monodacna edentula (portion of the mollusc in the ground).

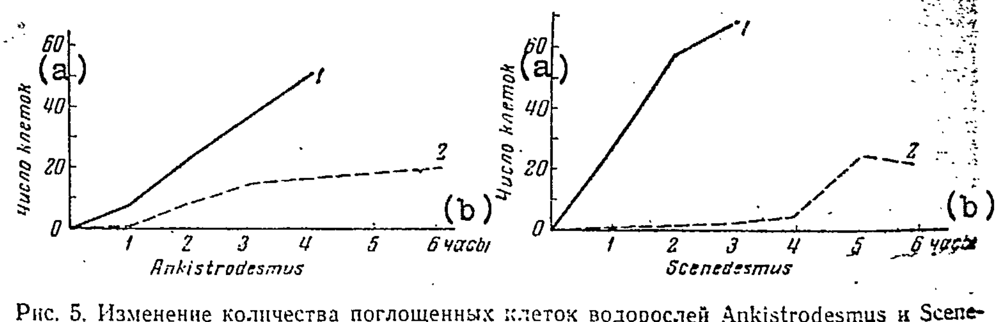

Рис. 5. Изменение количества поглощенных клеток водорослей Ankistrodesmus и Scenedesmus у Monodacna edentula
(Обозначения те же, что на рис. 3)

Figure 5. Variation of the number of absorbed cells of the algae Ankistrodesmus and Scenedesmus in Monodacna edentula. Symbols as in Figure 3).

to turn the openings of the siphons toward the surface of the ground permits capturing slowly settling algae cells. Since the main sources of food for Monodacna edentula are suspended nutrients, that mollusc can be considered a filtrator. Under natural conditions phytoplankton plays a large role in the food of the closely related species Monodacna caspia, according to the data of Briskina (1952).

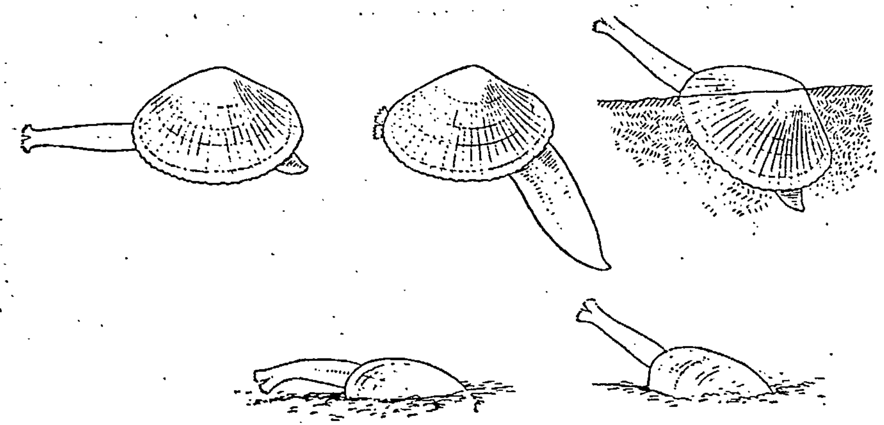

Рис. 6. Adacna plicata minima (положение моллюска в грунте)

Figure 6. Adacna plicata minima (position of the mollusc in the ground).

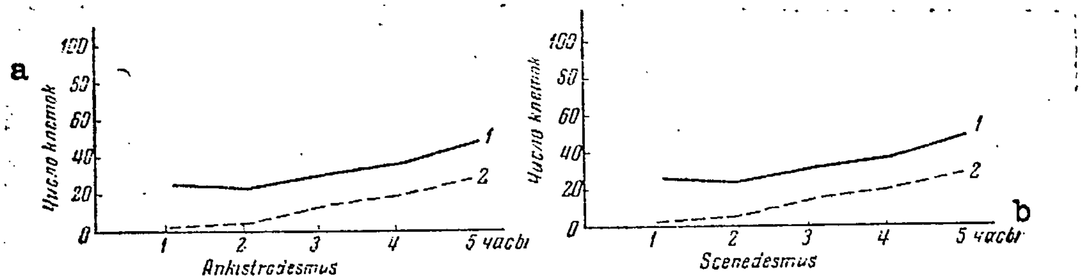

Рис. 7. Изменение количества поглощенных клеток водорослей Ankistrodesmus и Scenedesmus у Adacna plicata minima

Figure 7. Variation of the number of absorbed cells of the algae Ankistrodesmus and Scenedesmus in Adacna plicata minima. (Designations as on Figure 3).

3. Adacna plicata minima is characterized by great mobility and its united siphons can be extended considerably, being arranged parallel to the surface of the ground (Figure 6). The mollusc usually takes food in a suspended state and so in its method of feeding is a filtrator (Figure 7). However, as is rather clear from Figure 7, settled nutrient par- 152
ticles also are accessible to this species. They can be captured, as with Monodacna edentula, either when the surface of the ground is made turbid by the mollusc itself during movement or when the siphon openings approach the surface of the gound. This makes it possible to add Adacna plicata minima to the group of molluscs to which are accessible both food in a suspended state and food particles of the surface layer of the ground.

4. Cardium edule [the common cockle] is a very mobile form. The mollusc moves continuously over the bottom (in an aquarium), making turbid the light particles of the surface layer of the ground.

With binoculars it could be observed how the mollusc 153
during movement as it were "blows" particles of ooze away from the surface of the ground with a stream of water from the outlet siphon and then draws them in with its incurrent siphon. A sequence of contraction and opening of the siphon openings is noticeable in that case. When the feet are extended the siphon openings are open, but no flow of water is observed. Then, when the feet are contracted and the body extended, the rear end of the shell, together with the siphons, as it were inclines toward the surface of the ground; at that moment the

opening of the incurrent siphon closes, and then the water from the exhalent siphon of the mollusc as it were "blows" particles away from the surface of the ground. After that the exhalent siphon opening contracts and the opening incurrent siphon sucks in the stirred up food particles. Then the mollusc continues to move, and the activity of the siphons is repeated in the same sequence or slackens; it buries itself in the ground and only a small portion of the shell and siphon, directed upward, remains visible on the surface (Figures 1 and 8). The great mobility of Cardium edule, and also its ability to "blow" food particles out of the ground, were also noted by Khusainova (1958).

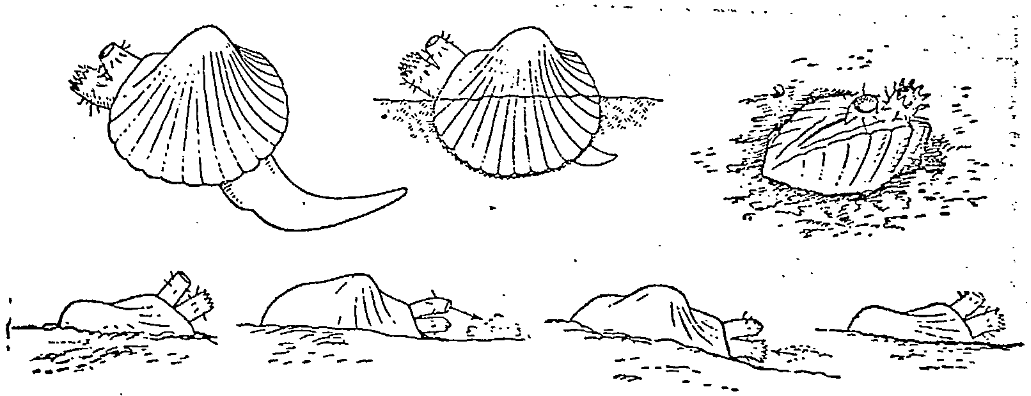

Рис. 8. Cardium edule (положение моллюска в грунте и различные стадии передвижения)

Figure 8. Cardium edule (position of the mollusc in the ground and different stages of movement).

It is evident from the results of experiments to make clear the method of feeding of Cardium (Figure 9) that, in contrast with previously considered species, food in both the suspended state and on the ground is accessible to the cockle. This becomes understandable if the just-described behavior of the mollusc is taken into consideration. However, in spite of the fact that food lying on the ground is accessible to the cockle, 154 it cannot be considered a gatherer of settled detritus (Turpaeva, 1948), since the cockle is not in any way adapted for gathering food from the surface of the ground (its siphons are too short and the labial palpi are weakly developed). It can capture food only when it is in a suspended state. Therefore Cardium edule is a filtrator, but the surface layer of the ground can also serve as a source of food for it. According to Briskina, a considerable quantity of soil is present in the intestinal content of the cockle, and this is confirmed by our data.

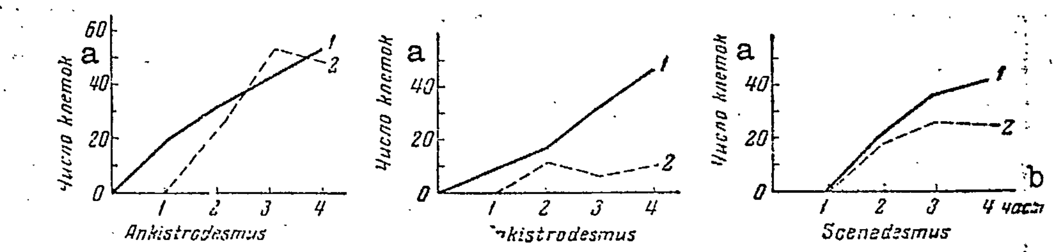

Рис. 9. Изменение количества поглощенных клеток водорослей Ankistrodesmus и Scenedesmus у Cardium edule

Figure 9. Variation of the number of absorbed cells of the algae Ankistrodesmus and Scenedesmus in Cardium edule (Symbols as in Figure 3). a - Number of cells; b - Hours

5. Syndesmya ovata, in contrast with the species considered earlier, usually buries itself completely in the ground, exposing on the surface long worm-like siphons many times longer than the shell of the mollusc. The siphons of Syndesmya are very mobile; passing its incurrent siphon over the surface of the ground, the mollusc takes in food particles lying on the bottom

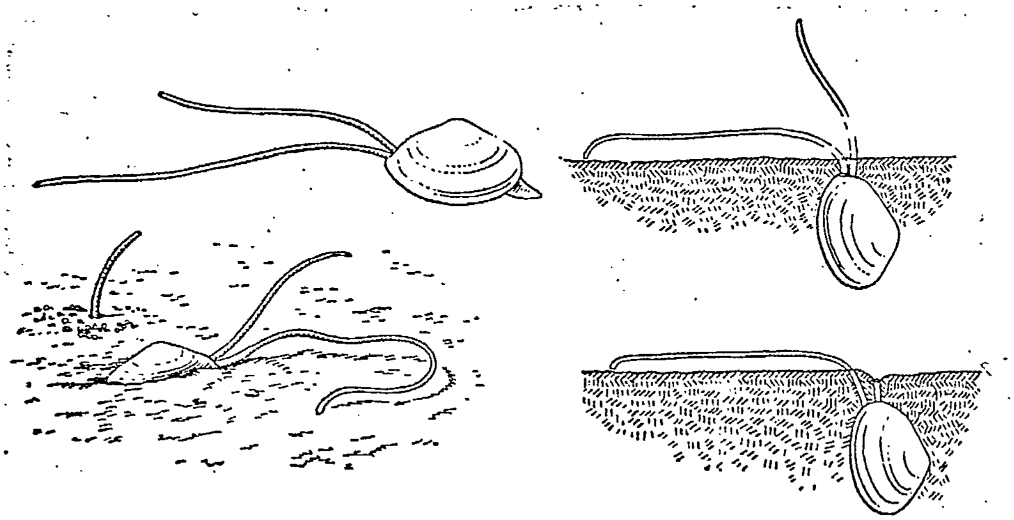

Рис. 10. Syndesmya ovata (положение моллюска в грунте)

Figure 10. Syndesmya ovata (position of the mollusc in the ground).

(Figure 10). Observations of the behavior of molluscs in an aquarium show that Syndesmya ovata is a gatherer and consumes food lying on the surface of the ground (Figure 11). The number of cells in the anterior section of the intestines increases rapidly in proportion to the gathering of food, whereas in an experiment with food in a suspended state the intestines are not well filled with food. Under natural conditions, according to Yablonskaya's data (1955), in the intestinal content of Syndesmya an important role is played by fine detrital suspension with a small admixture of sand particles and algae.

The above-cited facts permit considering Syndesmya ovata 155
in its method of acquiring food to be a gatherer of detritus, and the surface layer of the ground serves the mollusc as the source of food.

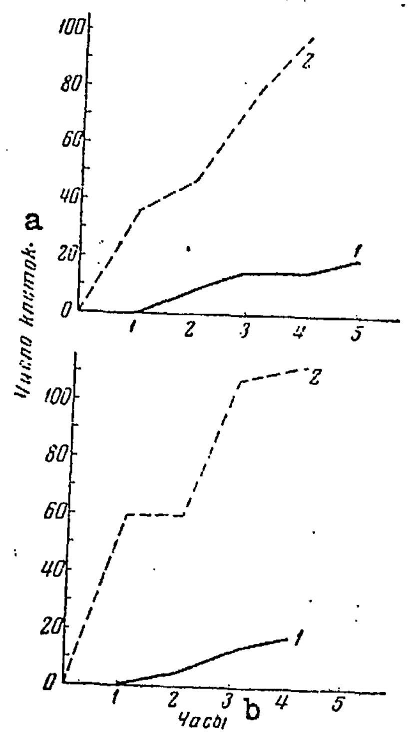

Рис. 11. Изменение количества поглощенных клеток водорослей Ankistrodesmus (вверху) и Scenedesmus (внизу) у Syndesmya ovata (Обозначения те же, что на рис. 3)

Figure 11. Variation of the number of absorbed cells of the algae Ankistrodesmus (above) and Scenedesmus (below) in Syndesmya ovata (Symbols as in Figure 3).

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6. Dreissena polymorpha and Mytilaster lineatus. We have not conducted experimental observations of the behavior of these two species of molluscs. However, it is known that mature forms of both species lead an immobile mode of life, fastening themselves by the byssus to underwater objects, and only the young has a more developed foot and is capable of moving over the substrate (Figure 12). According to the literature data (Kudinova-Pasternak, 1951; Voskresenskii, 1948 and 1957), Mytilaster lineatus and Dreissena polymorpha are filtering molluscs.

It is known that mainly intracellular digestion is characteristic of bivalves (Yonge, 1928), and so they can use relatively light and small particles as food. Most researchers studying the mechanism of the nutrition of bivalves consider that the

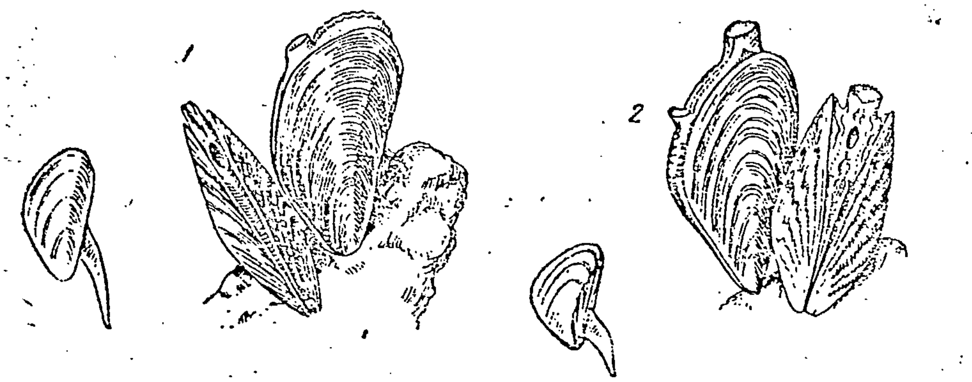

Figure 12. Mytilaster lineatus (1) and Dreissena polymorpha (2, 3).

food particles are sorted only by particle size, form and density, and not by food value. Nevertheless, some of them (Buley, 1936; Fox, 1936) think that there also can be a qualitative selection of food particles. Thus, for example, the composition of phytoplankton residues in the intestinal contents of oysters differs from the phytoplankton composition of the surrounding water. Buley (1936), in comparing the phytoplankton composition from the water surrounding molluscs and the intestinal content of Mytilus caliphornianus, found some differences in them. Thus, Chaetoceras, which was absent in the intestines of Mytilus, was present in great abundance in water samples. It can be thought that in this case Chaetoceras was not taken by the molluscs because of its large cell dimensions. Loosanoff (1949) observed that oysters are capable of selecting yeast cells from an aqueous mixture of microorganisms. However, the mechanism of qualitative selection of food particles is still not clear.

In the literature on the nutrition of molluscs considerable attention has been given to the question of which particle sizes can be filtered by molluscs. Galtsoff (1928) established that *Ostrea virginica* filters 70-90% of the diatoms and dinoflagellates from water passed by the mollusc through its gills, 156
whereas *Bacterium colli* is not retained by the filtering mechanism. Jorgensen and Goldber (1953) established for the same species that graphite particles with sizes of 2 to 3 microns are almost completely filtered from water, whereas particles of 1 to 2 microns pass through the gills quite freely and are not retained. The filtration apparatus of *Mytilus edulis* can retain finer particles, according to these authors. Pieces of graphite 1 to 2 microns in size are trapped almost completely by the filtration apparatus of this mollusc. The dimensions of particles filtered by the mollusc depend on the distance between the individual lateral-frontal cilia of the gills. In *Ostrea edulis* and *O. virginica* the distance between the cilia of the gill filaments is 1.5-3.7 microns, which corresponds completely to the maximum particle size of 2 - 3 microns which can be retained by these species.

The possibility of sorting food particles by sizes was established by us also for Northern Caspian bivalves. We fed the molluscs a mixed feed -- *Chlorella*, *Scenedesmus*, *Navicula*, *Rhizosolenia* (a disappearing culture), pulverized dried *Conferva* and pondweed. The dimensions of the food organisms and particles permitted us to draw certain conclusions. Of the Caspian molluscs *Syndesmya ovata* has the most refined mechanism of sorting food particles by size. Particles from 3 to 35 microns in size are of dominant importance in the feeding of this species. The presence in the surface film of the ground of a large quantity of larger food particles usually causes in this mollusc the formation of abundant "pseudofeces". Thus if a mixed feed consisting mainly of large *Navicula* (40-53 microns) and *Scenedesmus* (10-30 microns) was presented to *Syndesmya*, ranging from 1 to 1.5 cm in size usually the pseudofeces consisted almost entirely of large *Navicula* and large mineral particles (50-80 microns), whereas the contents of the anterior section of the intestines consisted of *Scenedesmus* (10-30 microns) with a small admixture of small *Navicula* about 20 microns in size and mineral particles of the same size.

Monodacna edentula and *Adacna plicata minima* also consume as food larger algae such as *Navicula* and *Pleurosigma* of large dimensions (35-195 microns). The *Monodacna* can also partially filter *Rhizosolenia*, but only small cells (about 190 and 300 microns) and, evidently, only in the case where the cells of *Rhizosolenia* during passage through the filtration apparatus are arranged along the oral groove and mouth opening of the mollusc. In most cases, however, in *Monodacna* and *Adacna*, when they are fed *Rhizosolenia*, a large quantity of pseudofeces form which 157
represent clusters of *Rhizosolenia* cells.

Of the molluscs investigated by us, Didacna trigonoides can filter the largest particles. If a suspension of moribund cells of Rhizosolenia are added to an aquarium containing molluscs, 1 hour after the start of the experiment, when the siphons of all the molluscs have already opened and motion of the water around them is noticeable, in the anterior section of their intestines from 3 to 8 fragments of Rhizosolenia cells can be discovered. Thus our rather crude experiments have shown that the alga Rhizosolenia, which is present in massive quantities in the southern part of the Northern Caspian, is poorly utilized by molluscs. It should be noted, however, that, according to the data of M. M. Briskina (1952), besides Didacna trigonoides, Rhizosolenia can be encountered in the intestinal contents of Cardium edule, Dreissena polymorpha and Mytilaster lineatus. Nevertheless, the nutritional importance of Rhizosolenia to molluscs is doubtful, since it is known (Jordan, 1913) that in bivalves (with the exception of Teredo and Bankia) there are no enzymes which cleave cellular tissue and are capable of acting on the siliceous shell of diatoms.

Amphipoda

Most amphipods of the Caspian Sea are demersal and bottom animals. Only two species of Caspian amphipods, of the family Lysianassidae, are known which should be classed as pelagic species. The remaining amphipods inhabiting the Caspian either bury themselves in the ground (gammarids) or construct tubules of particles of mud and sand on the surface of underwater objects and algae (corophiids).

Ya. A. Birshtein (1945) pointed out that the gammarids are omnivorous animals which use moribund aqueous vegetation and also the corpses of water animals as food. Young fresh *Enteromorpha* is consumed more eagerly by gammarids than coarse and rough Enteromorpha (Karpevich, 1946). M.M. Briskina, in studying the development and reproduction of Black Sea and Caspian amphipods under aquarium conditions, used *Enteromorpha* and *Cladophora* as food. Normal development and reproduction of gammarids were observed. In some cases the author offered the gammarids live larvae of Chironomidae, which they ate eagerly. 158

Ponyi (1956), in studying the feeding methods of some gammarids, showed that feeding by filtering small food particles (3-4 microns) and biting off large pieces of food is characteristic of four forms of freshwater amphipods.

The Caspian gammarids are forms capable of moving actively over the substrate in searches for suitable shelter or food and also of making horizontal and vertical migrations when the quantity of oxygen in the near-bottom layers of water decreases (Segerstrâle, 1940). Some species of gammarids are connected with the ground by their behavior and feeding. They either wander over the surface of the ground in searches for food or bury themselves in the ground, exposing the anterior part of the cephalothorax on the surface of the ground (*Stenogammarus similis*, *Gmelina pusilla* and some representatives of the genus *Pontogammarus*). Others (*Amathillina cristata*) dwell mainly among thickets of macrophytes and algae, finding shelter and food there (Benning, 1938).

1. Stenogammarus similis. This species is among the most common species of Caspian crustaceans, is encountered in all the northern part of the sea and avoids only water with a salinity below .1% (Romanova, 1958). Our observations while keeping Stenogammarus similis in an aquarium showed that this species eats detritus, tender filaments of Conferva and also overgrowths (encrusting organisms) on the aquarium walls. Moving around the aquarium, the small crustaceons, when they encounter pieces of detritus on their way, grasp them with their maxillopeds and, holding them with their gnathopods, direct them into the mouth. If the crustaceans buried themselves in the ground, it was clearly visible how by unusual movements of their antennas, mouth parts and gnathopods they created a flow of water and thereby as it were drove towards themselves the pieces of detritus and scraps of algae floating past which were then held by the gnathopods and maxillopeds (Figure 13).

The method of feeding and type of food of Stenogammarus similis was made clear by observation of the behavior of the amphipods in crystallizers with Gaevskaya bays. The number of crustaceans which had appeared on a given feed was recorded at definite time intervals. The results of the distribution of crustaceans by different feeds, expressed in percentages of the total number of crustaceans in the experiment, are presented in Table 2. It is clearly evident that Stenogammarus similis prefers detritus in the presence of different feeds. Six or seven hours after the experiment began, all the gammarids assembled

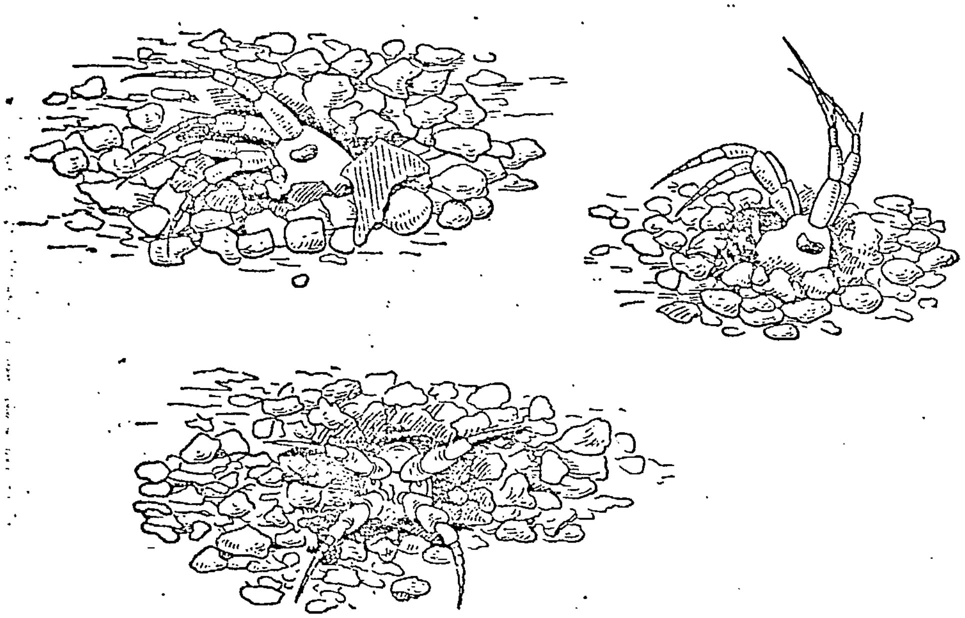

Рис. 13. Положение в грунте Stenogammarus similis

Figure 13. Position of Stenogammarus similis in the ground.

Table 2. Distribution of Stenogammarus similis in Gaevskaya bays with different types of feed (as % of the total number of specimens in the experiment)

Таблица 2

Распределение Stenogammarus similis по дворикам Гаевской с разным видом корма (в % от общего числа экземпляров в опыте)

Серия опытов a	I (8 экз.) b			II (10 экз.)			III (12 экз.)		
Продолжительность опыта, час c	1	3	5	3	5	7	2	4	6
Виды корма d									
1 Энтероморфа	0	0	0	0	0	0	0	0	0
2 Урути (молодые веточки)	0	0	0	—	—	—	—	—	—
3 Спирогира	—	—	—	0	0	0	8,5	8,5	0
4 Корневище сусака с обрастаниями	12,5	12,5	0	40	30	0	0	0	0
5 Детрит	75	75	100	60	70	100	75	90	100

a - Series of experiments; b - specimens; c - Duration of experiment, hrs; d - Types of feed. 1 - Enteromorpha; 2 - Myriophyllum (young ramuli); 3 - Spirogyra; 4 - Butomus rootstock with overgrowths; 5 - Detritus.

in the part of the aquarium where detritus had been placed on the surface of the ground. Dissection of the intestines of the crustaceans showed that in 74% of the test gammarids the intestinal content consisted of detritus, and in only 4% were filaments of Spirogyra clearly noticeable in the anterior section.

Stenogammarus similis thus actively gathers and to some degree filters food particles. The main food source is detritus of the surface layer of the ground. Also of some importance in the feeding of Stenogammarus similis are overgrowths of higher water vegetation. Diatoms identical to those of Butomus rootstock 159
overgrowth were found in 22% of the test amphipod in the anterior section of the intestine. It can be considered that Gmelina pusilla and Stenogammarus macrurus acquire food similarly.

2. Stenogammarus compressus, like the preceding species, is an often encountered amphipod, but in contrast with it is more euryhaline; its distribution is not limited to just the Northern Caspian, it is encountered in the delta of the Volga and the Central Caspian (N. N. Romanova, 1958). The behavior of Stenogammarus compressus under aquarium conditions and its feeding biology are similar to those of the preceding species -- the crustaceans feed on overgrowths, detritus and filaments of Conferva.

The results of the experimental observations (the procedure of the observations was the same as in work with the preceding species) showed that, in spite of external similarity, there is a difference in the feeding of the two species (Table 3). 160

Table 3. Distribution of Stenogammarus compressus in Gaevskaya bays with different types of feed

a Серии опытов	b I (15 экз.)					II (10 экз.)			III (15 экз.)				IV (13 экз.)				
c Продолжительность опыта, час.	2	2,5	4	4,5	5	1	3	5	2	4	5	7	1	2	5	7	8
d Виды корма																	
1 энтероморфа	0	0	6,6	0	12,5	0	0	0	0	0	0	0	0	0	0	0	0
2 Урути (молодые веточки)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3 Корневище сусака с обрастанием	20	0	26,6	60	60	60	80	90	—	—	—	—	—	—	—	—	—
4 Нитчатка	—	—	—	—	—	—	—	—	13,3	13,3	13,3	13,3	15,3	15,3	7,7	15,3	7
5 Детрит	0	26,6	26,6	26,6	26,6	20,0	10,0	10,0	60,0	60.0	66,6	86,6	48	48	53,3	61,5	92

a - Series of experiments; b - specimens; c - Duration of experiment, hrs; d - Types of feed. 1 - Enteromorpha; 2 - Myriophyllum (young ramuli); 3 - Butomus rootstock with overgrowths; 4 - Conferva; 5 - Detritus.

Whereas the species Stenogammarus similis showed a preference for flocculent detritus, Stenogammarus compressus fed mainly on overgrowth of Butomus rootstock. In bays with Butomus, where up to 90% of the amphipoda gathered, it could be observed how the crustaceans clung to the rootstock by means of the gnathopods and bit off pieces of overgrowths with their mandibles. However, in the absence of overgrowths (series III and IV) the crustaceans went over to feeding on detritus.

Stenogammarus compressus thus can acquire food in two ways -- by biting off overgrowths of water vegetation and by gathering pieces of detritus and scraps of algae from the surface of the ground.

3. Pandorites platycheir, a widespread form, is encountered from the middle course of the Volga and Ural rivers to the

Central and Southern Caspian. In the Northern Caspian Pandorites platycheir is confined to the area near the delta.

In an aquarium, in the absence of any sort of accumulations of algae or plants, Pandorites platycheir buries itself in the ground, exposing only the anterior end of its trunk and moving its antennae, gnathopods and maxillipeds, creates a flow of water, driving towards itself flocs of detritus and scraps of algae. If a cluster of algae or the rootstock of a plant is placed in an aquarium, all the crustaceans assemble either on the algae or on the lower surface of the rootstock. Here, besides shelter, they find abundant food: like Stenogammarus compressus the crustaceans hold onto the surface of the rootstock and bite off the overgrowths.

In experiments with Gaevskaya bays the crustaceans were offered five types of food: Enteromorpha, water thyme (Elodea), fennel (sago) pondweed, Butomus rootstock with overgrowths and detritus. As is evident from Table 4, Pandorites platycheir prefers the overgrowths. In all series of experiments the crustaceans accumulated on the rootstocks with overgrowths. Dissection of the intestines of crustaceans gathered from the overgrowths showed that in 94% of the gammarids the food consisted of a gray-greenish flocculent mass with an admixture of diatoms.

It should be noted that the crustaceans also gathered in bays with fennel pondweed and water thyme. Possibly the appearance of amphipods on the fennel pondweed and water thyme is connected with the feeding of the crustaceans on overgrowths which rather abundantly cover the stem and twigs of plants. Thus both Stenogammarus compressus and Pandorites platycheir are species feeding mainly on overgrowths.

Table 4. Distribution of Pandorites platycheir in Gaevskaya bays with different types of feed

1 Число экз.	2 Продолжительность опыта, час	3 Энтероморфа	4 Элодея	5 Рдест гребенчатый	6 Корневище сусака с обрастанием	7 Детрит
20	7	—	20	—	80,0	—
23	7	—	—	16,6	83,4	—
25	9	—	—	28,0	72	—
15	10	—	—	26,6	73.4	—

Key: 1 - Number of specimens 2 - Duration of experiment, hrs 3 - Enteromorpha 4 - Elodea 5 - Fennel pondweed 6 - Butomus rootstock with overgrowths 7 - Detritus

Table 5. Distribution of Pontogammarus robustoides in Gaevskaya bays with different types of food

1 Число экз.	2 Продолжительность опыта, час.	3 Хирономиды	4 Уруть	5 Корневище сусака с обрастанием	6 Детрит
24	4	8,2	20,8	71,0	—
26	6	—	26,9	73,1	—
35	6	8,5	31,5	60,0	—
25	8	4	24,0	72,0	—
15	11	—	33,3	66,7	—

Key: 1 - Number of specimens 2 - Duration of experiment, hrs 3 - Midges 4 - Myriophyllum 5 - Butomus rootstock with overgrowths 6 - Detritus

4. Pontogammarus robustoides, like most representatives 161
of that genus, is an inhabitant of the splash zone and well-aerated regions with a rapid flow and shallow depths. Pontogammarus robustoides is encountered in large quantities in the

Volga delta on sand banks and on underwater parts of water vegetation. There are no other data on the biology of Pontogammarus robustoides, but there is rather a large amount of information about the biology of the closely related species Pontogammarus maeoticus which also is encountered mainly in shallow places and leads the larger part of its life buried in sand. According to Reznichenko (1957), Pontogammarus maeoticus actively seizes pre-ejected algae accumulated at the water line. Besides this, the author notes that Gammarus transported to a pseudo-littoral by waves bury themselves in the ground and feed on the wastes of algae. But the author considers the main method of feeding to be the passive filtration of water and takeup of suspensions.

The behavior of Pontogammarus robustoides under aquarium conditions is to a certain degree similar to the described behavior of Pontogammarus maeoticus. Just like the latter, they bury themselves in the ground, leaving at the surface either part of the cephalothorax or the last segments of the abdomen with the uropods. If algae or scraps of macrophytes are placed in the aquarium, however, the crustaceans come out of the ground and dot the placed objects in clusters.

Analysis of the experimental investigations (Table 5) conducted with the Gaevskaya "bays" shows that of all the offered feeds Pontogammarus robustoides prefers Butomus rootstock with overgrowths. Dissections of the intestines of gammarids from the compartment containing Butomus rootstock showed in 90% of the

crustaceans the presence of diatoms and detritus, and also of fine pieces of tissues of the rootstock, and only in 8% residues of tissues of *Myriophyllum*. One should also note the greater importance of higher water vegetation in their nutrition, in contrast with all the species of gammarids considered earlier. Besides this, *Pontogammarus robustoides* is capable of feeding on animal food (midges in our experiments). This also is understandable if it is taken into consideration that *Pontogammarus robustoides* has well developed gnathopods and maxillopeds, by means of which it can hold such a relatively large and mobile prey as *Chironomus*. It must be noted that it is precisely *Pontogammarus* which does considerable damage to a fishery. Clustering in large quantities on the nets, they damage the nets and
the fishes in them. But under the conditions of our experiment 162
animal food had no great importance in the nutrition of *Pontogammarus robustoides*, and this species fed mainly on overgrowths and macrophytes.

Thus in the character of its nutrition *Pontogammarus robustoides* is close to *Pandorites platycheir* and *Stenogammarus compressus* and is included in gammarids feeding mainly on overgrowths, but higher water vegetation is starting to acquire greater importance in the nutrition of *Pontogammarus robustoides*.

5. *Dikerogammarus haemobaphes* and *Amathillina cristata* are encountered in large quantities among beds of eelgrass in the region of the Mangyshlak peninsula and Kulaly island, and also in the Volga delta. The experimental data (Tables 6 and 7) permit

Table 6. Distribution of Dikerogammarus haemobaphes in Gaevskaya bays with different types of food

1 Число экз.	2 Продолжительность опыта, час	3 Зостера	4 Энтероморфа	5 Лауренсия	6 Детрит
21	5	76,2	23,8	—	—
29	5	72.4	27,6	—	—
27	8	74,0	18,6	7,4	—
30	9	75,8	10,5	13,7	—
29	9	73,4	13,3	13,3	—
23	10	78,2	21,8	—	—
32	12	71,8	18,7	9,5	—

Key: 1 - Number of specimens 2 - Duration of experiment, hrs 3 - Eelgrass 4 - Enteromorpha 5 - Laurencia 6 - Detritus

Table 7. Distribution of Amathillina cristata in Gaevskaya bays with different types of food

1 Число экз.	2 Продолжительность опыта, час.	3 Зостера молодая	4 Зостера старая	5 Энтероморфа	6 Лауренсия
23	4	52,1	34,7	13,2	—
26	6	57.7	30,7	7,6	4
26	8	57,7	26,7	7.6	8
20	9	45,0	40,0	10,0	5,0
18	10	27.7	50,0	22,3	—
18	10	61,2	33,3	5,5	—
31	12	51,6	32,2	12,9	3,3
31	24	61,3	38,7	—	—

Key: 1 - Number of specimens 2 - Duration of experiment, hrs 3 - Young eelgrass 4 - Old eelgrass 5 - Enteromorpha 6 - Laurencia

considering Dikerogammarus haemobaphes and Amathillina cristata to be vegetarians. The largest concentration of gammarids was observed in bays with eelgrass. The experiments with Amathillina cristata permit the assertion that the crustaceans consume both young shoots of eelgrass and last year's. Dissection and inspection of the intestinal contents of the gammarids confirm that eelgrass is preferred to the other foods offered: the food consisted of well-disintegrated eelgrass in 76% of the gammarids, pieces of Enteromorpha tissues in 22% and Laurencia in 2%. However, just like all the above-considered amphipods, Dikerogammarus haemobaphes and Amathillina cristata can feed on detritus and overgrowths. We happened to observe how Dikerogammarus haemobaphes uses the claw (dactylus) of the gnathopod to scrape away the overgrowths of the eelgrass stalk and directs the clusters of overgrowth into its mouth with its maxillipeds. Of interest are the differences noted by Briskina in the composition of the food of Dikerogammarus haemobaphes caught in the sea and on the coast. The author points out that, whereas detritus and bottom diatoms predominated in the food of the former, algae did so in that of the latter.

To ascertain the possibility of the feeding of Amathillina cristata on detritus the gammarids were offered feed consisting of hollow valves of Rhizosolenia, on the surface of which diatoms developed in a large quantity. After 30 minutes the intestines were dissected and their contents examined. Analysis
of the intestinal contents of this species of gammarids showed 163
that the crustaceans can use as food detritus formed by Rhizosolenia: it was possible to distinguish rather clearly in the contents fine surviving fragments of valves of Rhizosolenia and Navicula. It must be noted that, according to the data of Yablonskaya (1955) and Briskina (1952), who analyzed the intestinal

contents of the above-mentioned two species of gammarids, flocculent detritus predominated in the food of gammarids and bottom diatoms were encountered; true, the admixture of diatoms was .... smaller in that of *Amathillina cristata*.

Thus the literature data on the composition of the food, our observations and experiments indicate considerable euryphagy of *Dikerogammarus haemobaphes* and *Amathillina cristata*. Depending on various conditions of habitation these species can use as food macrophytes (eelgrass) and overgrowths of macrophytes, and also detritus; under experimental conditions they fed mainly on eelgrass. It can be thought that in both the region of Mangyshlak Peninsula and that of Kulaly Island the main food source is eelgrass. Our observations of the feeding process of *Dikerogammarus haemobaphes* have shown that the gammarids gnaw eelgrass leaves and are capable of biting off large pieces of food (Figure 14).

6. *Pandorites podoceroides* and *Niphargoides quadrimanus*. It was shown above that the gammarids widespread in the delta and fore-delta of the Volga, in the region of Kulaly island, are connected in their distribution with macrophytes and eat mainly overgrowths of macrophytes and some algae (*Spirogyra*), and also detritus. However, there is an entire group of gammarids widespread in the region of the Ural submarine trench where, as is known, there are no macrophyte thickets of any kind, and torn-off eelgrass is brought in only by the current. *Pandorites podoceroides* and *Niphargoides quadrimanus* always bury themselves
in the ground and never gather on the underwater vegetation or 164

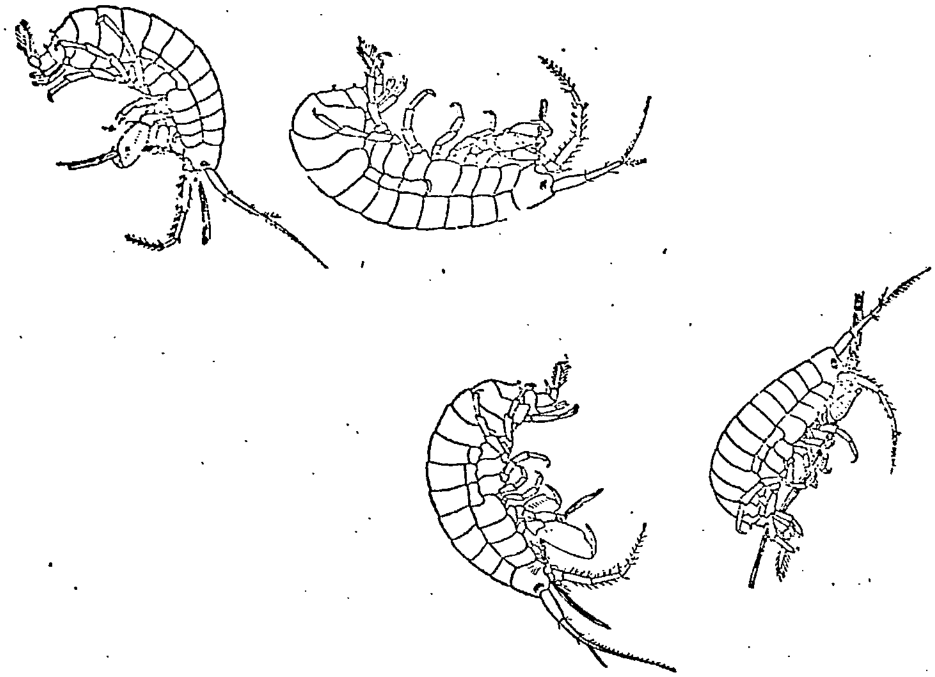

Рис. 14. Dikerogammarus haemobaphes

Figure 14. Dikerogammarus haemobaphes.

its residues. In an aquarium it can be observed how the crustaceans construct small holes from which only their antennae are visible. By moving their antennae the crustaceans create motion of the water around the hole and stir up light particles of the surface layer of the ground. By the movement of the antennae and maxillopeds the flow of water is directed toward the mouth and then all the particles which have settled on the bristles of the antennae and gnathopods are swept away by other bristles into small clusters and swallowed. The species under consideration are also capable of filtering a suspension to some degree. Thus, upon the addition of a suspension of Ankistrodesmus or pulverized Conferva to the water of an aquarium containing crustaceans, the crustaceans start waving their antennae and oral appendices energetically and after some time (1-1.5 hours) the algae can be detected in the anterior section of the intestine of the crustaceans. However, in the case of a long absence of suspensions in the water Pandorites podoceroides, sitting in a hole, starts to rake in with gnathopod pair I the detritus lying close at hand. If a large mineral particle or a coarse piece of macrophyte falls in the hole, the crustaceans expel it.

The data presented in Tables 8 and 9 show rather clearly that of all the presented feeds (the experiments were conducted with the use of Gaevskaya bays; the distribution of crustaceans by different compartments is expressed in percentages) the two species preferred detritus gathered in the region of the channel of the Ural submarine trench. At the end of the experiment almost all the crustaceans proved to be in the compartment with gray-green flocculent detritus, and the motion of water around the holes of the crustaceans was clearly visible. Only Pandorites podoceroides was encountered at times on Butomus rootstock. However, in the intestines of most crustaceans (87%) gathered in the compartment containing the rootstock there was a flocculent mass, and in only 13% was there a brown mass with a small admixture of Navicula of identical diatom overgrowths. In the experiments, when the crustaceans were offered Spirogyra and rootstock with overgrowths,
in only 10% of Niphargoides quadrimanus and 22% of Pandorites 165
podoceroides was a brown mass with Navicula discovered in the intestines, and in the remaining crustaceans the intestines

Table 8. Distribution of Pandorites podoceroides in Gaevskaya bays with different food

1 Число экз.	2 Продолжительность опыта, час.	3 Детрит	4 Спирогира	5 Корневище с обрастаниями	1 Число экз.	4 Спирогира	5 Корневище с обрастаниями
18	4	100	—	—	15	33	67
22	8	95	—	5	10	—	100
20	8	100	—	—	20	50	50
20	10	85	—	15	12	30	70
20	12	100	—	—	12	50	50
20	12	75	—	25	12	18	82

Key: 1 - Number of specimens 2 - Duration of experiment, hrs 3 - Detritus 4 - Spirogyra 5 - Rootstock with overgrowths

Table 9. Distribution of Niphargoides quadrimanus in Gaevskaya bays with different food

1 Число экз.	2 Продолжительность опыта, час.	3 Детрит	4 Спирогира	5 Корневище с обрастаниями	1 Число экз.	4 Спирогира	5 Корневище с обрастаниями
15	8	100	—	—	12	50	50
20	8	100	—	—	12	20	80
20	10	100	—	—	10	100	—
20	10	100	—	—	10	40	60

Key: 1 - Number of specimens 2 - Duration of experiment, hrs 3 - Detritus 4 - Spirogyra 5 - Rootstock with overgrowths

were empty. This indicates that the gammarids under consideration can also feed on overgrowths.

And so the gammarids inhabiting the region of the Ural submarine trench are filtrators and feed mainly on flocculent detritus.

Gammarids can thus consume particles of different size as food. Following Ponyi (1956), among the gammarids of the Northern Caspian one can distinguish species consuming as food: 1) small particles (Stenogammarus similis, Stenogammarus compressus, *Pandorites podoceroides* and *Niphargoides quadrimanus*) and 2) large food particles (*Dikerogammarus haemobaphes*, *Pontogammarus robustoides*, *Pandorites platycheir* and *Amathillina cristata*).

7. Corophiidae. Corophiidae live in tubules which they construct of a cobweb-like net covered with a layer of mud or sandstones. Under unfavorable conditions crustaceans abandon the tubules and construct new homes when they find suitable conditions for habitation.

Among the Corophiidae there are species which usually construct tubules which are raised above the surface of the ground or attached to underwater objects (*Corophium curvispinum*, *C. mucronatum* and *C. monodon*). In contrast to these species, *Corophium nobile* constructs homes, not on the surface of the ground but, like *Corophium volutator* (Thamdrup, 1935; Segerstråle, 1940; Jonge, 1952) in the form of a U-shaped tubule buried several centimeters in the ground. Such tubules are open at both ends; the crustacean lies in them back downward, and its pleopods are in continuous motion to maintain the flow of water.

It is known from the literature data (Jonge, 1952; Thamdrup, 1935; Segerstråle, 1940) that the Corophiidae feed on detritus on the bottom and in the mass of the water and in their method of feeding are filtrators. Serving as the filter for the Corophiidae are the long elastic bristles with which the gnathopods are covered in large quantity. Of no less importance in holding small particles are the oral organs, especially the maxillae and maxillopeds. The Corophiidae lack any sort of adaptations for the "mastication" of food.

Actually, our observations showed that Corophium nobile and Corophium mucronatum eat only suspended food substances, extracting them from the water which the crustations pass through the tubule of their home by means of their pleopods. After the addition of Chlorella, Scenedesmus or Ankistrodesmus to the aquarium containing the crustaceans, invariably it was possible to discover those algae in the intestines of the Corophiidae after a short time interval (30 minutes or 1 hour). However, whereas Corophium nobile is capable of capturing Chorella cells 4 microns in size, Chorella occurred extremely rarely in the dissected intestines of Corophium mucronatum, while Scenedesmus and Ankistrodesmus were always encountered in the intestines. It is known from the literature data that Corophiidae can capture even finer particles with the above-described filtration apparatus. Thus, Corophium volutator is capable of filtering particles 2-4 microns in size. It should also be noted that in the absence of nutrients suspended in the water the Corophiidae (especially Corophium mucronatum emerge from the tubules, stir up with antenna pair II the detritus which has settled near their home and then filter the suspended particles.

Corophiidae, besides small food particles, can use certain 166
filamentous algae as food. Separate filaments of the algae are simply swallowed without any sort of "mastication". This is especially characteristic of the Northern Caspian Corophiidae, Corophium curvispinum. The data of Yablonskaya (1955) confirm

our observations. It is characteristic that this species is encountered oftener than other species, in overgrowths and among accumulations of Spirogyra, finding here a substrate for the base of the tubulé and food. Thus the principal method of feeding of Corophiidae of the Northern Caspian, as of the Corophiidae of other waters, consists in the filtration of detritus of the layer of water near the bottom.

Cumacea

Although the Cumacea lead a mobile form of life they are capable of burying themselves in the ground; the anterior part of the cephalothorax and the uropods remain above the ground (Zimmer, 1933; Forsmann, 1938).

To judge from the few investigations, most cumaceans are mud-eaters. Predominant in their food are detritus and various bottom diatoms (Briskina, 1952; Yablonskaya, 1955). According to Zimmer and Forsmann, the crustacean Diastylis rathkei, sitting in the shelter dug out by it, carries up the ends of pair III of the maxillopeds and pair I of the pereopods to the mouth pieces of mud gathered not far from the hole. The authors consider such a method of feeding characteristic of all cumaceans dwelling in mud. Dwellers in sand, according to the observations of Zimmer, such as Diastylis brandyi and Lampros fasciata, for example, have a somewhat different type of feeding. They grasp sandstones with the ends of pair III of the maxillopeds and, turning constantly, raise them to the mouth and then, evidently, scrape bacterial and algal overgrowths with the mandibles. Zimmer

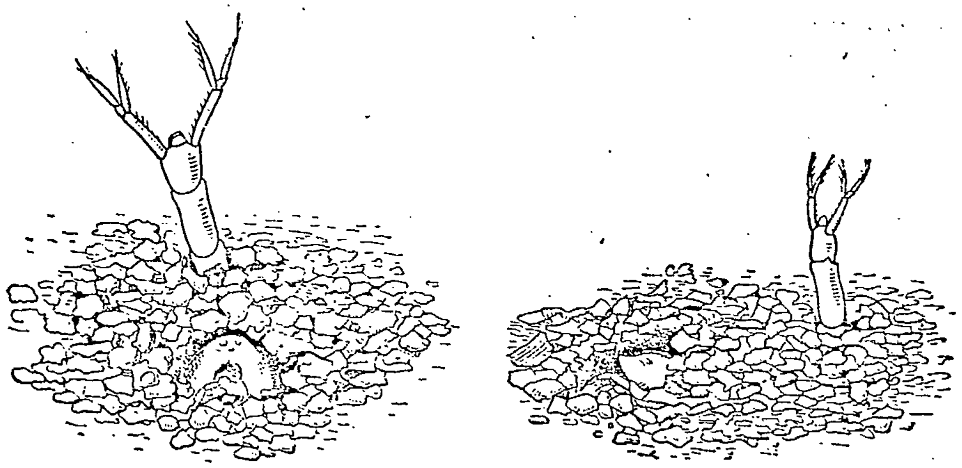

Рис. 15. Положение в грунте Pterocuma pectinata

Figure 15. Position of Pterocuma pectinata in the ground.

(1933) notes, however, that among the cumaceans, to judge by the structure of the mouth parts (for example, Campylaspoides), there are predators, or in any case forms capable of eating larger pieces of detritus or residues of algae.

We did not conduct special observations of the feeding of Caspian cumaceans. It is known from literature data that in the food of some cumaceans of the Caspian (Pterocuma pectinata and Pt. sowinskyi) detritus and diatoms of the type of Navicula have predominant importance (Yablonskaya, 1955; Briskina, 1952; Maksimova, 1958).

Our indirect observations of the behavior of Pterocuma 167
pectinata and Schizorhynchus bilamellatus under aquarium conditions showed that the crustaceans bury themselves in the ground, exposing the uropods and often a part of the cephalothorax on the surface (Figure 15). When danger draws near the crustacean

quickly abandons the hole and buries itself at another place. It is quite evident that the crustaceans sitting in the holes gather the clusters of detritus around the hole.

Oligochaeta

The Oligochaeta are one of the common groups of bottom fauna of the Northern Caspian. They develop in large quantity on various grounds and are encountered over the entire area of the Northern Caspian. As is well-known, the tubificids of fresh waters have no special organs of respiration, and gas exchange in them takes place through the surface of the posterior part of the body, which they thrust out of the ground, making rhythmic oscillating movements. It has also been established by many researchers that the tubificids bury the anterior ends of their bodies in the ground and, grasping particles of organic matter in the deep layers of the ground, pass it through the intestine and transport it onto the surface (Izosimov, 1940; Pobegailo, 1955). This biological characteristic of worms was used in studying the method of their feeding and in determining the source from which they draw food material.

1. Tubifex sp. We conducted several series of experiments with two species of algae (Scenedesmus and Ankistrodesmus). The presence or absence in the excrements of test Oligochaeta or of residues of algae and the times of their appearance were taken into consideration in the experiments. The results of the experiments, presented in Table 10, show rather clearly that the range of penetration of the Oligochaeta into the ground

Table 10. Results of experiments to make clear the depth of penetration of tubificids of the Northern Caspian for food into the ground

Глубина залегания корма, см (a)	Scenedesmus (50 олигохет) (b)														Ankistrodesmus (30 олигохет) (b)													
	Время появления водорослей в экскрементах олигохет (часы с начала постановки опыта) (c)																											
	1,2	1	2	3	4	5	6	7	8	9	10	11	12	13	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Поверхность (d)																			×			+						
1	+														+													
2	+														+													
3		+													+													
4		×			+												+											
5					×	×											×	+										
6							×	×									×				+							
7					×					+												+						
8										+											+							
9																							+					
10										+		×										+						
11														×										×				
12																										×		
13										Водоросли в экскрементах отсутствовали (e)																		

Примечание. + означает появление водорослей у большинства олигохет; × — то же, у единичных олигохет.

Key: a - Depth of location of food, cm b - Oligochaeta c - Time of appearance of algae in the excrement of Oligochaeta (in hours from the beginning of the experiment). d - Surface, e - No algae present in experiments Note: + designates the appearance of algae for most Oligochaeta; x - the same, for single Oligochaeta is rather broad. Accessible to them is food both lying on the surface of the ground and lying at a certain depth. However, as is evident from the time of appearance of algae in the experiments, the most favorable conditions for obtaining food from the ground are at a depth of about 1-3 cm. In this experiment, algae cells could be found in the excrements of Oligochaeta already after one half hour. In the absence of nutrient particles in the ground the Oligochaeta appear on its surface and feed on the surface layer. In this case food is captured through partial eversion of the pharynx, which according to the data of Izosimov (1940) has a rather strong musculature.

Thus the main source of food of tubificids of the Northern Caspian is the organic matter of the intermediate layer of the ground, and of its surface layer only in some cases. In their method of feeding the Oligochaeta, like most free-living worms, are swallowers.

Polychaeta

Feeding and the structure of the feeding organs have been described in detail for Polychaeta of the Sabellidae family (Nicol, 1931). The Sabellidae excite a flow of water by beating their bronchial cilia and settle out fine particles contained in the water, which are driven toward the mouth by means of the gill cilia along the ventral groove of the "lips". Mac Ginitie (1939) described the feeding of the sedentary polychaetous worm Chaetopterus varipedatus. The worm lives in a U-shaped tube constricted at both ends, passing water through it. Inside the tube

the worm produces mucus which forms a peculiar catching net with very fine pores; fine food particles are held by this net. Every 15 minutes a ball of mucous net containing food particles 169
is directed along the dorsal ciliar groove toward the mouth. Dales (1955, 1957) and Sutton (1957), in work on the feeding of some Polychaeta, gave special attention to the method of getting food and digestion of the group Terebellidae. In contrast with Sabellidae, these worms feed by means of extremely mobile and contractible tentacles. Food particles adhere to the mucus produced by the tentacles and are transported by the motion of the cilia toward the upper lip and further toward the mouth. When the particles reach the upper lip, on tentacles which have a groove, covered with cilial epithelium, on their lower surface, they are sorted by sizes. Food is taken by the Nereidae, according to the data of many researchers, including Yablonskaya (1952) and Beklemishev (1950) by eversion of the pharynx, which is equipped with chitinized maxillae.

As is well-known (Anenkova, 1930; Zenkevich, 1922), in the Caspian Sea polychaetous worms are represented by three families: Nereidae, Ampharetidae and Sabellidae. The first family belongs to the errant (Errantia) and the last two to the sedentary (Sedentaria) Polychaeta. Sedentary Polychaeta live in tubes of mud and lead a relatively immobile form of life. The family Nereidae is represented in the Northern Caspian by a single species, *Nereis diversicolor*; of the family Ampharetidae, widely represented here are *Hypania invalida* and *Hypaniola kowalewskyi*. The family Sabellidae is represented by two species

-- Manajunkia caspica and Fabricia sabella. Since the feeding of Nereis has been analyzed in detail in the work of Yablonskaya, we gave special attention to study of the method of feeding of Hypania, Hypaniola and Manajunkia.

1. Hypania invalida and Hypaniola kawalewskyi. As is well-known, both species of Polychaeta belong to the order Terebellidae. In representatives of that order, in connection with the transition to an immobile mode of life (in tubules), the palps have been modified into slightly contractible filiform tentacles. By means of tentacles which creep over the ground in all directions from the head of the worm, Hypania invalida and Hypaniola kowalewskyi (Figure 16) gather food particles lying around the tubule.

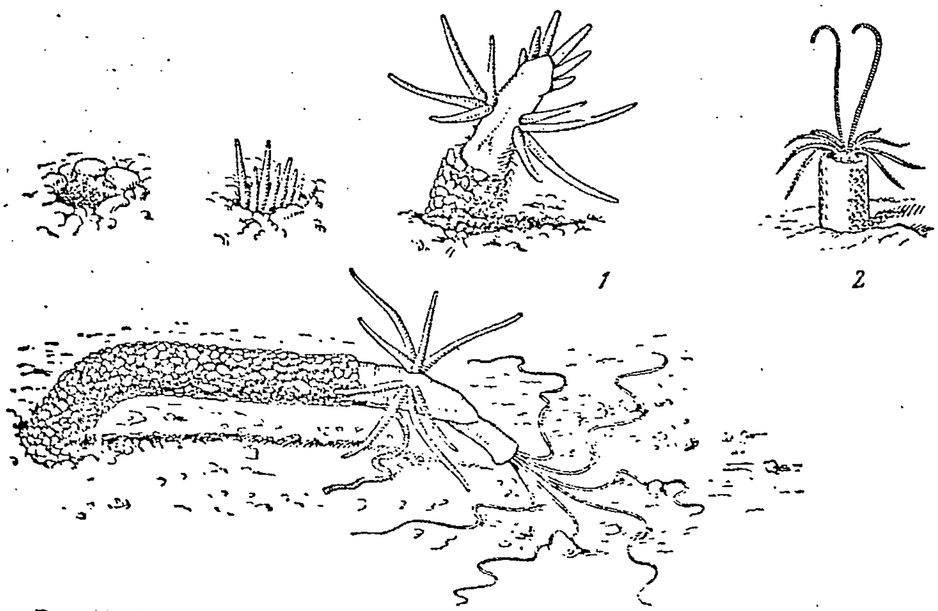

Рис. 16. Положение в грунте Hypania invalida (1) и Manajunkia caspica (2)

Figure 16. Position in the ground of Hypania invalida (1) and Manajunkia caspica (2).

Table 11. Experimental observations to explain the food source of Hypania invalida and Hypaniola kowalevskyi

a Продолжительность опыта, час.	Hypania invalida (50 экз.) b (Scenedesmus) взвешен в воде c	Hypania invalida (50 экз.) b (Scenedesmus) положен на грунт d	Hypaniola kowalewskyi (50 экз.) b (Scenedesmus) взвешен в воде c	Hypaniola kowalewskyi (50 экз.) b (Scenedesmus) положен на грунт d	a Продолжительность опыта, час.	Hypania invalida (50 экз.) b (Scenedesmus) взвешен в воде c	Hypania invalida (50 экз.) b (Scenedesmus) положен на грунт d	Hypaniola kowalewskyi (50 экз.) b (Scenedesmus) взвешен в воде c	Hypaniola kowalewskyi (50 экз.) b (Scenedesmus) положен на грунт d
1/4	—	×	—	×	2	—	×	—	×
1/2	—	×	—	×	3	—	×	—	×
3/4	—	×	—	×	4	—	×	+	×
1	—	×	—	×	5	+	×	—	×

Key: a - Duration of experiment, hrs. b - specimens c - suspended in water d - placed on the ground
Note. + -- single cells in excrement; x -- many cells (the same for Table 12)

Table 12. Experimental observations to explain the food source of Manajunkia caspica

a Продолжительность опыта, час.	b Корм (Scenedesmus) взвешен в воде c	b Корм (Scenedesmus) положен на грунт d	a Продолжительность опыта, час.	b Корм (Scenedesmus) взвешен в воде c	b Корм (Scenedesmus) положен на грунт d
1/4	×	—	2	×	—
1/2	×	—	3	×	+
1	×	—	4	×	—

Key: a - Duration of experiment, hrs. b - Food c - suspended in water d - placed on the ground

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Specially arranged experiments, the results of which are presented in Table 11, testify that for the above species of worms food is accessible only when it is on the surface of the ground. Algae which had been in a suspended state were not present in the excrement of the worms. In only two cases were single cells of floating algae discovered in the intestines of worms at the end of experiments, and this evidently is explained by the settling of those cells on the ground. This conclusion agrees well with the above-described observations and the data of Briskina (1952), Yablonskaya (1955) and Maksimova (1958), according to which the food of *Hipania* and *Hipaniola* consists of flocculent detritus with a considerable admixture of mineral particles. Thus the main food source of *Hipania* and *Hipaniola* is the surface layer of the ground. In their method of feeding the two species are gatherers which gather food particles by means of mobile contractible tentacles.

2. *Manajunkia caspica*. This species belongs to the family Sabellidae of the order Serpulomorpha. In contrast with Terebellamorpha, the palps of *Manajunkia caspica* are modified into a pair of lobes directed forward and equipped with filiform plumose excrescences covered with cilial epithelium. *Manajunkia*, according to our observations, lives in mud or sand tubules raised a little above the surface of the ground and by beating the cilia creates a flow of water containing food particles toward the mouth (Figure 16).

The data presented in Table 12 confirm the conclusion drawn on the basis of the observations: *Manajunkia*, in contrast with the species of worms discussed above, feeds only on food particles in the near-bottom layer of water and is a filtrator. Actually, in experiments in which the food (*Scenedesmus*) was placed on the ground, the algae were completely absent in either 171
the intestinal contents or in the excrement, whereas algae in the suspended state were discovered in the excrement of the worms already after a half hour.

Investigators describing the feeding of various Polychaeta have also directed attention to a certain selection of food particles by size. Thus, Mac Ginitie (1945) established that Urechis and Chaetopterus are capable of entrapping molecules of hemocyanin by means of catching nets. Thus he was able to calculate that the pore size of the catching net is 0.004 micron. Dales (1955) observed the selection of finer food particles by Amphitorite jonstoni. The author discovered that small particles are moved along the grooves of the tentacles exclusively by the cilia, whereas solid and large particles are moved by contraction of the groove.

In the worms investigated by us there also is a certain selection of consumed food particles by size. The data were obtained by feeding worms with algae of different sizes and a macrophytic suspension with subsequent measurement of the dimensions of food and mineral particles in the intestinal contents and excrement. Direct observations were also made with binoculars of the consumption of food particles of different sizes by the worms. Worms feeding on suspended nutrients have the most delicate mechanism of particle selection. Thus, Manajunkia caspica is capable of selecting particles with dimensions of 1 to 20 microns. Polychaeta gathering food with slimy tentacles (Ampharetidae) can consume as food even larger food particles from 3 to 140 microns in size. Oligochaeta can seize particles up to 200 microns in size and swallow larger particles with difficulty. This is clearly traced in the observation of Oligochaeta with binoculars: usually, when larger particles are encountered on the path of movement of Oligochaeta, they rather energetically hurl them to one side with their prostomium.

Food Groupings

On the basis of the obtained results of experimental investigations to clarify the method of feeding and food source of some bottom animals of the Northern Caspian we attempted to classify them by the character of feeding. The basis of the proposed groupings was the scheme of Zernov (1940) with refinements and additions introduced by Turpaeva (1949). The scheme was constructed on the division of animals according to sources and method of capture of food. By food sources the bottom invertebrates of the Northern Caspian can be subdivided into four groups, two of which are broken down in turn into smaller groupings.

1. Animals Whose Main Source of Food is Thickets of Macrophytes

The first group includes gastropods, gammarids and some other crustaceans. The gammarids belonging to this group are distributed over the entire Northern Caspian, but the largest accumulations form in the delta and fore-delta of the Volga, in the region of the slope, and also in the region of Mangishlak peninsula. Such a distribution undoubtedly is connected with their feeding, as it is precisely there that macrophytes and certain green algae develop in a large quantity. Among amphipods there are species feeding both on overgrowths of macrophytes (mainly) and on various parts of the macrophytes themselves. Their methods of feeding are correspondingly different.

Among them we distinguish biting species which scrape away overgrowths (*Pontogammarus robustoides*, *Pontogammarus abbreviatus* and *Pandorites platycheir*) and gnawing species which bite off relatively large pieces of leaves and stems of macrophytes (*Dikerogammarus haemobaphes* and *Amathillina cristata*). 172

2. Animals Feeding Mainly on Suspended Nutrients

The second group includes animals of different systematic groups: crustaceans (corophiids and some gammarids), molluscs and worms. Representatives of this group are filtering animals, which actively catch or precipitate suspended food particles of small dimensions from flows of water created by them (Turpaeva, 1948). Thus feed most molluscs of the Caspian -- *Dreissena polymorpha*, *Mytilaster lineatus*, *Didacna trigonoides*, *Monodacna edentula*, *Adacna plicata minima* and *Cardium edule*. The first two species lead an attached mode of life, forming large accumulations on rocks and shells and feeding exclusively on suspended nutrients. The remaining species live in the surface layer of the ground, burying themselves either completely (*Monodacna*, *Adacna* and *Syndesmya*) and leaving only siphons at the surface, or to a depth of about half the size of the shell (*Didacna*), rising as it were above the ground.

The polychaete worm *Manajunkia caspica* also filters food. The worms live in mud tubules, which rise slightly above the surface of the ground, and by beating the cilia of the oral lobes create a flow of water directed toward the mouth. In such a method of capturing food the settled detritus becomes inaccessible to *Manajunkia caspica*.

We also class corophiids (Corophium nobile, C. mucronatum and C. monodon) in the group of invertebrates feeding mainly on detritus suspended in the water. Crustaceans rarely appear on the surface of the ground and only when there are no food particles suspended in the water do the corophiids emerge from their tubules and stir up the detritus settled around their home with antenna pair II.

3. Animals Whose Main Source of Food is the Surface Layer of the Ground

Representatives of this group, connected in their feeding with the surface of the ground, in their method of feeding (Turpaeva, 1948) are gathering, swallowing and filtering [animals].

The grouping of gathering animals includes animals of different systematic groups and naturally with a different morphological structure of the organs of feeding. Thus, Syndesmya ovata sucks in food particles with long thin siphons which it passes over the surface of the ground. The organs of feeding of Hypania invalida and Hypaniola kowalewskyi are readily contractible filiform tentacles with which the worms gather food particles lying around their homes. Cumaceans, sitting in a hole, gather fragments of detritus around their shelter with pair III of the maxillopeds and pair I of the pereopods. When all the food around the hole has been eaten, the crustaceans abandon the hole and bury themselves in a new place. Gammarids of this grouping (Stenogammarus similis) move actively over the ground and gather with their maxillopeds clumps of detritus and scraps of algae lying on the surface of the ground.

Among the gammarids whose main food source is the surface layer of the ground we distinguished species similar in their method of feeding to filtrators: *Pandorites podoceroides*, *Niphargoides quadrimans*, *N. aequimanus*, etc. Placing themselves in holes, the crustaceans by moving their antennae and maxillopeds create a flow of water around themselves. It should be noted that filtration (extraction of food particles from a flow of water created by the crustacean) is to some degree characteristic of all the gammarids. Whereas filtration is not of great importance to representatives of group I, the gammarids of group III feed mainly on filtered food particles. 173

Classed in the grouping of swallowing animals, according to the investigations of Yablonskaya (1952) is *Nereis diversicolor*, which captures food by everting its pharynx, which is equipped with chitinous jaws.

4. Animals Whose Main Source of Food is the Mass of the Ground

This group of the bottom population of the Northern Caspian includes the Oligochaeta, which in their method of feeding are swallowers, feeding on organic matter of the mass of the ground. In contrast with *Nereis* which, according to the classification of Sokolova (1958) swallows ground whole, unselectively, some sorting of the particles by sizes is characteristic of the Oligochaeta.

As is evident from what has been said, the four groups of bottom animals distinguished on the basis of their food source and the method of obtaining it should be divided into five groupings: filtering, gathering, swallowing, biting (scraping) overgrowth and gnawing (biting off relatively large pieces of food) (Table 13).

Table 13. Distribution by food groupings of the most common bottom animals of the Northern Caspian

	Группировки A	Виды B
1	Фильтрующие	**Mollusca.** Dreissena polymorpha, Mytilaster lineatus, Didacna trigonoides, Didacna barbot-de-marny, Cardium edule, Monodacna edentula, Adacna plicata minima. **Polychaeta** Manajunkia caspica **Amphipoda** Corophium curvispinum, C. nobile, C. mucronatum, C. chelicorne, Pandorites podoceroides, Niphargoides quadrimanus, N. aequimanus, Pontogammarus maeoticus
2	Собирающие	**Mollusca** Syndesmya ovata **Polychaeta** Hypania invalida, Hypaniola kowalewskyi **Amphipoda** Stenogammarus similis, Gmelina pusilla, Stenogammarus macrurus **Cumacea** Pterocuma pectinata, Pt. sowinskyi, Schizorhynchus bilamellatus, Stenocuma gracilis.
3	Глотающие	Nereis diversicolor, Tubificidae
4	Обкусывающие (соскребывающие)	**Mollusca** Vivipara viviparus, Theodoxus **Amphipoda** Stenogammarus compressus, Pandorites platycheir, Pontogammarus robustoides, Pontogammarus abbreviatus
5	Грызущие (откусывающие большие куски пищи)	**Amphipoda** Dikerogammarus haemobaphes, Amathillina cristata

Key: A - Grouping B - Species
1 - Filtering 2 - Gathering 3 - Swallowing
4 - Biting (scraping) 5 - Gnawing (biting off large pieces of food)

Of greatest importance in the benthos of the Northern Caspian are the first three: filtering, swallowing and gathering (Table 14). In 1949 filtrators amounted to 87.5% of the total biomass. The remaining groupings were poorly represented in the benthos of the Northern Caspian. Recently, due to the settlement of Syndesmya ovata in the Northern Caspian, the role of gathering animals has increased considerably.

Table 14. Biomass of various food groupings* in the benthos of the Northern Caspian (as %)

	Группировки A	1948 г.	1949 г.	1950 г.	1951 г.	1952 г.	1953 г.
1	Фильтрующие	85,4	87,54	84,0	80,5	77,0	69,0
2	Собирающие	1,67	2,56	4,7	3,12	7,75	10,63
3	Глотающие	10,77	7,8	8,0	11,7	10,02	16,2
4	Обкусывающие (соскребывающие)	1,80	1,87	2,9	4,46	3,62	3,37
5	Грызущие (откусывающие)	0,36	0,23	0,40	0,22	1,61	0,9

Key: A - Grouping 1 - Filtering 2 - Gathering 3 - Swallowing 4 - Biting (scraping) 5 - Gnawing (biting off)

*To compile Table 14 we used materials published in the works of Ya. A. Birshtein and N. N. Spasskii (1952) and L. G. Vinogradov (1959).

On the basis of the data on the distribution of animals (during 1948-1953) we attempted to subdivide the Northern Caspian into five food zones:

I - the zone of predominance of animals which bite (scrape) and gnaw macrophytes;

II - the zone of predominance of filtering animals;

III - the zone of predominance of gathering and swallowing animals;

IV - the zone of predominance of swallowing animals;

V - the zone of predominance of filtering and gathering animals.

A schematic map of the distribution of the food zones is presented in Figure 17.

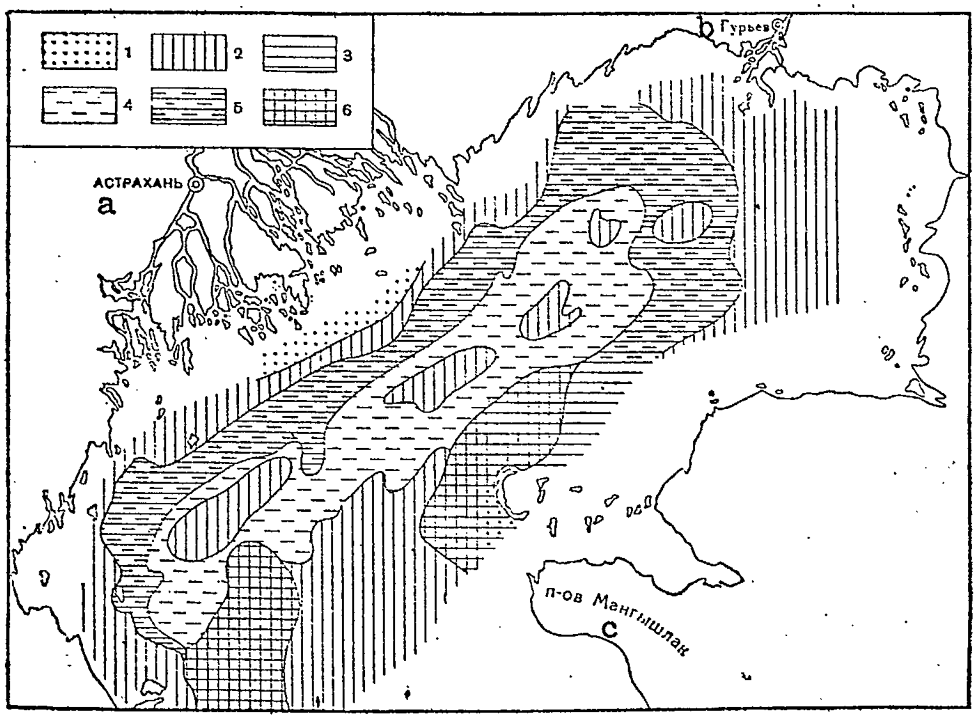

Рис. 17. Расположение пищевых зон в Северном Каспии

Figure 17. Location of food zones in the Northern Caspian. 1 - Zone I; 2 - Zone II; 3 - Zone of predominance of gathering animals; 4 - Zone IV; 5 - Zone III (equally); 6 - Zone V. a - Astrakhan b - Gur'ev c - Mangyshlak peninsula.

The zone of accumulation of animals, the main food source of which is thickets of macrophytes and which feed on overgrowths and various parts of the macrophytes themselves, is situated in the Volga delta and the region of Mangyshlak

peninsula -- Kulaly Island. The zone of predominance of fil-
tering animals extends from Tyulen'i Island along the area near
the Volga delta to the area in front of the Ural River mouth
and then turns south along the eastern coast. Considerable
accumulations of filtering animals are observed in the region
adjacent to the Central Caspian. In the part of the zone near
the delta, *Dreissena*, *Adacna* and corophiids achieve their greatest
quantitative development; in the southwestern region of the zone, 174
Monodacna; in the region of the eastern coast and near the mouth
of the Ural River, *Dreissena* and corophiids predominate among
the bottom population. In the region adjacent to the Central
Caspian there are considerable accumulations of *Mytilaster*,
Cardium and *Didacna*.

The zone inhabited equally by gathering and swallowing
animals is situated in the region of the slope, extends to
Zaburun'e and then turns toward the Ural submarine trench and
Kulaly Island. In this zone, among benthonic animals, of the
gathering animals the cumaceans and some gammarids (*Stenogam-
marus similis* and *Gmelina pusilla*) attain the greatest quanti-
tative development, and of the swallowing animals, the Oligo-
chaeta.

The zone of predominance of swallowing animals occupies 175
the central part of the Northern Caspian, from the region of
Tyulen'e Island to the Ural submarine trench *Nereis* and Oligo-
chaeta dominate among the bottom population here. In places
in this zone are interspersed spots of predominance of filtering

animals, consisting of Monodacna (western and central spots) and Dreissena (the two remaining spots).

The zone inhabited by filtering and gathering animals is in the region bordering the Central Caspian and consists of two parts. One part of the zone is at Kulaly Island and is formed of Didacna and Mytilaster (filtering) and Syndesmya 176
(gathering); the other part is in the southwestern part of the boundary region and is formed of Cardium and Mytilaster (filtering) and Syndesmya (gathering).

Bibliography

1. Anenkova, N. P. 1930. Fresh-and brackish-water Polychaeta of the USSR. Key to Freshwater Organisms of the USSR, No. 2.
2. Beklemishev, K. V. 1950. "The Feeding of Nereis pelagica and the Functional Importance of its Maxillary Apparatus." Doklady AN SSSR, Vol. 73, No. 5.
3. Bennig, L. L. 1938. "The Amphipod Amathillina cristata in the Southeastern Region of the Caspian Sea." Priroda, Nos. 7-8.
4. Birshtein, Ya. A. 1945. "Annual Variations of the Benthos of the Northern Caspian." Zoologicheskiy zhurnal, Vol. 24, No. 3.
5. Birshtein, Ya. A., and Spasskii, N. N. 1952. "The Bottom Fauna of the Caspian Sea Before and After the Establishment of Nereis succinea." Proceedings of the Moscow Society of Naturalists, Zoological Department, No. 33.

6. Briskina, M.M. 1952. "Composition of the Food of Bottom Invertebrates in the Northern Part of the Caspian Sea." Proceedings of the All-Union Scientific Research Institute of Sea Fisheries and Oceanography (VNIRO), No. 1.

7. Vinogradov, L.G. 1959. "Perennial Variations of the North Caspian Benthos." Ibid., Vol. 38.

8. Voskresenskii, K. A. 1948. "The Belt of Filtrators as a Biohydrological System of the Sea.' Proceedings of the State Oceanographic Institute, No. 6 (18).

9. Idem. 1957. "The Intensity of Water Exchange of Dreissena." Theses of the Conference on Biological Problems of New Bodies of Water.

10. Gaevskaya, N.S. 1939. "Some New Methods in Studying the Feeding of Water Organisms." Zoologicheskii zhurnal, Vol. 18, No 6.

11. Zernov, S.A. 1940. General Hydrobiology. Moscow.

12. Zenkevich, L.A. 1922. "Fabricia sabella subsp. caspica." Russkii gidrobiologicheskii zhurnal, Vol. 1.

13. Izosimov, V.V. 1940. "Oligochaeta." Handbook of Zoology, Part 2.

14. Karpevich, A.F. 1946. "The Consumption of Food of Pontogammarus maeoticus of the Caspian Sea." Zoologicheskii zhurnal, Vol. 25, No. 6.

15. Kudinova-Pasternak, R.K. 1951. "The Question of the Interaction of Biofilters With Masses of Water." Voprosy geografii, Collection No. 26.

16. Maksimova, L.P. 1958. "The Feeding of Invertebrates Established in the Tsimlyansk Reservoir from the Lower Reaches of the Don." Izvestiya Vsesoyuzn. nauchno-issled. in-ta ozern. i rech. rybnogo khoz-va, Vol. 11.

17. Pobegailo, I.P. 1955. "The Role of Bottom Organisms in the Process of Self-purification of Bodies of Water Contaminated by Waste Waters." Candidate's Dissertation.

18. Reznichenko, O.G. 1957. "The Ecology and Nutritional Importance of Pontogammarus maeoticus of the Sea of Azov." Zoologicheskii zhurnal, Vol. 36, No. 9.

19. Romanova, N.N. 1958. "Distribution and Ecological Characterization of North Caspian Amphipoda and Cumacea." Doklady AN SSSR, Vol. 121, No. 3.

20. Sokolova, M.N. 1958. "The Feeding of Deep-sea Bottom Invertebrate Detritus-eaters." Proceedings of the Institute of Oceanology of the USSR Academy of Sciences, Vol. 27.

21. Turpaeva, E.P. 1948. "The Feeding of Some Bottom Invertebrates of the Barents Sea." Zoologicheskii zhurnal, Vol. 27, No. 6.

22. Idem. "Food Groupings of Benthos and Their Importance in Bottom Biocenoses of the Barents Sea." Candidate's Dissertation.

23. Khusainova, N.Z. 1958. Biological Characteristics of Some Mass Bottom Food Invertebrates. Kazan' State University Press, Alma-Ata.

24. Chugunov, N.L. 1923. "Experience in the Quantitative Investigation of the Productivity of the Bottom Fauna in the Northern Caspian and Typical Bodies of Water of the Volga Delta." Proceedings of the Astrakhan Ichthyological Laboratory, Vol. 5, No. 1.

25. Yablonskaya, E.A. 1952. "The Feeding of Nereis succinea in the Caspian Sea." Proceedings of the Moscow Society of Naturalists, No. 33.

26. Idem. 1955. "Possible Changes of the Food Supply of Fishes of the Sea of Azov During Regulation of River Runoffs." Proceedings of VNIRO, Vol. 31, No. 1.

27. Buley. 1936. "Consumption of Diatoms and Dinoflaggellates by the Mussel." Bulletin Scripps Institute of Oceanography, Vol. 4.

28. Dales, P. 1955. "The Feeding and Digestion in Terebellid Polychaetes." J. Marine Biol. Assoc., Vol. 34.

29. Idem. 1957. "Preliminary Observation on the Role of the Coelomic Cells in Food Storage and Transport in Certain Polychaetes." Ibid., Vol. 1.

30. Forsmann, B. 1938. "Investigations of the Cumaceans of the Skagerak." Zool. Bidrag. Uppsala, Vol. 18.

31. Fox, D. 1936. "The Habitat and Food of the California Mussel." Bull. Scripps Institute of Oceanography, Vol. 4.

32. Galtsoff, P. 1928. "Experimental Study of the Function of the Oyster Gills and Its Bearing on the Problems of Oyster Culture and the Sanitary Control of the Oyster Industry." Biol. Bur. Fish., Vol. 44.

33. Jordan, H. 1913. Comparative Physiology of Invertebrate Animals [in German]. Vol. 1.

34. Jorgensen and Goldber. 1953. "Particle Filtration in Some Ascoidians and Lamellibranchs." Biol. Bull., Vol. 105, No. 3.

35. Yonge, C. 1952. Aspects of Life on Muddy Shores. Essays in Marine Biology.

36. Loosanoff, V. 1949. "On the Food Selectivity of Oysters." Science, 110.

37. Mac Ginitie, G. 1939. "The Method of Feeding of Chaetopterus." Biol. Bull., Vol. 77.

38. Idem. 1945. "The Size of the Mesh Openings in Mucous Feeding Nets of Marine Animals." Biol. Bull., Vol. 88.

39. Nicol. E. 1931. "The Feeding Mechanism, Formation of the Tube and Physiology of Digestion in Sabella povonina." Trans. Roy. Soc. Edinb., 56.

40. Ponyi, E. 1956. "Ecological, Feeding, Biological and Systematic Investigations of Various Genera of Gammarus." Arch. fuer Hydrobil. Vol. 52, No. 3.

41. Segerstråle, S. 1940. "On the Biology of the Amphipoda Corophium volutator Together With Information About the Development and

42. Sutton, M. 1957. "The Feeding Mechanism, Functional Morphology and Histology of the Alimentary Canal of Terebella lapidaria L. (Polychaeta)." Proceedings of the Zoological Society, Vol. 129, No. 4, London.

43. Thamdrup, H. 1953. "On the Ecology of Fauna on Experimental Principles." Medd. Kommis. fören Dansk fiskeri. Ser. Fiskeri, Vol. 10, No. 2.

44. Zimmer, C. 1933. "Observatións of Living Mysidaceans and Cumaceans." Sitzen ber. Ges. Naturforsch., Vol. 1, Leipzig.

1 Аненкова Н. П. 1930. Пресноводные и солоноватоводные Polychaeta СССР.— Определитель организмов пресных вод СССР, вып. 2.

2 Беклемишев К. В. 1950. Питание Nereis pelagica и функциональное значение его челюстного аппарата.— Докл. АН СССР, т. LXXIII, № 5.

3 Бенинг Л. Л. 1938. Бокоплав Amathillina cristata в юго-восточном районе Каспийского моря.— Природа, № 7—8.

4 Бирштейн Я. А. 1945. Годовые изменения бентоса Северного Каспия.— Зоол. журн., т. XXIV, вып. 3.

5 Бирштейн Я. А. и Спасский Н. Н. 1952. Донная фауна Каспийского моря до и после вселения Nereis succinea.— Труды МОИП., отд. зоол., вып. 33.

6 Брискина М. М. 1952. Состав пищи донных беспозвоночных в северной части Каспийского моря.— Труды Всесоюзн. научно-исслед. ин-та морск. рыбн. хоз-ва и океаногр., вып. 1.

7 Виноградов Л. Г. 1959. Многолетние изменения северокаспийского бентоса.— Труды ВНИРО, т. XXXVIII.

8 Воскресенский К. А. 1948. Пояс фильтраторов, как биогидрологическая система моря.— Труды Гос. океаногр. ин-та, вып. 6 (18).

9 Воскресенский К. А. 1957. Интенсивность водообмена у дрейссены.— Тезисы совещ. по биол. проблемам новых водоемов.

10 Гаевская Н. С. 1939. О некоторых новых методах в изучении питания водных организмов.— Зоол. журн., т. XVIII, вып. 6.

11 Зернов С. А. 1940. Общая гидробиология, М.

12 Зенкевич Л. А. 1922. Fabricia sabella subsp. caspica.— Русский гидробиол. журн., т. I.

13 Изосимов В. В. 1940. Oligochaeta. Руководство по зоологии, ч. II.

14 Карпевич А. Ф. 1946. Потребление корма Pontogammarus maeoticus Каспийского моря. Зоол. журн., т. 25, вып. 6.

15 Кудинова-Пастернак Р. К. 1951. К вопросу о взаимодействии биофильтров с водными массами.— Вопросы географии, сб. 26.

16 Максимова Л. П. 1958. Питание беспозвоночных, вселяемых в Цимлянское водохранилище из лиманов Дона.— Изв. Всесоюзн. научно-исслед. ин-та озерн. и речн. рыбного хоз-ва, т. XI.

17 Побегайло И. П. 1955. Роль донных организмов в процессе самоочищения водоемов, загрязненных сточными водами. Канд. дисс.

18 Резниченко О. Г. 1957. Экология и кормовое значение Pontogammarus maeoticus Азовского моря.— Зоол. журн., т. XXXVI, вып. 9.

19 Романова Н. Н. 1958. Распределение и экологическая характеристика северокаспийских Amphipoda и Cumacea.— Докл. АН СССР, т. 121, № 3.

20 Соколова М. Н. 1958. Питание глубоководных донных беспозвоночных детритоядов.— Труды Ин-та океанологии АН СССР, т. XXVII.

21 Турпаева Е. П. 1948. Питание некоторых донных беспозвоночных Баренцева моря.— Зоол. журн., т. XXVII, № 6.

22 Турпаева Е. П. 1949. Пищевые группировки бентоса и их значение в донных биоценозах Баренцева моря. Канд. дисс.

23 Хусаинова Н. З. 1958. Биологические особенности некоторых массовых донных кормовых беспозвоночных. Изд-во Казахск. Гос. ун-та. Алма-Ата.

24 Чугунов Н. Л. 1923. Опыт количественного исследования продуктивности донной фауны в Северном Каспии и типичных водоемах дельты Волги.— Труды Астрах. ихтиол. лабор., т. V, вып. 1.

25 Яблонская Е. А. 1952. Питание Nereis succinea в Каспийском море.— Труды МОИП, вып. 33.

26 Яблонская Е. А. 1955. Возможные изменения кормовой базы рыб Азовского моря при зарегулировании стока рек.— Труды ВНИРО, т. XXXI, вып. 1.

27 Buley. 1936. Consumption of diatoms and dinoflagallates by the mussel.— Bull. Scripps Inst. Oceanogr., v. 4.

28 Dales P. 1955. The feeding and digestion in terebellid polychaetes.— J. Marine Biol Assoc., v. 34.

29 Dales P. 1957. Preliminary observation on the role of the coelomic cells in food storage and transport in certain polychaetes.— J. Marine Bion. Assoc., v. 1.

30 Forsmann B. 1938. Untersuchungen über die Cumaceen des Skageraks.— Zool. Bidrag. Uppsala, Bd. 18.

31 Fox D. 1936. The habitat and food of the California mussel.— Bull. Scripps Ints. Oceanogr., v. 4.

32 Galtsoff P. 1928. Experimental study of the function of the oyster gills and its bearing on the problems of oyster-culture and sanitary control of the oyster industry.— Biol. Bur. Fish., v. 44.

33 Jordan H. 1913. Vergleichende Physiologie wirbelloser Tiere. Bd 1.

34 Jorgensen a. Goldber. 1953. Particle filtration in some ascoidians and lamellibranchs.— Biol. Bull., v. 105, N 3.

35 Yonge C. 1952. Aspects of life on Muddy shores. Essays in Marine Biology.

36 Loosanoff V. 1949. On the food selectivity of oysters.— Science, 110.

37 Mac Ginitie G. 1939. The method of feeding of Chaetopterus.— Biol. Bull., v. 77.

38 Mac Ginitie G. 1945. The size of the mech openings in mucous feeding nets of marine animals.— Biol. Bull., v. 88.

39 Nicol E. 1931. The feeding mechanism formation of the tube and physiology of digestion in Sabella povonina.— Tranc. Roy. Soc. Edinb., 56.

40 Ponyi E. 1956. Ekölogische, ernährung, biologische und systematische Untersuchungen auf verschiedenen Gammarus — Arten.— Arch. für Hydrobil. Bd 52, H. 3.

41 Segerstrale S. 1940. Zur biologie des Amphipoden Corophium volutator nebst Angaben über die Entwicklung und Rückbildung des Oostegitenborsten bin diesen Art.— Commentat. Biol., v. 11, N 6.

42 Sutton M. 1957. The feeding mechanism functional morphology and histology of the alimentary canal of Terebella lapidaria L. (Polychaeta).— Proc. Zool. Soc., v. 129, N 4. London.

43 Thamdrup H. 1953. Beiträge zur Ökologie der Wattenfauna auf experimentaller Grundlage.— Medd. Kommıs. fören Dansk fiskeri. Ser. Fiskeri, Bd. X, N 2.

44 Zimmer C. 1933. Beobachtungen der lebenden Mysidaceen und Cummaceen. Sitzenber. Ges. Naturforsch., Bd. 1, Leipzig.