Free-living Marine Nematodes as a Component of the Meiobenthos of Chupa Inlet of the White Sea

Introduction

165 In the last decade interest in the study of small benthic organisms (meiobenthos), the size of which does not exceed 0.1 to 3.0 mm, has significantly increased. In the quantitative assessment of macrofauna these organisms are generally overlooked. Peterson and Boysen-Jenson (1911) pioneered the study of benthos on the shores of Denmark. However, early studies were biased toward the fish industry and concentrated on those benthic forms which serve as food for fish. An analysis of test samples was usually conducted by hand right at the site or the test samples washed through sieves with a mesh size larger than 2.0 mm. Smaller organisms consequently eluded detection.

In the 1920's and 1930's almost no work was done on the quantitative distribution of meiofauna. But one should not construe that the study of minute multicellulur organisms was entirely ignored. During the period several taxonomic and morphological works appeared on separate groups, particularly on Nematoda, Harpacticoida, Ostracoda, Turbellaria, and Halacarida. In this context the works of Wieser (1959), Purasjoki (1945), Delamare Deboutteville (1960), Swedmark (1964), and a few others are quite noteworthy. An important contribution (Remane, 1933, 1952), which stimulated further interest in the study of the ecology of small benthic organisms as a whole, discussed the morphological adaptations of different groups of meiofauna to specific conditions of habitat.

The work of Mare (1942) was also a pioneering effort; she was the first to identify meiofauna as an estimable category of the benthos. In the 1950's and 1960's a significant number of reports on the quantitative distribution of meiobenthos and groups of organisms constituting it in littoral and deeper waters appeared in other countries. McIntyre (1969) has given quite a comprehensive list of these works in his review.

A study of the meiobenthos is of both theoretical and practical value. Large populations of organisms of meiobenthos in the superficial layers of the ground play an important role in the balance of organic substances in bottom sediments (Rauzer-Chernousova, 1935). Participating in the mineralization of the organic substances of bottom deposits, meiofauna contribute greatly to the formation of the biological regime of the sea.

166 Meiobenthic organisms represent an "intermediate" link between

micro- and macrobenthos, accumulating and processing minute food particles, the direct utilization of which by macroforms would otherwise be wasted in the trophic structure (Kiseleva, 1965). As observed by Gilyarov (1944), extremely minute food does not justify the consumption of energy spent on its ingestion. Organisms of meiobenthos available in the surface layer of the ground (1.0 to 2.0 cm) (Mare, 1942; Brotskaya, 1951) become a source of nutrition for predatory forms of macrobenthos (Rees, 1940). Information is available on the direct utilization of meiofauna (Nematoda and Harpacticoida) by the young of fishes (Mironova, 1951; Perkins, 1958; Milovidova, 1961). As evaluation of the trophic role of meiofauna in the ecosystem has been based on little information, assessment of their energetics is much more difficult. According to different authors, 3.0 to 30.0% of the amount of oxygen required by the entire community is consumed by meiobenthos (Wieser and Kanwisher, 1961; Teal and Wieser, 1966; McIntyre, 1969). The species composition of individual groups of meiobenthos is an important aspect in a study of meiofauna. In spite of the fact that a large number of works on individual groups of meiobenthos have been published, such organisms as Nematoda, Copepoda, Ostracoda, and a number of others are still not fully understood.

Existing works touch mainly on the distribution of meiobenthos in very large areas; this, in my opinion, interferes with the explanation of the general phenomena of distribution of organisms. It may be more pertinent to commence work on the study of meiobenthos as a pilot project in more restricted areas. A study of meiofauna is further complicated by the necessity for combining field and research station investigations. Such investigations are best conducted where there is a biological station. Guided by these considerations, the place selected for the present analysis was the Biological Station of the Institute of Zoology, Academy of Sciences, USSR, on the coast of the White Sea. It is extremely difficult to conduct thorough studies in the sublittoral zone; for this reason I worked in the littoral zone in small areas and collected frequent samples with respect to time and place.

During the course of my work I had to decide on the volume and number of representative samples to be taken from a small area which would later determine the frequency of collection of samples in a pilot study of the littoral zone.

Variation in methods usually adopted for the collection and processing of samples of meiobenthos, also makes a comparison of quantitative data from different regions of the world oceans difficult. One problem during the course of my studies was to make the method of processing of meiobenthos samples more precise. This process is extremely laborious. Improving methods of collection of sediment samples facilitates processing a larger quantity in a comparatively shorter period of time.

Meiobenthos should not be considered an accidental grouping of organisms taken together on the basis of their size or methodological peculiarities of their study. Meiobenthos constitute a complex of specific organisms adapted to conditions of living in capillary spaces between sediment particles. First of all, the general collective character of meiobenthos and the group of organisms entering into their composition is of great interest because one must know the limits of population dynamics of the biotope under study, in order to assess the role of meiofauna in the ecosystem.

It is also very important to know the character of distribution of meiofauna in the littoral zone and its seasonal variations. It may be assumed that organisms of the meiobenthos are uniformly distributed in the entire littoral zone or, contrarily, that their distribution is patchy.

167 As already mentioned, the dominant group of meiobenthos usually comprises free-living marine nematodes and harpacticoids. Chislenko (1961, 1965, 1967) has published a number of works on harpacticoids of the coastal region of the White Sea, in which the species composition and quantitative distribution of this group of organisms have been detailed. The nematode fauna of the White Sea contrarily has hardly been touched; only two works exist—Filip'ev (1927) and Frolov (1972). In the former a few new species of nematodes from the isthmus (narrow part) of the White Sea have been described, and in the latter publication a list of nematodes from the sandy littoral zone is presented. Taking into account these facts, it is very important to analyze the species composition of this dominant group of meiobenthos. Moreover, it is interesting to postulate the natural phenomena governing the distribution of these organisms in the littoral zone, and to analyze the seasonal dynamics of their population and biomass.

Meiofauna of the littoral zone is of special interest because it has adapted to life in a zone periodically exposed to low and high tides, having an unstable regime with respect to temperature, salinity, availability of food, and other factors. As such, it is important to determine how some of these factors influence the population dynamics of meiofauna (on the basis of some dominant species of nematodes).

It appears possible to determine zoogeographic zones on the basis of the effect of temperature on the speed of multiplication of individual species of nematodes in different seasons. The problem of the zoogeographic origin and distribution of free-living marine nematodes is very complex. Some authors consider these free-living marine nematodes cosmopolitan (Steiner, 1916a; Kreis, 1934; Allgen, 1954). Others assume that such a wide distribution of nematodes is the result of inaccurate identification in a number of cases (Platonova, 1967). In practice, it often turns out that the wide area attributed to one species is occupied by two or three species. At present, it is difficult to give the zoogeographic characters of free-living marine nematodes due to insufficiency of studies. However, guided by their adaptation to particular temperatures and the temperature limits of their multiplication, some inferences can be drawn about their zonal associations. As the entire area of my investigations is situated in the region of distribution of species belonging to the north Atlantic Ocean and the Atlantic sector of the polar basin, zonal association determined to a significant degree the zoogeographic characters.

It is very interesting to analyze the extent of influence of such factors as granulometric composition of sediments, presence and distribution of food material, and salinity on population dynamics and the nature of distribution of marine nematodes. In this work I do not attempt to comprehend the impact of all such factors on meiofauna and have only selected those which visibly influence its development.

Collection of material was carried out from different localities with similar physico-chemical conditions, oxygen regime, etc. during the period of investigation. Oxygen content obviously does not remain constant during a prolonged period of time, but taking into account the fact that studies were done in the littoral zone, it can be assumed that it would always be sufficiently high and not a factor limiting the distribution of these organisms in the littoral zone during the summer and autumn seasons.

This work was accomplished through the constant friendly help, support, and care of my research supervisor, Tatyana Alekseevna Platonova. A.A. Strelkov assisted extensively in editing the manuscript. Comments given by A.N. Golikov and Ya.I. Starobogatovyi on various occasions were extremely helpful in the preparation of this article. Lastly, 168 this work could not have been completed without the organizational support of V.K. Khlebovich, Director of the White Sea Biological Station, ZIN, Academy of Sciences, USSR.

PHYSICAL AND GEOGRAPHIC CHARACTERS OF THE REGION UNDER STUDY

The White Sea is a water mass in which features of the Arctic and boreal basin are combined, as evidenced in the temperature regime and composition of its fauna and flora (Gur'yanova, 1949). In summer the surface layer of the water heats up to 10°C and above, but in shallow waters and closed inlets may be as high as 23°C; in winter intense freezing continues for 7.0 to 8.5 months (Gur'yanova, 1949; Chernovskaya, 1956). Thus, if during winter conditions in shallow waters are arctic, they approach boreal conditions during summer. Sharp seasonal changes in temperature occur as the result of the geographic position and topography of the White Sea; it is situated almost completely to the south of the polar circle in the temperate belt. This determines the boreal character of littoral and deeper waters. At the same time the distance of the sea in the east from the effect of the warm North Cape current leads to more severe conditions in the winter regime compared to the Barents Sea, which is outside the polar circle. Gur'yanova (1949) divided the White Sea into seven regions. My studies were conducted in the second one, i.e., shallow waters of the western half of the sea, from Cape Tur in the west up to Kandalaksha, south coast of Kandalaksha Bay, Karelian coast up to Onega Bay, Salovetskii Islands, and the Letnii coast up to Unskaya inlets. The coastal line of this zone is very cut up by shallow inlets and bays, high granite banks which protect them from turbulence, and breakers. Shallow calm waters of the coastal lagoons warm up to the very bottom.

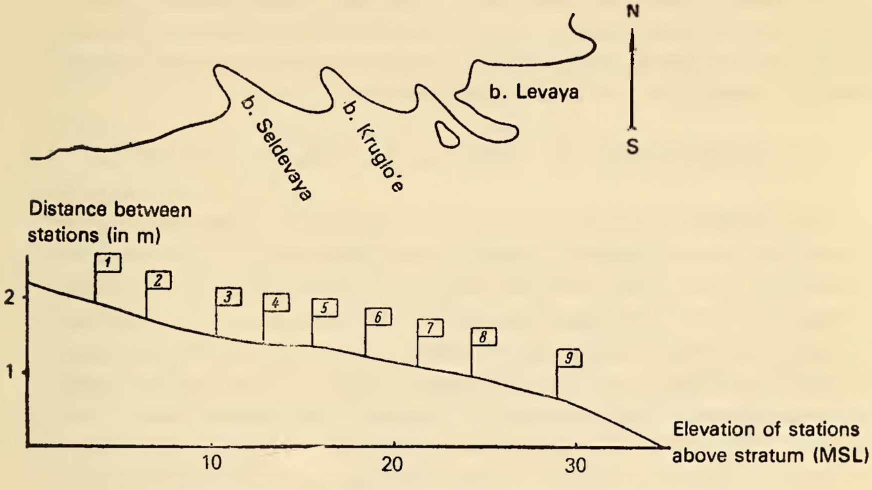

Figure 1. Diagrammatic depiction of stations in the littoral zone of Kruglo'e Bay.

The littoral zone of Kruglo'e Bay, which is a part of the inlets of Chupa Kandalaksha Gulf of the White Sea, was selected for my studies. The littoral zone of Kruglo'e Bay is a small stony-sandy beach 25 m × 35 m.

The upper part of the littoral zone is more stony than the lower. Among macrofauna only periwinkles are seen here during summer. As
169 observed by Gur'yanova (1949), the upper horizon of the littoral zone of the White Sea is a "dead zone" because hummocked ice on the banks

adversely affects the entire macrofauna. The middle horizon is situated within the limits of fluctuations of the sea level, i.e., throughout the course of a month in syzygy as well as in quadrature it is daily flooded with water which dries up every day. Here on separate boulders clumps of fuci with colonies of mytilus are seen. Almost all the stones are seeded with cirripedian barnacles.

The lower horizon of the littoral, in contrast to the first two, is exposed for only a short time. Almost the entire horizon is covered with dense fuci.

Control points (areas) taken for study were selected in such a way as to cover all the conditions of living of meiofauna in all the horizons of the littoral zone. For this purpose a number of stations were established along the maximum length of the beach ranging from supralittoral to sublittoral. In each horizon there were not less than three stations. The selected stations were situated at different levels from zero depth and the distance between them did not exceed two to three meters (Figure 1).

To study the seasonal dynamics of population and biomass of meiofauna and their dependence on some factors of the surrounding medium, collection of material at the stations was done during the course of two seasons, namely, summer of 1970 and autumn of 1971.

TERMINOLOGY, MATERIAL, AND METHODOLOGY

Terminology. Mare (1942) introduced the term meiobenthos from the Greek word *meiŏn* meaning "lesser". As a criterion of size, she used the size of the gauze sieve through which the test samples were washed. According to Mare all organisms passing through a sieve with a mesh of 1.0 mm × 1.0 mm but retained in a sieve with a mesh 0.1 mm × 0.1 mm belong to meiobenthos. All protozoans, except for Foraminifera, which pass through a sieve with a mesh of 0.1 mm × 0.1 mm, come under microbenthos, whereas all those organisms retained in a sieve with a mesh of 1.0 mm × 1.0 mm are classed as macrobenthos. Such a categorization of benthos on the basis of size has been done purely from a practical point of view, as each category of benthos requires a special method of collection and separation of organisms from the ground. In this way meiofauna defined on the basis of sieve size is a purely statistical quantum related more or less to an arbitrarily selected part of the general size spectrum of the organisms. It includes not only species which remain within the limits of the given category during the course of their life cycle, but also sexually immature individuals of macrobenthos.

Bougis (1950) distinguishes permanent and temporary components within the limits of meiofauna. Permanent elements are those organisms which during the course of their life cycle belong to meiobenthos. These include such groups as ostracods, kynorhynths, water mites, nematodes, harpacticoids, and others. Most of the species of these groups pass through a sieve with a 1.0 mm mesh; hence it is better to regard permanent meiofauna not as a statistical but as a taxonomic category. This group of small multicellular organisms according to measurements, number and time of multiplication, and adaptation, may be considered separate from larger components of the benthos. Temporary elements comprise many representatives of macrofauna with benthic juvenile stages and hence could be related to meiobenthos in the earlier stages of their development.

Chislenko (1961) proposed the term eumeiobenthos (eumesobenthos) for the first category and pseudomeiobenthos (pseudomesobenthos) for the second. These two terms reflect the taxonomic composition and not the temporary or permanent nature of meiobenthos.

170 Sometimes the terms microbenthos, microfauna (Remane, 1933; Arnol'di, 1940; Brotskaya, 1951), and mesobenthos (Chislenko, 1961; Gurvich, 1967; Dekhtyar, 1969) are wrongly used to express the idea of meiobenthos. It seems to me extremely appropriate to use the terminology adopted at the First International Conference on Meiofauna, held at Tunisia in 1969 (Hulings, 1971). The basis of this terminology is the classification of benthos proposed by Mare (1942).

Using universally accepted international terminology avoids vagueness in defining meiofauna.

Material and Methodology. At present three types of equipment are used for the collection of meiofauna: a tubular device, bottom grab, and dredge. The choice of equipment depends on the zone of the sea under investigation (littoral, sublittoral, or deep waters). Collection of material from the littoral zone is generally effected with tubular devices operated manually. Many researchers use a simple metallic or plastic tube, which is cored into the bottom and then withdrawn, pruning the basic column of the bottom (Tseeb, 1937; Brotskaya, 1951; Jansson, 1967b; Dzyuban, 1968; Dekhtyar, 1969; Frolov, 1971).

Collection of samples from silted sediments poses a special problem. A number of authors have described tubular devices designed for this purpose (Moore and Neill, 1930; Krogh and Spärck, 1936; Mare, 1942). Similar devices are utilized for the collection of meiofauna at shallow depths, as most of the components of the meiofauna reside in the upper few centimeters of the bed (Smidt, 1951; Muus, 1964). A similar but slightly modified appartus for the collection of meiofauna from sandy sediments has been described by Willimoës (1964), Craib (1965) and Fenchel (1967).

Larger types of collecting devices—bottom grabs (Purasjoki, 1945; Kiseleva, 1965; Thiel, 1966; Stripp, 1969)—are mostly used at greater depths. These are the least satisfactory because they stir the substratum and, while hauling, the organisms are apt to be washed away. These deficiencies are partially removed if the bottom grabs are provided with bags made of fine gauze (Smith and McIntyre, 1954), Dredges for the collection of meiofauna are quite limited (Foster, 1953; Sanders, Hessler and Hampson, 1965).

For maximum value, the sample should contain a sufficient quantity of fauna—from the largest form to the smallest—so that it is possible to define the density of meiofauna more precisely. According to Gray (1971) the most rational device for the collection of meiobenthos on sandy ground is a tube 37 mm in diameter.

I used a tube with a diameter of 50 mm, height of 25 mm, with a lid of standard ground glass for the collection of meiobenthos. As 90 to 95% of the meiofauna in spring, summer, and autumn are found in the upper layer of sediment (1.0 to 2.0 cm) (Brotskaya, 1951; Stripp, 1969), core samples of the sediment included complete meiofauna of the littoral area under study. In samples of the volume mentioned 300 to 4,000 specimens were usually present, which were quite enough to characterize the density of meiobenthos at a point of investigation. As for Gray's statement that the most rational diameter of the tube is 37 mm, it is necessary to establish empirically the minimum volume of a sample which will characterize the population of meiobenthos in each specific region of study and in each biotype.

The second important aspect of meiobenthos collection is frequency of sampling from a definite area. To elucidate this problem three areas
171 one square meter each were selected and five random samples taken. In samples of the upper horizon of the littoral zone the total number of specimens (nematodes and other organisms combined) was 230, 605, 234, 314, and 323 per sample. On the basis of this data, I hypothesized that in 75% of the samples drawn from an area one square meter primarily organisms of one type would prevail, i.e., 200 to 300 specimens per sample.* This hypothesis was verified on the basis of results of selective investigations by way of calculating the degree of reliability in the difference between empirical and theoretical parts (t_{p-P}) according to the formula $t_{p-P}=p-P\sqrt{\frac{PQ}{n}}$ (Plokhinskii, 1970): where $p-P$ = difference between selected parts. The reliability coefficient of the difference (t_{p-P}) in this case is equal to 0.3 with the degree of freedom (v) equal to 4 ($v=n-1$), and the standard value of Student's test (t_{st}) is equal to 2.8 to 4.6 to 8.6, i.e., $t_{p-P}<t_{st}$, which means that the difference between the general and the selected parts is insignificant. In other words, in 75% of

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*Meaning not clear in Russian original—General Editor.

a small number of samples collected from an area one square meter a correct picture of the meiofauna population is obtained.

In the middle horizon of the littoral zone 1,305, 497, 1,391, 1,253 and 1,010 organisms were collected in each sample. Taking for granted the hypothesis advanced in the first case and calculating the criterion of reliability, the difference between the general (combined) and the selected lots was t_{p-P} equals 0.8 and $t_{p-P} < t_{st}$, i.e., that in this case one to two samples from one square meter with a probability of 0.75 reflect the size of the organism population in the selected area.*

In the lower horizon of the littoral zone 741, 539, 653, 628 and 765 specimens were recorded in each probe. The coefficient of reliability in the difference between the general and the selected lots, as in the first case, was equal to 0.3 and less than the standard value for Student's test.

Hence one to two probes from one square meter will give the real population of meiofauna at a given spot in the littoral zone with 75% accuracy.

Core samples were washed in the laboratory through a fine mesh (No. 68) three to four times in order to separate finer fractions of the substratum.

For further processing of the samples of meiobenthos in the laboratory several methods were followed: 1. "Plankton" method (Dzyuban, 1968) in which the sample is taken in a beaker, diluted with water, stirred, and then withdrawn by means of a 5-ml pipette provided with a bulb. The sample so processed is examined in 15 to 20 portions. The main drawback of this method is the difference in sedimentation rate of various groups of meiobenthos, as a result of which organisms with a small specific gravity usually enter the pipette in larger numbers, which may lead to a wrong interpretation of the ratio of groups of meiobenthos in the sample.

2. Organisms can also be separated from the sample by the flotation method. Sugar (Fast, 1970) or salt (Monakov and Mordukhai-Boltovskii, 1959) can be used to make a flotation solution. But this method too has limitations as it is possible to separate only individual groups. For example, in a flotation solution of sugar oligochaetes and mollusks can be separated from the sample, but it is absolutely impossible to isolate nematodes. A salt solution is useful for the separation of copepods and water mites, but unsuitable for ostracods, oligochaetes, and nematodes.

3. Screening the entire sample or some part in the chamber of Bogorova under binoculars is a third method of processing. To expedite analysis of the sample it should be stained. I used Rose Bengal for staining samples, which method more or less coincides with the staining

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*Meaning not clear in Russian original—General Editor.

technique of Thiel (1966). The preparation is simple: to 100 ml water add 0.5 ml concentrated solution of Rose Bengal and 2.0 to 3.0 ml concentrated solution of phenol. The stain persists for three to four hours. With such a preparation all groups of meiobenthos are stained, which helps in
172 distinguishing them from soil particles at the time of screening.

If the sample is rich in meiofauna, it is advisable to examine only a part of the sample at one time and not the whole. To divide the sample into ten approximately similar parts, Chislenko devised an apparatus (Figure 2) which consists of a container and a divider. The divider has ten sections or compartments almost equal in area (from 8.15 to 11.28 cm²). It is technically quite difficult to prepare a divider in which all the walls or septa of the divider and the container ideally approximate each other, and for this reason the problem of the parametrical data of the divider was examined.

For this purpose a series of counts were done. To simplify, each series of counts were done with one and the same sample. The sample was introduced in the container, stirred, the divider then lowered to the bottom, and the sample allowed to settle. After settling organisms were sorted from each compartment by means of a pipette and counted under binoculars in the chamber of Bogorova.

I was interested in the following aspects: 1) distribution of organisms

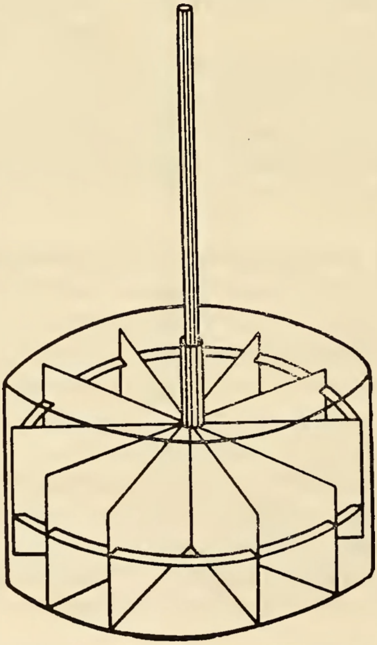

Figure 2. Divider equipment of L.L. Chislenko.

1.0 to 2.0 mm long, i.e., those which could not pass through the chinks between the septa (walls) of the divider and the container; 2) influence of the manner of selection of organisms on the ultimate results; and 3) distribution of organisms below 1.0 mm in each section.

Copepods, crustaceans of genus *Calanus* (1.0 to 2.0 mm), exemplified large organisms, 2,500 specimens of which were present in the sample (Gal'tsova, 1971). The least number of organisms (159) fell into the compartment with an area of 8.87 cm^2 and the greatest number (302) fell into the compartment with an area of 10.55 cm^2. Relative variations in the number of *Calanus* within the limits of each compartment ranged from 1.25 to 2.00, and in the whole series 1.49 on the average.

As the areas of all the compartments differ slightly from each other, the question arose as to what relation exists between the area of the compartment and the number of organisms in it. With this in mind, I calculated σ_1 and σ_2—mean square deviation of the number of organisms in each compartment and of the area, along with r—the correlation coefficient expressing the relation between the area of the compartment and the number of organisms falling into a given compartment. These values for the first series of counts were $\sigma_1 = 36.0$, $\sigma_2 = 0.71$ and $r = 0.603$. For a level of 0.05 no relation between number of organisms in a compartment and area of compartment was found.

On the whole the relative variation in copepod number in the compartments of the divider did not exceed 1.5. In other words, if counting of large organisms is done in only two or three compartments of the divider and, on the basis of this, the number in the whole sample determined, then the probable figure will differ from the actual maximum by 1.5 times.

Hence the predicted number of organisms in the sample will differ insignificantly from the actual one. Time spent on processing the sample is significantly shortened. The limit of absolute number of organisms for 173 which such error is insignificant is calculated on the basis of a hundred individuals.

The second aspect—parameters of the divider—depicts the influence of the order of selection of organisms from the compartments on the end results. Samples were drawn, containing about 2,000 copepods, from alternate compartments. The first samplings were taken from compartments 1, 3, 5, 7, and 9 and the second series from 2, 4, 6, 8, and 10. The minimum number of copepods was recorded in compartments with an area of 9.12 cm^2 (165) and the maximum in compartments with an area of 10.09 cm^2 (248). Relative variations in number of copepods ranged from 1.19 to 1.70, equal to 1.40 on the average for the counts of these series. Squares of standard deviation of specimen number for the first and second series of collection were: $\sigma_1 = 22.4$, $\sigma_2 = 25.6$. The correlation coefficient (r), expressing the relation of order of selection to number of organisms in compartments, was 0.137. At a level of 0.05 significance no relation between these two features was found.

In an ideal case 10% of the total number of organisms contained in a sample must fall in each compartment. Practically, less than 10% fall in some compartments and more than 10% in others, yet almost the same results are obtained in the sum total as anticipated for an ideal case. It follows that the order of separating organisms from the sectors does not affect the results obtained (coefficient of correlation confirms the same). Organisms may be sorted from two or three compartments successively or selectively form different places in the divider, and the error will not exceed 1.4 to 1.5 in either case.

Larvae of copepods (Nauplii) (average size of individual 0.2 mm) served as a model for smaller organisms. Organisms were selectively drawn from five sectors. The least number of larvae was recorded for a compartment with an area of 8.15 cm^2 (185) and the maximum number in a compartment with an area of 10.09 cm (290). Relative variations in the compartments constituted 1.32 to 1.66 and for this series on the average 1.52. When the results obtained were compared with the two preceding series, the quantities were of the same order (1.4 to 1.5).

Standard deviations and correlation coefficient for the third series were: $\sigma_1=34.1$, $\sigma_2=0.81$, and $r=0.633$. As in the first series, the correlation coefficient revealed an absence of relation between the area of the compartment and the number of organisms falling into it. Hence small differences in the areas of the compartments of the divider may be disregarded, and the distribution of organisms taken as equal for all compartments.

To ensure a more uniform distribution of samples in this device, a subsidiary divider with smaller diameter of septa than in the main one may be added, but the plates of this divider must be cut like teeth in a comb.

The method of processing samples of meiobenthos in this case is as follows: the sample is placed in the container, diluted with water up to the mark, mixed with the supplementary divider, which is then quickly withdrawn and the main divider with septa reaching up to the container walls substituted. The sample is allowed to settle for a period of 10 to 15 minutes. Subsequently the contents of two or three compartments are drawn out and examined in the Bogorov chamber and differential counts according to groups carried out. The number of organisms in the whole sample is determined on the basis of these sortings. For organisms fewer in number in the sample, it is advisable to examine the sediments of the sample.

In this way the Chislenko divider may be recommended for processing

sample in the Bogorov chamber. It expedites counts of organisms of meiobenthos. In using the Chislenko divider the error in number of organisms does not exceed 1.4 to 1.5 times; the lower limit of the absolute number of organisms for which such an error is inconsequential is measured in hundreds of individuals. The distribution of organisms in
174 the compartments of the divider may be considered equal irrespective of minor differences in the area of individual compartments. The order of selection of organisms from compartments of the divider exerts almost no influence on the ultimate result. In order to obtain more precise information, a supplementary divider may be used for agitating the sample.

The average weight of a single individual in each group had to be established in order to determine the biomass. For this purpose 50 to 100 specimens of each group were measured, the average length of each individual determined, and the average weight calculated according to nomograms (Chislenko, 1968). The young of mollusks (50 to 100 specimens) were weighed directly and the average individual weight then determined. The average weights derived for various groups were as follows:

Group	Length, mm	Weight 10^{-2} (mg)
Foraminifera	0.5	1.300
Nematoda	1.1	0.014
Polychaeta	1.5	5.100
Oligochaeta	1.0	1.100
Harpacticoida	0.5	0.800
Ostracoda	0.5	0.650
Isopoda	1.3	2.500
Nauplii	0.2	0.063
Tardigrada	0.3	0.065
Halacarida	0.8	6.800
Bivalvia	1.4	40.000
Gastropoda	1.2	63.000

My data correspond very well with the scanty data available in literature on the average weight of representatives of meiofauna. For example, Stripp (1969) gives the weight of nematodes as 0.03×10^{-2} mg and that of harpacticoids 0.8×10^{-2}.

In calculating biomass the number of specimens was multiplied by the average weight of a given group of organisms in the meiofauna.

As mentioned earlier, material for the present work was collected during the course of two seasons at one and the same control points (summer of 1970 and autumn of 1971). In all, 114 samples were collected, processed, and fixed in 4.0% formalin. Together with collection of material, temperature and salinity of water in the littoral zone (see pp.

331, 348) were also measured by methods usually followed in studies of hydrobiology (Bruevich and Demenchenok, 1944; Voronkov 1953). Control samples for an analysis of granulometric composition of the bottom were collected from stations at which meiofauna was being studied. Analysis of the granulometric composition was undertaken by the central laboratory of SZGU (Table 1). To compare the results composite curves were drawn (Figure 3). On the abscissa log measurements of sediment granules are given (in mm) and on the ordinate the percentage content of one or the other fraction. To interpret the data of granulometric analysis served granulometric coefficients were calculated, namely, the average
175 (median) size of the granules and the coefficients of sorting and asymmetry (Table 2). To calculate the coefficients quadrants were first made: hori-

Table 1. Granulometric composition of the substratum (*d* in mm) in the littoral stations of Kruglo'e Bay (in %)

Height of stations over 0-depth (m)	>10 mm	10–5 mm	5–2 mm	2–1 mm	1–0.5 mm	0.5–0.25 mm	0.25–0.1 mm	0.1–0.01 mm	<0.01 mm
1.95	2.1	10.5	10.2	4.7	16.3	31.0	22.0	2.6	0 6
1.78	10.7	14.5	10.7	3.3	3.6	9.7	39.0	6.9	1.6
1.55	—	5.0	9.9	4.3	7.0	14.1	42.2	13.5	4.0
1.44	—	3.8	11.9	7.2	12.5	21.2	33.7	7.6	2.1
1.41	—	20.5	21.9	7.2	12.1	17.3	15.6	3.9	1.5
1.37	19.1	14.1	19.1	5.4	11.6	14.6	12.4	2.3	1.4
1.25	—	5.0	8.8	5.4	11.0	15.6	36.4	14.1	3.7
1.15	—	6.1	6.5	4.0	14.3	37.8	27.6	3.1	0.6
0.99	—	1.0	5.7	7.2	22.4	24.2	29.8	8.4	1.3

176 **Table 2. Granulometric coefficients for samples collected September 9, 1977 from the littoral zone of Kruglo'e Bay at different heights over 0-depth**

Height in m (station No.)	Q_3	Q_1	S_o	M_d	S_k
1.95 (1)	2.09	0.31	2.6	0.64	1.56
1.78 (2)	5.37	0.22	4.9	0.40	7.37
1.55 (3)	0.79	0.18	2.1	0.29	1.65
1.44 (4)	1.52	0.23	2.8	0.50	1.36
1.41 (5)	7.50	0.44	4.1	1.32	1.89
1.37 (6)	8.71	0.62	3.8	2.27	1.04
1.25 (7)	0.79	0.21	1.9	0.37	1.16
1.15 (8)	0.79	0.31	1.6	0.52	0.88
0.99 (9)	0.79	0.25	1.8	0.51	0.72

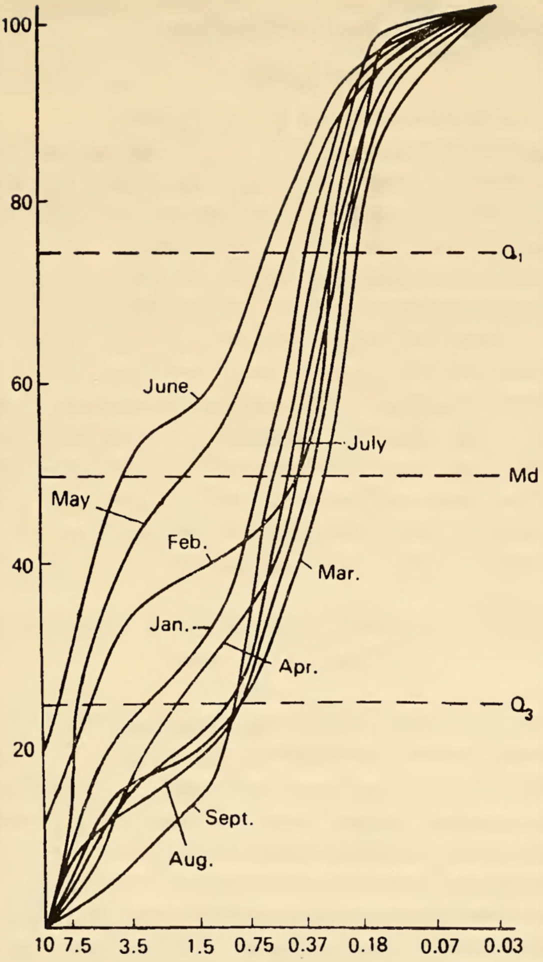

Figure 3. Granulometric composition of substratum samples collected from Kruglo'e Bay September 17, 1971.

Abscissa—grain size of substratum (*d* in mm); Ordinate—percentage content of fractions.

zontal lines were drawn on graph paper from the points on the axis of the ordinate correponding to 25, 50 and 75%. The abscissa of the points of intersection of the horizontal and cumulative curve provided the initial data for calculating granulometric coefficients (Rukhin, 1953). The two extreme numbers represent quadrants and the middle number the median. The coefficient of sorting was determined according to the formula—

$$S_0 = \sqrt{Q_3/Q_1}$$

where Q_1 and Q_3 are the first and third quadrants. Coefficients of asymmetry were calculated according to the formula—

$$S_k = Q_1 Q_3 / Md^2$$

where Md is the median and Q_1 and Q_3 the quadrants.

Medium sand with an average size of 300 to 600 μm predominated in almost all the stations investigated. Large sand granules, average diameter 1,000 to 2,000 μm, predominated only at two stations (5 and 6) situated in the middle horizons of the littoral zone.

All nine cumulations were represented by extremely steep curves, bespeaking the homogeneity of the ground. Coefficients of sortings confirmed this. According to Trask (Trask et al., 1932), if S_0 is <2.5, the sand is well sorted, if S_0 is 2.5 to 4.5 moderately well sorted, and if S_0 is >4.5, poorly sorted. Sediment at the selected section is well or moderately sorted sand if S_k (coefficient of asymmetry) shows the position of the maximum ordinate (mode) in relation to average diameter (median), i.e., asymmetry of distribution of granules in relation to median. If S_k is more than 1.0, then finer fractions predominate in the sediment, i.e., the mode is situated in this case in the finely granular part of the spectrum.

QUANTITATIVE CHARACTERS OF THE MEIOBENTHOS OF KRUGLO'E BAY

In the last 10 to 15 years rather numerous studies have appeared on the population and biomass of small benthic organisms. Yet little infor-
176 mation is available on the systematics and populations of different groups of meiobenthos. Attempts to carry out a collateral analysis of meiofauna while investigating macrobenthos have not been successful. A need thus arose to undertake specialized studies of minute benthic organisms, not exceeding 2.0 to 3.0 mm in size. Such studies usually consisted of a "once only" collection of samples from an area, or larger areas were subjected to study from which an extremely insignificant number of samples were taken (Krogh and Spärck, 1935; Mare, 1942; Bougis, 1946; Purasjoki, 1945; Brotskaya, 1951; Wieser, 1960; Chislenko, 1961; Wieser and Kanwisher, 1961; Kiseleva, 1965; Muus, 1967; Tietjen, 1969, 1971; Belogurov and Koroleva, 1970; Belogurova, 1970; Gray and Rieger, 1971; Thiel, 1971; Gal'tsova, 1971a).

If one takes into account that the methods of collection and processing adopted in every concrete case differ, then it is not difficult to predict that the data on population of meiobenthos as a whole and its different groups are highly heterogeneous. For the sandy littoral zone of the Baltic Sea for example, 5,000 specimens/m^2 (Purasjoki, 1945), 376,000 specimens/m^2 (Fenchel and Jansson, 1966), and 968,000 specimens/m^2 (Muus,

1967) have been recorded. With respect to density of an individual group (for example, marine nematodes), 2,000 (Purasjoki, 1945), 789,000 (Bregnballe, 1961), and 658,000 (Muus, 1967) specimens/m^2 have been recorded.

Subsequent stages of study attempted to investigate the population dynamics of meiobenthos and its different groups with respect to seasons and for the whole year (Smidt, 1951; McIntyre, 1964; Hopper and Meyers, 1966; Yeates, 1968; Tietjen, 1969; Schmidt, 1969; Stripp, 1969; Coull, 1970; Warwick and Buchanan, 1971; Skoolmun and Gerlach, 1971; Frolov, 1971; Harris, 1972). For the coast of the North Sea various authors have given different data on the population of meiofauna as a whole during the course of one year: Schmidt (1968–1969) indicates that the limits of fluctuation in density of meiofauna range from 131,000 to 375,000 specimens/m^2, while Stripp (1969) gives the figures 500,000 to 1,000,000 specimens/m^2. McIntyre (1964) indicates that the average population of meiobenthos during the course of one year is 1,959,000 specimens/m^2.

It follows from these examples that a "once only" collection of material cannot reflect the picture of distribution of organisms of meiofauna with sufficient accuracy because such samples were usually collected from points separated by rather long distances. With regard to seasonal and year-round observations (even when sample collecting was done from strictly defined points), sampling was not done often enough—only once in one or two months (Skoolmun and Gerlach, 1971; Warwick and Buchanan, 1971; and others). Such minimal sampling, in my opinion, cannot yield an objective assessment of the population dynamics of meiobenthos and its different groups. Taking all this into account I decided to initiate a study of meiofauna of the White Sea in just a small
177 section of the littoral zone. Distances between stations did not exceed two to three meters and samples were collected from them not less than once in seven to ten days. Work continued in the same area for two years and was conducted in different seasons. In 1970 the population dynamics and biomass of meiobenthos were assessed during the spring-summer season and in 1971 during the summer-autumn season.

Spring-Summer Season of 1970 (Table 3)

The following groups of meiobenthos were found in the littoral zone of Kruglo'e Bay in the spring-summer season of 1970: eumeiobenthos (Foraminifera, Nematoda, Harpacticoida, Halacarida, and Turbellaria), pseudomeiobenthos (Oligochaeta, Polychaeta, and the young of mollusks Bivalvia and Gastropoda). The population of the entire meiofauna ranged from 70,600 to 2,606,640 specimens/m^2. When the distribution of orga-

178–184 **Table 3. Population (N, specimens/m²) and biomass (B, mg/m²) of meiobenthos of Kruglo'e Bay during the summer of 1970 at different heights of stations over 0-depth**

Group		1.95 m	1.78 m	1.55 m	1.44 m	1.41 m	1.37 m	1.25 m	1.15 m	0.99 m
1		2	3	4	5	6	7	8	9	10
July 7th										
Foraminifera	N	—	2,540	—	2,540	—	10,160	2,540	—	15,240
	B	—	33.02	—	33.02	—	132.08	33.02	—	198.12
Nematoda	N	111,760	142,748	59,436	687,324	482,640	1,117,600	424,180	411,480	1,097,280
	B	15.66	20.02	8.32	96.32	67.56	156.46	59.39	57.61	153.62
Harpacticoida	N	21,500	40,700	8,630	561,000	81,280	635,000	66,040	43,180	121,920
	B	172.00	325.60	69.04	4,488.00	650.24	5,080.00	528.32	345.44	975.36
Ostracoda	N	—	1,016	—	5,080	2,540	55,880	48,260	—	25,400
	B	—	6.60	—	33.02	16.51	363.22	313.69	—	165.10
Halacarida	N	—	4,070	—	10,160	5,080	10,160	10,160	—	5,080
	B	—	276.76	—	690.88	345.44	690.88	690.88	—	345.44
Turbellaria	N	—	—	—	—	—	—	17,780	—	15,240
	B	—	—	—	—	—	—	711,20	—	609.60
Eumeiobenthos	N	133,400	197,074	66,066	1,266,104	571,540	1,828,800	568,980	454,660	1,280,160
	B	187.66	662.00	77.36	5,341.24	1,079.75	6,422.64	2,336.50	403.05	2,447.34
Oligochaeta	N	10,900	6,600	1,520	10,160	12,240	30,480	2,540	12,700	15,240
	B	119.90	72.60	16.72	111.76	134.64	335.28	27.94	139.70	167.64
Bivalvia	N	5,080	—	—	10,160	—	20,320	5,080	22,860	35,500
	B	2,032.00	—	—	4,064.00	—	8,128.00	2,032.00	9,144.00	14,224.00
Gastropoda	N	—	4,070	1,016	5,080	7,620	—	20,320	5,080	40,640
	B	—	2,564.10	640.08	3,200.40	4,800.60	—	12,801.60	3,200.40	25,603.20

Pseudomeio-benthos	N	15,980	10,640	2,530	25,400	22,860	40,800	27,940	40,640	91,440
	B	2,151.90	2,636.70	656.80	7,376.16	4,935.24	8,463.28	14,861.54	12,887.15	39,994.84
Meiobenthos (total)	N	149,240	201,744	70,602	1,291,504	594,400	1,879,600	596,900	495,300	1,371,600
	B	2,339.56	3,298.70	734.16	12,717.40	6,014.99	14,885.92	17,198.04	13,290.20	42,442.08
July 16th										
Foraminifera	N	—	20,770	—	10,160	10,160	35,560	15,240	15,240	2,540
	B	—	270.01	—	132.08	132.08	462.28	198.12	198.12	33.02
Nematoda	N	396,240	751,840	736,600	1,183,640	985,520	1,188,720	1,371,600	187,960	469,900
	B	55.44	105.26	103.13	165.62	137.97	166.42	192.02	26.31	45.52
Harpacticoida	N	52,400	290,000	154,900	487,000	436,880	411,480	426,720	154,940	93,980
	B	419.20	2,320.00	1,239.20	3,896.00	3,495.04	3,291.84	3,413.76	1,239.52	751.84
Ostracoda	N	—	—	—	—	5,080	10,160	—	7,620	2,540
	B	—	—	—	—	33.02	66.04	—	49.53	16.51
Helacarida	N	1,520	10,160	20,340	—	5,080	—	—	—	—
	B	103.36	690.88	1,383.12	—	345.44	—	—	—	—
Turbellaria	N	—	10,160	—	—	—	—	—	—	—
	B	—	406.40	—	—	—	—	—	—	—
Eumeiobenthos	N	450,160	1,082,930	911,840	1,680,800	1,442,720	1,645,920	1,813,560	365,760	568,960
	B	485.00	3,792.55	2,725.45	4,193.7	04,143.55	3,986.58	3,803.90	1,513.48	846.89
Oligochaeta	N	11,690	15,240	2,500	—	35,560	25.400	25,400	10,160	17,780
	B	128.59	167.64	27.94	—	391.16	279.40	279.40	111.76	195.58
Bivalvia	N	—	15,240	10,160	5,080	10,160	15,240	10,160	2,540	7,620
	B	—	6,096.00	4,064.00	2,032.00	4,064.00	6,096.00	4,064.00	1,016.10	3,048.00
Gastropoda	N	6,600	106,900	43,208	30,500	20,320	15,240	116,840	35,560	20,320
	B	4,158.00	67,347.00	27,221.04	41,456.02	12,801.60	9,601.20	73,609.20	22,402.80	12,801.60
Pseudomeio-benthos	N	18,290	137,380	55,908	35,580	66,040	55,880	152,400	48,260	45,720
	B	4,286.59	73,610.64	31,312.98	43,468.02	17,256.76	15,976.60	77,952.60	23,530.56	16,045.18
Meiobenthos (total)	N	468,450	1,220,310	967,748	1,716,380	1,508,760	1,701,800	1,965,960	414,020	614,680
	B	4,771.59	77,403.19	34,038.43	47,661.72	21,400.31	19,963.18	81,756.50	25,044.04	16,892.07

(Contd.)

1		2	3	4	5	6	7	8	9	10
July 27th										
Foraminifera	N	—	—	30,500	5,080	15,240	10,160	20,320	25,400	—
	B	—	—	396.50	66.04	198.12	132.08	264.16	330.20	—
Nematoda	N	562,356	645,160	619,760	1,310,640	808,228	970,289	695,960	838,200	609,600
	B	78.64	90.32	86.77	183.54	113.08	135.84	97.43	117.34	85.34
Harpacticoida	N	89,400	142,200	111,850	334,900	266,700	467,360	360,680	274,320	20,320
	B	715.20	1,137.60	894.80	2,679.20	2,133.60	3,738.88	2,885.44	2,194.56	162.56
Ostracoda	N	—	—	—	—	—	35,560	30,480	10,160	—
	B	—	—	—	—	—	213.14	198.12	66.04	—
Halacarida	N	—	20,770	—	15,240	2,540	—	—	—	—
	B	—	1,412.36	—	1,036.32	172.72	—	—	—	—
Eumeiobenthos	N	651,756	688,130	762,110	1,665,860	1,092,708	1,483,360	1,107,440	1,148,080	629,920
	B	793.84	2,640,28	1,378.07	3,969.10	2,617.52	4,237.94	3,445.15	2,708.14	247.90
Oligochaeta	N	25,400	5,080	5,080	5,080	43,180	25,400	5,080	20,320	—
	B	279.40	55.88	55.88	55.88	474.98	279.40	55.88	23.52	—
Bivalvia	N	5,080	5,080	20.770	25,400	2,540	20,320	20,320	60,960	10,160
	B	2,032.00	2,032.00	8,308.00	10,160.00	1,016.0	8,128.00	8,128.00	24,384.00	4,064.00
Gastropoda	N	84,300	66,044	198,100	228,500	76,200	157,480	162,560	187,960	5,080
	B	53,109.00	41,607.72	124,803.00	123,955.00	48,006.00	99,212.40	102,412.80	118,414.80	3,200.40
Pseudomeio-benthos	N	114,780	76,204	223,950	258,980	121,920	203,200	187,960	269,240	15,240
	B	55,420.40	43,695.60	133,166.88	154,170.88	49,496.98	107,619.80	110,596.68	142,822.32	7,264.40
Meiobenthos (total)	N	766,536	884,334	986,060	1,924,840	1,214,628	1,686,560	1,295,400	909,320	645,160
	B	56,214.24	46,335.88	134,544.95	158,135.98	52,114.50	111,857.74	114,041.83	145,530.46	7,512.30

August 6th										
Foraminifera	N	—	—	10,160	86,360	45,720	5,080	—	15,240	—
	B	—	—	132.08	1,122.68	594.36	66.04	—	198.12	—
Nematoda	N	939,800	508,000	970,280	863,600	792,480	787,400	949,960	685,800	1,889,760
	B	131.60	71.12	135.97	120.96	110.95	110.24	132.99	96.01	254.57
Harpacticoida	N	126,000	421,920	229,000	279,000	299,720	254,000	111,760	116,840	71,120
	B	1,008.00	3,375.36	1,832.00	2,236.00	2,397.76	2,032.00	894.08	934.72	568.96
Ostracoda	N	2,540	—	—	10,160	10,160	5,080	—	—	20,320
	B	16.51	—	—	66.04	66.04	32.02	—	—	132.08
Halacarida	N	—	5,080	—	—	—	—	—	—	—
	B	—	345.34	—	—	—	—	—	—	—
Turbellaria	N	17,790	—	—	—	40,640	5,080	—	—	—
	B	711.20	—	—	—	1,625.60	203.20	—	—	—
Eumeiobenthos	N	1,086,130	935,000	1,209,440	1,239,620	1,188,720	1,056,640	1,061,720	817,880	1,981,200
	B	1,867.31	3,791.92	2,100.05	3,545.68	4,794.71	2,444.50	1,027.07	9,641.33	965.61
Oligochaeta	N	12,000	15,240	5,080	5,080	55,880	25,400	10,160	45,720	5,080
	B	132.00	167.64	55.88	54.88	558.80	279.40	111.76	502.92	55.88
Polychaeta	N	—	—	—	—	5,080	—	—	—	—
	B	—	—	—	—	259.08	—	—	—	—
Bivalvia	N	7,610	10,160	15,240	10,160	—	20,320	10,160	86,360	45,720
	B	3,044.00	4,064.00	6,096.00	4,064.00	—	8,128.00	4,064.00	34,544.00	18,288.00
Gastropoda	N	160,000	609,610	386,360	300,000	111,760	127,000	142,240	76,200	35,560
	B	100,800.00	384,054.30	243,406.80	189,000.00	70,408.80	80,010.00	46,939.20	48,006.00	22,402.80
Pseudomeiobenthos	N	179,610	635,010	406,680	315,240	172,720	172,720	162,560	208,280	86,360
	B	103,976.00	388,285.94	249,558.68	193,119.88	71,226.68	88,417.40	51,114.96	83,052.92	40,746.68
Meiobenthos (total)	N	1,265,740	1,570,010	1,616,120	1,554,360	1,361,440	1,229,360	1,224,280	1,026,160	2,067,560
	B	105,843.31	392,077.86	251,658.73	196,665.56	76,021.39	90,861.96	52,142.03	92,694.25	41,712.29

(*Contd.*)

1		2	3	4	5	6	7	8	9	10
August 17th										
Foraminifera	N	—	—	48,960	60,960	106,680	20,320	20,320	2,540	10,160
	B	—	—	636.48	792.43	1,386.84	264.16	264.16	33.02	132.08
Nematoda	N	307,340	965,200	415,020	1,259,840	1,137,920	1,209,040	1,773,000	306,060	949,960
	B	43.12	135.10	58.08	176.40	159.31	169.27	248.92	54.05	133.63
Harpacticoida	N	71,100	147,300	188,000	310,000	375,920	375,920	508,000	68,580	40,640
	B	568.80	1,178.40	1,504.00	2,480.00	3,007.36	3,007.36	4,064.00	548.64	325.12
Ostracoda	N	—	5,080	5,080	10,160	15,240	5,080	60,960	—	—
	B	—	33.02	33.02	66.04	99.06	33.02	396.24	—	—
Halacarida	N	—	—	5,080	5,080	5,080	15,240	5,080	—	—
	B	—	—	345.44	345.44	345.44	1,036.32	345.44	—	—
Turbellaria	N	—	30,500	—	—	5,080	20,320	—	—	—
	B	—	1,220.00	—	—	203.20	812.80	—	—	—
Eumeiobenthos	N	378,440	1,148,080	662,140	1,646,040	1,645,920	1,945,920	2,372,360	457,200	1,000,760
	B	611.92	2,556.52	2,577.02	3,860.36	5,201.21	5,322.93	5,318.76	635.71	590.83
Oligochaeta	N	40,600	35,588	12,700	15,240	10,160	55,880	—	22,860	10,160
	B	446.60	391.47	139.70	167.64	111.76	614.68	—	251.46	11.76
Polychaeta	N	—	—	—	10,160	5,080	—	—	—	—
	B	—	—	—	518.16	259.08	—	—	—	—
Bivalvia	N	—	5,080	149,800	76,200	50,800	40,640	25,400	2,540	—
	B	—	2,032.00	59,920.00	30,480.00	20,320.00	16,256.00	10,160.00	1,016.00	—
Gastropoda	N	2,540	137,200	310,000	859,000	330,200	132,080	127,000	81,280	40,640
	B	1,600.20	86,436.00	195,300.00	541,170.00	208,026.00	83,210.40	80,010.00	51,206.00	25,603.20
Pseudomeio-benthos	N	43,140	177,868	472,500	960,600	396,240	228,600	152,400	106,680	50,800
	B	2,046.80	88,859.47	255,359.70	572,335.80	228,716.84	100,081.08	80,111.60	52,473.86	25,714.96

Meiobenthos (total)	N	421,580	1,325,948	1,134,640	2,606,640	2,042,160	1,874,520	2,524,760	563,880	1,051,560
	B	2,658.72	91,425.99	257,936.72	576,196.16	233,918.05	105,104.01	85,430.36	53,109.57	26,305.79
August 25th										
Foraminifera	N	3,560	30,500	25,400	132,000	127,000	45,720	—	5,080	5,080
	B	46.28	396.50	330.20	1,716.00	1,651.00	594.36	—	66.04	66.04
Nematoda	N	193,548	497,840	584,200	1,076,960	1,295,400	899,160	782,320	619.760	238,760
	B	27.45	69.74	83.19	151.06	181.36	125.88	109.53	86.77	33.43
Harpacticoida	N	77,600	99,150	106,900	142,100	401,320	177,800	198,120	69,040	25,400
	B	620.80	793.20	855.20	1,137.60	3,210.56	1,422.40	1,584.96	528.32	203.20
Ostracoda	N	5,080	—	10,160	—	10,160	20,320	25,400	—	2,540
	B	33.02	—	66.04	—	66.04	132.08	165.10	—	16.51
Halacarida	N	1,520	—	—	5,080	—	—	5,080	—	—
	B	103.56	—	—	345.44	—	—	345.44	—	—
Turbellaria	N	21,820	7,610	—	—	5,080	40,640	—	—	—
	B	872.80	304.40	—	—	203.20	1,625.60	—	—	—
Eumeiobenthos	N	303,131	635,100	726,660	1,356,140	1,838,960	1,183,640	1,010,920	690,880	271,780
	B	1,703.91	1,563.84	1,334.63	3,350.10	5,312.16	3,900.32	2,106.03	681.13	319.18
Oligochaeta	N	10,160	12,700	20,770	5,080	15,240	55,880	5,080	10,160	12,700
	B	111.76	139.70	22.85	55.88	167.64	614.68	55.88	111.76	139.70
Polychaeta	N	—	—	5,080	5,080	5,080	—	—	—	—
	B	—	—	259.08	259.08	259.08	—	—	—	—
Bivalvia	N	21,820	20,770	55,900	60,960	30,480	60,960	—	10,160	10,160
	B	8,728.00	8,308.00	22,360.00	24,384.00	12,192.00	24,384.00	—	4,064.00	4,064.00
Gastropoda	N	11,700	86,361	218,000	335,200	340,360	147,320	132,080	152,400	86,360
	B	7,040.88	54,407.43	137,340.00	211,176.00	214,426.90	92,811.60	83,210.40	96,012.00	54,369.00
Pseudomeiobenthos	N	43,680	119,831	299,750	406,320	391,160	264,160	137,160	172,760	109,220
	B	15,880.64	62,855.13	159,981.93	235,874.96	227,045.92	117,810.28	83,266.28	100,187.76	58,572.70

(*Contd.*)

1		2	3	4	5	6	7	8	9	10
Meiobenthos (total)	N	346,808	754,931	1,026,460	1,762,460	2,230,120	1,447,800	1,148,080	863,600	381,000
	B	17,584.55	64,418.97	161,316.56	239,225.06	232,357.68	121,710.60	85,372.31	100,868.89	58,891.88
September 3rd										
Foraminifera	N	2,540	5,080	15,240	10,160	312,420	17,780	5,080	—	2,540
	B	33.02	66.04	198.12	132.08	4,061.46	231.14	66.04	—	33.02
Nematoda	N	259,080	660,400	624,840	751,840	970,250	668,020	939,800	645,160	4,572
	B	36.40	92.46	87.48	105.26	135.84	93.52	131.57	90.32	0.64
Harpacticoida	N	97,600	137,200	132,100	152,400	228,600	154,940	269,240	66,040	2,540
	B	780.80	1,097.60	1,056.80	1,219.20	1,828.80	1,239.52	2,153.92	528.32	20.32
Ostracoda	N	5,080	—	2,540	10,160	5,080	53,340	10,160	—	—
	B	33.02	—	16.51	66.04	33.02	346.71	66.04	—	—
Halacarida	N	—	—	5,080	10,160	5,080	—	—	—	—
	B	—	—	345.44	690.88	345.44	—	—	—	—
Turbellaria	N	17,800	15,240	—	—	2,540	—	10,160	—	—
	B	12,140.40	1,036.32	—	—	172.72	—	690.88	—	—
Eumeiobenthos	N	382,100	817,920	779,800	934,720	1,523,970	894,080	1,234,440	711,200	9,652
	B	2,093.64	2,292.42	1,704.35	2,213.46	6,577.28	1,910.89	3,108.45	618.64	53.98
Oligochaeta	N	15,270	50,800	15,240	5,080	12,700	43,180	—	10,160	—
	B	167.64	614.68	167.64	55.88	139.70	474.98	—	111.76	—
Polychaeta	N	—	—	10,160	—	—	—	—	—	—
	B	—	—	518.16	—	—	—	—	—	—
Bivalvia	N	32,800	25,400	30,500	20,770	93,980	20,320	30,480	5,080	—
	B	13,120.00	10,160.00	12,192.00	8,308.00	37,592.00	8,128.00	12,192.00	2,032.00	—
Gastropoda	N	2,540	55,880	259,000	71,120	160,020	25,400	111,760	203,200	104,140
	B	1,600.20	35,204.40	163,171.00	44,805.60	100,812.60	160,000.20	70,408.80	128,016.00	65,608.20

Pseudomeio-benthos	N	50,610	132,080	314,900	96,970	266,700	88,900	142,240	218,440	104,140*
	B	14,887.84	45,979.08	176,047.48	53,169.48	138,544.30	168,603.18	82,600.80	130,159.76	65,608.20*
Meiobenthos (total)	N	432,710	950,000	1,094,700	1,031,690	1,790,670	982,980	3,176,680	929,640	113,792
	B	16,981.48	48,271.50	177,752.15	55,382.94	145,121.58	170,514.07	85,709.25	130,778.40	65,662.18

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*These figures duplicate the ones immediately above and probably are a misprint in the Russian original—General Editor.

nisms of meiofauna was examined according to sections its irregularity even within the limits of a single horizon was notable. For example, at the three stations located at a distance of not more than 2.7 to 2.9 m in the middle horizon the lowest population was recorded (July 7, 1970) in the middle station (594,400/m^2), the highest at the lower one (1,879,600/m^2), and an intermediate population (1,291,500/m^2) at the junction of the upper and middle horizons. Moreover the same pattern was observed for the lower horizon on July 16, 1970, the upper horizon on August 25, 1970, and so no. One possible reason for this unequal distribution of meiobenthic organisms must have been unequal distribution of food resources (p. 346).

During the course of the entire season the greatest density of meiobenthos was associated with the middle horizon of the littoral zone, rarely going below 1,000,000 specimens/m^2. This tallies very well with the data of some authors (Meadows and Anderson, 1968) concerning the maximum density of bacteria in the middle (intermediate) horizon of the littoral zone. Bacteria, as is known, enter into the food composition of many representatives of meiobenthos (constituting up to 50% of the food of marine nematodes). The upper horizon of the littoral zone is the most poorly populated, although here too the population does not drop below 400,000 specimens/m^2 from the end of July to the end of August. The lower horizon of the littoral occupies an intermediate position with respect to density of meiofauna.

The population dynamics for the entire summer were as follows: during the first half of July the density of meiofauna remained at approximately the same level, from the middle of July to the middle of August the density gradually increased throughout the whole section, the highest being recorded on August 17, 1970 (1,300,000 to 2,600,000 specimens/m^2), followed by a gradual decline at the beginning of September, going down to 950,000 to 1,790,000 specimens/m^2 (p. 340). August is considered the warmest month of the White Sea (Chernovskaya, 1956) and probably large-scale multiplication of organisms of meiofauna, which prefer warmer temperatures for reproduction, is associated with this period.

Of the two large subdivisions of meiobenthos, eumeiobenthos plays a leading role, constituting not less than 80 to 95% of the general population; this is because it includes permanent representatives which do not exceed 2.0 to 3.0 mm in size. It is difficult to say anything about the population dynamics of pseudomeiobenthos as after growing out of the dimensional limits they become members of macrobenthos. Consequently, it appears advisable to dwell in greater detail on the population dynamics of different groups of eumeiobenthos.

Foraminifera[1] constituted 2.0 to 7.0% of the total number of meiobenthos. During the summer season their number ranged from 2,540 to 312,420 specimens/m². In the littoral zone their distribution was irregular mainly in the middle and lower horizons. Their greatest density was recorded in the middle horizon at the end of August.

185 Harpacticoids constituted 10 to 20% of the total population of meiofauna. During summer their population ranged from 8,630 to 635,000 specimens/m². Their occurrence was considerably irregular on the beach. Such a varied picture of distribution is associated to some degree with their great mobility (up to 10 cm/min). In spite of this it should be noted that during the course of the entire summer they preferred to stay on the lower stratum of the upper horizon, and the midupper levels of the
186 lower horizon. The maximum population throughout the entire section was recorded in the middle of July (411,000 to 487,000) and in the middle of August (310,000 to 508,000 specimens/m²).

Ostracods constituted 0.5 to 1.5% of the total number of meiobenthos or 1,016 to 60,960 specimens/m²; they were found mainly in the middle and lower horizons of the littoral zone. The maximum density of population throughout the entire section was recorded on August 17, 1970.

Halacarids (marine mites) constituted about 1.0% of the total number of meiofauna or 1,520 to 20,770 specimens/m². They were found mainly in the upper and middle horizons of the littoral zone. The maximum population throughout the section was recorded in the beginning to the middle of July.

Turbellarians also constituted 1.0 to 2.0% of the meiofauna population, or 2,540 to 40,640 specimens/m². They localized in the upper and middle horizons of the littoral zone.

Nematodes constituted 50 to 80% of the entire population of meiofauna. The leading role of nematodes in sandy beaches has been observed by many researchers (Purasjoki, 1945; Smidt, 1951; Wieser, 1960; Fenchel and Jansson, 1966; Muus, 1967; Tietjen, 1969; Coull, 1970). During the summer of 1970 the nematode density was 4,570 to 1,778,000 specimens/m². The lowest population was recorded at the end of summer in the lower horizon of the littoral zone. Nematodes were distributed very irregularly in the littoral zone (Figure 4, Table 3). At the beginning of summer two peaks in the population were noted in the middle (1,117,600) and lower (1,097,280 specimens/m²) horizons. Population was lowest

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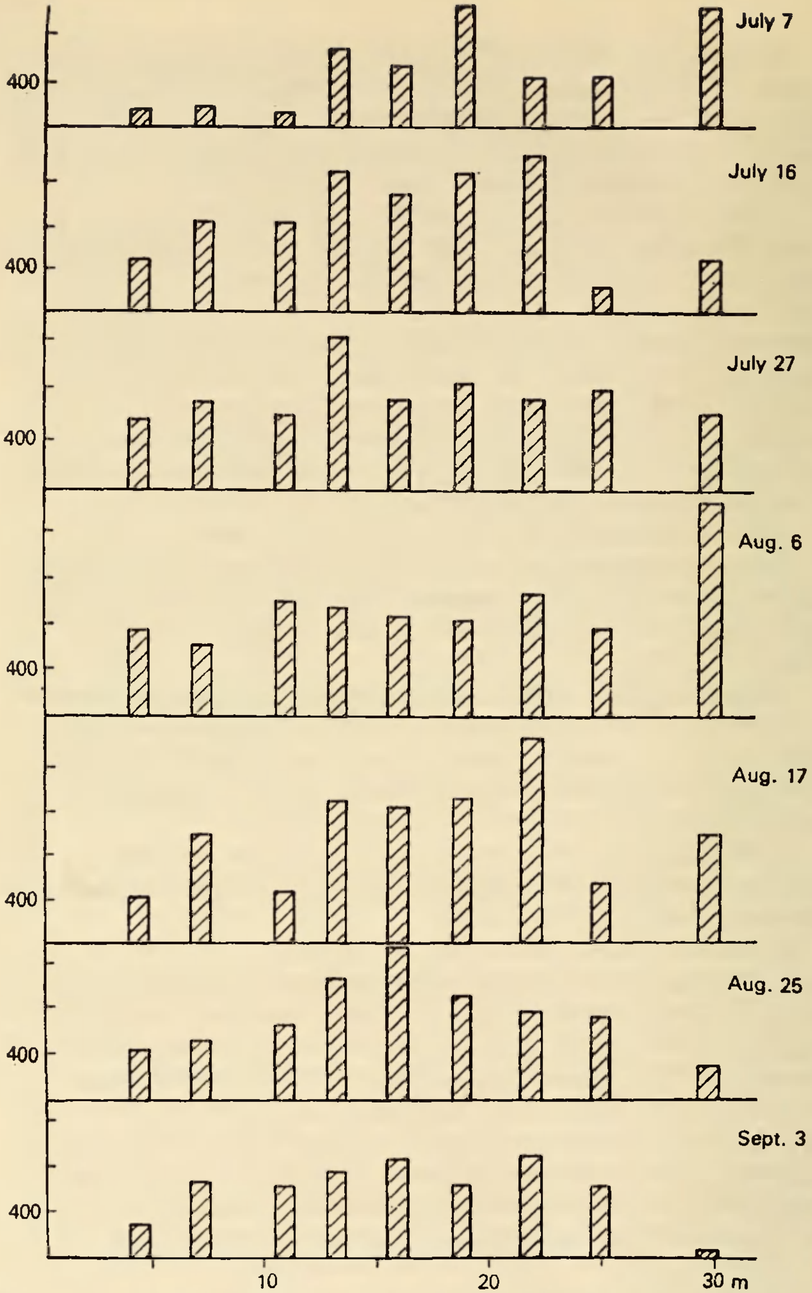
[1] Only live specimens, well-stained with Rose Bengal were taken into consideration.



185 Figure 4. General population dynamics of marine nematodes in the littoral zone of Kruglo'e Bay.[2]

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[2] In Figures 4, 5, and 41 to 54 the abscissas give the distance in meters between stations, and ordinates the organism population in thousand specimens/m^2.

in the upper horizon (59,436 to 112,740 specimens/m^2). Increase in numbers throughout the section took place toward the middle of July, but the maximum remained in the middle (intermediate) horizon as before (1,188,720 specimens/m^2). The peak disappeared in the lower horizon, which was characterized by very low density. Toward the end of July the number of nematodes reduced a little, on the average 600,000 to 900,000 specimens/m^2. A peak population continued in the middle horizon. At the beginning of August it was more or less the same as at the end of July, but the maximum during this period shifted to the lower horizon of the littoral zone. The highest number of nematodes throughout the section was 900,000 to 1,200,000 specimens/m^2 in the middle of the month, when the maximum population shifted again from the lower horizon to the middle. At the end of August and beginning of September a gradual fall in population throughout the section was observed. During this period the highest concentration remained in the middle (intermediate) horizon of the littoral zone.

Pseudomeiobenthos comprised, on the average, 5.0 to 20.0% of the population of meiofauna.

Oligochaetes constituted 2.0 to 3.0% of the total meiofauna (1,520 to 55,880 specimens/m^2) and were recorded in all horizons of the littoral zone. The lowest population was recorded in the month of July.

Polychaetes constituted less than 1.0% of the meiobenthos. Maximum population (on the basis of a few samples) did not exceed 10,160 specimens/m^2. They were not found in the month of July and in the month of August only a few in isolated samples were recorded from the middle horizon.

Young of lamellibranchs constituted 1.0 to 9.0% of the total meiofauna, or 2,540 to 149,800 specimens/m^2. During the month of July their population remained approximately at the same level, i.e., 10,000 to 20,000. In August a gradual increase up to 20,000 to 40,000 specimens/m^2 took place and the maximum concentration was found in the middle horizon of the littoral zone.

Young of gastropods constituted 1.0 to 32.0% of the total population of meiofauna, or 1,010 to 859,000 specimens/m^2. The maximum appearance of the young was registered betweeen the end of July and the beginning of August (60,000 to 180,000 specimens/m^2). During August the density throughout the littoral zone remained high.

Brotskaya (1951) has given some estimates of population of some groups of meiobenthos of the White Sea: nematodes—718,000 to 1,700,000; harpacticoids—80,000 to 187,000; oligochaetes—20,000 to 60,000; turbellarians—70,000 to 170,000; and young of all mollusks
187 50,000 to 160,000 specimens/m^2. Frolov (1971) estimated the population of the entire meiobenthos of the White Sea on sandy littoral beds during

summer as 1,650,000 to 1,900,000 and nematodes alone as 1,000,000 to 1,600,000 specimens/m^2. The data of these two authors compare well with mine.

The biomass of each group was determined by multiplying the average weight of an individual by its number (Table 3). The total biomass of meiobenthos during the summer season was 0.7 to 576.2 g/m^2. In the biomass an inverse correlation to population was observed: 80 to 90% of the entire biomass was contributed by pseudomeiobenthos because young mollusks constituted its main bulk and the weight of one representative of pseudomeiofauna is ten to a hundred times more than the weight of representatives of eumeiobenthos. The dynamics of biomass of eumeiobenthos on the whole parallel the dynamics of population; for this reason I shall briefly discuss the values of biomass for different groups.

The biomass of forminiferans (in mg/m^2) comprised 33 to 1,716 (the highest throughout the entire section as recorded on August 25, 1970 was 300 to 10,000); of harpacticoids 69 to 5,080 (the highest in the section observed during the month of August was 1,000 to 3,000); ostracods 6.9 to 396.2 (the highest throughout the entire section was observed on August 17, 1970); halacarids (marine mites) 103.4 to 1,412.4 (the highest throughout the entire section was recorded on August 7, 1970); and turbellarians 203.2 to 1,625.

Nematodes constituted numerically the most predominent group of meiofauna, but the average weight of a single nematode was the least of all (0.14 μm); they occupied one of the lowest positions with respect to biomass. Extreme values of biomass for the season ranged between 0.6 to 264.6 mg/m^2 and the highest for the section was observed on August 17, 1970.

Values of biomass for pseudomeiobenthos during the season ranged between 6.5 to 527.3 g/m^2.

Summer-Autumn Season of 1971 (Table 4)

The meiofauna population during autumn of 1971 was 201,676 to 6,283,960 specimens/m^2, i.e., the range was significantly wider than during the summer of 1970. The highest density of meiofauna occurred in the middle of September, comprising 1,000,000 to 6,000,000 specimens/m^2. Organisms of meiofauna were irregularly distributed throughout the littoral zone. During this season the maximum density was observed in the upper and middle horizons, as distinguished from summer when the maximum population was recorded in the middle and lower horizons.

The composition of meiofauna with respect to groups was the same as during summer. I shall dwell in greater detail on the population dynamics of different groups.

Foraminiferans constituted 1.0 to 3.0% of the total population, or 1,520 to 33,020 specimens/m^2, and were found mainly in the middle and lower horizons. The maximum population was recorded at the end of September.

Harpacticoids constituted 3.0 to 30.0% of the total number of meiofauna, or 5,080 to 215,900 specimens/m^2. The highest population throughout the section in the first ten days of September was 80,000 to 200,000, followed by a gradual fall, so that during the month of October the number was 40,000 to 100,000 specimens/m^2, approximately twice less than in the summer season.

Ostracods constituted 1.0 to 4.0% of the entire meiofauna, or 1,520 to 35,560 specimens/m^2, and were recovered mainly from the middle or lower horizon.

Halacarids (marine ticks) constituted less than 1.0% of the entire meiofauna or 2,540 to 5,080 specimens/m^2. They inhabited the middle and lower horizons of the littoral zone.

Turbellarians constituted 1.0 to 5.0% of the total meiofauna or 1,520 to 60,960 specimens/m^2. Their maximum population was 10,000 to 20,000 in the middle of September. In the month of October the population decreased to 5,000 to 10,000 specimens/m^2.

Nematodes, as in the summer season of 1971, constituted the leading group in the entire meiobenthos, comprising 90 to 96% of the population or 77,720 to 6,156,900 specimens/m^2. Their distribution was more irregular in character but they were more numerous than during summer (Figure 5, Table 4).

The maximum concentration of all nematodes was recorded in the upper and middle horizons, as distinguished from the summer season
192 when their maximum density was observed in the middle and lower horizons. Only one population peak was observed in the middle horizon at the beginning of the autumn season. In the middle of September, the population peak shifted toward the limits of the upper and middle horizon (6,156,960 specimens/m^2) and at the end of September the density of population remained high in the upper horizon. In the upper level of the middle horizon of the littoral zone a sufficiently high density persisted (1,000,000 to 2,000,000 specimens/m^2). During the course of the entire season the population density in the lower horizon did not exceed
193 400,000 to 600,000 specimens/m^2. Thus a trend from the middle to the upper horizon of the littoral zone was observed in nematodes throughout the autumn season. Increase in number of organisms occurred due to intense multiplication of some species (pp. 334–343).

Table 4. Population (N, specimens/m^2) and biomass (B, mg/m^2) of meiobenthos in the littoral zone of Kruglo'e Bay during autumn of 1971 at different heights of stations over 0-depth

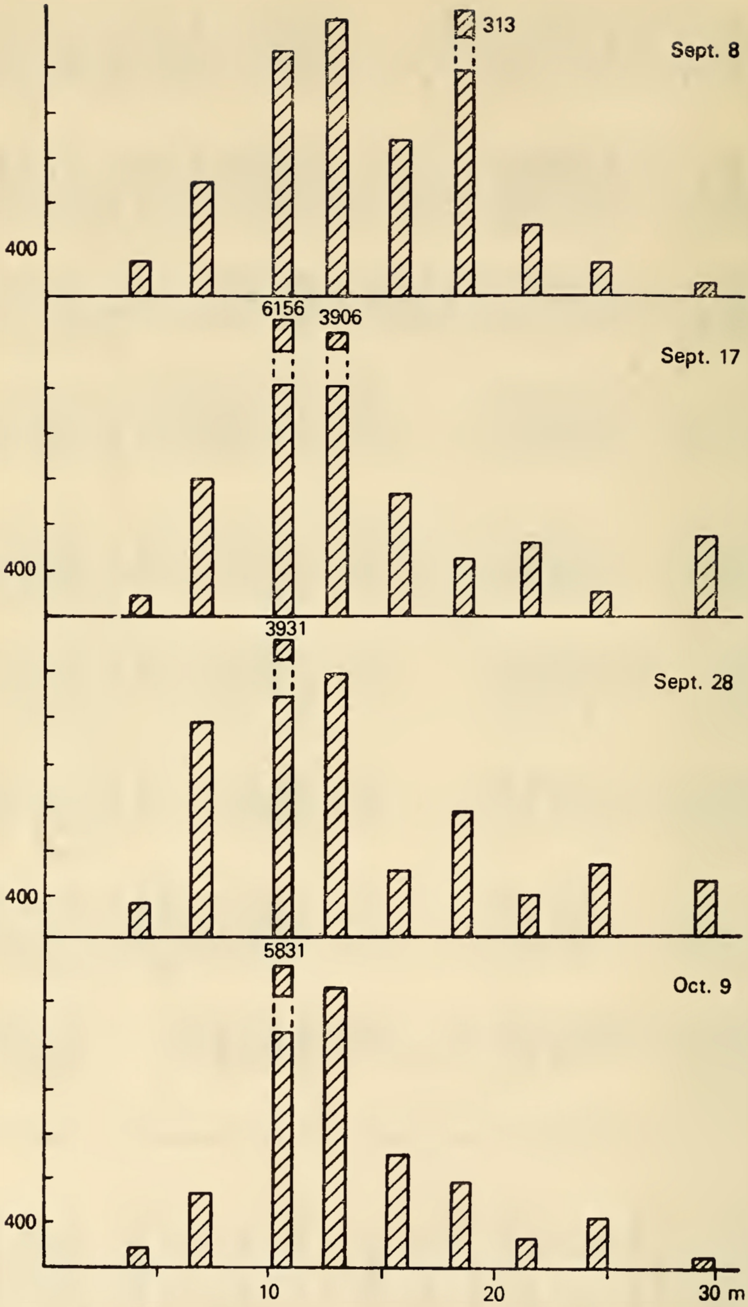
Group		1.95 m	1.78 m	1.55 m	1.44 m	1.41 m	1.37 m	1.25 m	1.15 m	0.99 m
1		2	3	4	5	6	7	8	9	10
September 8th										
Foraminifera	N	—	—	10,160	—	10,160	5,080	22,860	2,540	3,556
	B	—	—	132.08	—	132.08	66.04	297.13	33.02	44.23
Nematoda	N	292,100	955,040	2,194,560	2,341,880	1,341,120	3,139,440	671,576	238,760	77,724
	B	40.89	133.71	307.24	327.86	187.76	439.52	95.30	33.43	10.88
Harpacticoida	N	38,100	86,360	96,520	96,520	182,880	71,120	193,040	215,900	5,080
	B	304.80	690.88	772.16	772.16	1,463.04	568.96	1,544.32	1,727.20	40.64
Ostracoda	N	—	—	—	—	—	—	5,080	25,400	1,524
	B	—	—	—	—	—	—	33.02	165.10	9.91
Halacarida	N	—	—	—	—	5,080	—	5,080	—	—
	B	—	—	—	—	345.44	—	345.44	—	—
Turbellaria	N	2,540	—	—	—	25,400	20,320	2,540	15,240	—
	B	101.60	—	—	—	1,016.09	812.80	101.60	609.60	—
Eumeiobenthos	N	332,740	1,041,400	2,301,240	2,438,400	1,564,640	3,235,960	900,176	497,840	87,884
	B	447.29	824.59	1,211.48	1,100.02	3,144.32	1,887.32	2,416.86	2,568.35	107.66
Oligochaeta	N	56,388	15,240	—	111,760	81,280	157,480	10,160	43,180	10,160
	B	620.27	167.24	—	1,229.36	894.08	1,732.28	111.76	474.08	111.76
Polychaeta	N	—	—	—	—	—	—	—	2,540	—
	B	—	—	—	—	—	—	—	129.54	—
Bivalvia	N	2,540	5,080	20,320	—	5,080	10,160	83,820	10,160	42,164
	B	1,016.00	2,032.00	8,128.00	—	2,032.00	4,064.00	33,528.00	4,064.00	16,865.60
Gastropoda	N	5,080	10,160	66,040	15,240	30,480	25,400	124,460	68,580	1,524
	B	3,200,40	6,400.80	41,607.72	9,601.20	41,436.02	16,002.00	78,409.80	43,205.40	960.12

Pseudomeio-benthos	N	64,008	30,480	86,360	127,000	116,840	193,040	218,440	124,460	53,848
	B	4,836.67	8,600.44	49,735.72	10,830.56	44,432.10	21,798.28	112,049.56	47,873.92	17,937.48
Meiobenthos (total)	N	396,748	1,071,880	2,387,600	2,565,400	1,681,480	3,419,000	1,118,616	622,300	141,732
	B	5,283.96	9,425.03	50,947.20	11,930.58	47,476.42	23,685.60	114,466.42	50,442.27	18,045.14
September 17th										
Foraminifera	N	2,540	5,080	—	5,080	15,240	2,540	—	—	—
	B	33.02	66.04	—	66.04	198.12	33.02	—	—	—
Nematoda	N	194,056	1,239,520	6,156,960	3,906,520	1,173,480	543,560	660,400	204,724	675,640
	B	27.17	173.53	861.97	546.91	164.29	76.10	92.46	28.66	87.59
Harpacticoida	N	30,480	106,680	76,200	25,400	213,360	25,400	182,880	167,640	127,000
	B	243.84	853.44	609.60	203.20	1,706.88	203.20	1,463.04	1,341.12	1,016.00
Ostracoda	N	2,540	—	—	5,080	—	5,080	5,080	13,716	5,080
	B	16.51	—	—	33.02	—	33.02	33.02	89.15	33.02
Halacarida	N	—	—	5,080	5,080	5,080	—	—	—	—
	B	—	—	345.44	345.44	345.44	—	—	—	—
Turbellaria	N	2,540	—	5,080	10,160	60,960	20,320	10,160	1,524	5,080
	B	101.60	—	203.20	406.40	2,438.40	812.80	406.40	60.96	203.20
Eumeiobenthos	N	232,156	1,351,280	6,243,320	3,957,320	1,468,120	596,900	858,520	387,604	812,800
	B	422.14	1,093.01	2,020.21	1,601.01	4,853.13	1,158.14	1,994.92	1,519.89	1,339.81
Oligochaeta	N	8,128	5,080	—	215,360	160,680	187,960	45,720	30,480	25,400
	B	89.41	55.88	—	2,368.96	1,767.48	2,067.56	502.92	335.28	279.40
Polychaeta	N	—	—	—	—	—	—	—	1,524	—
	B	—	—	—	—	—	—	—	77.72	—
Bivalvia	N	2,540	30,480	15,240	—	5,080	22,860	76,200	8,636	25,400
	B	1,016.00	12,192.00	6,096.00	—	2,032.00	9,144.00	30,480.00	3,454.40	10,160.00
Gastropoda	N	2,540	162,560	25,400	—	111,760	33,020	86,360	79,756	45,720
	B	1,600.20	102,412.80	16,002.00	—	70,408.80	20,802.70	54,407.43	50,132.88	28,803.60

(*Contd.*)

1		2	3	4	5	6	7	8	9	10
Pseudomeio-benthos	N	13,208	198,120	40,640	215,360	277,520	243,840	208,280	120,396	96,520
	B	2,705.61	114,660.68	22,098.00	2,368.96	74,208.28	32,014.16	85,390.35	54,000.28	39,243.00
Meiobenthos (total)	N	245,264	1,549,400	6,283,960	4,172,680	1,745,640	840,740	1,066,800	508,000	909,320
	B	3,127.75	115,753.69	24,118.21	3,969.97	79,061.41	33,172.30	87,385.27	55,520.17	40,582.81
September 28th										
Foraminifera	N	—	15,240	—	15,240	10,160	30,480	33,020	—	—
	B	—	198.12	—	198.12	132.08	396.50	429.26	—	—
Nematoda	N	289,560	1,864,360	3,931,920	2,331,720	558,800	1,092,200	307,340	614,680	485,140
	B	40.54	261.01	550.47	326.44	78.23	152.91	43.03	86.06	67.92
Harpacticoida	N	71,120	96,520	101,600	91,440	45,720	152,400	48,260	193,040	43,180
	B	568.80	772.16	812.80	731.52	365.76	1,219.20	386.08	1,544.32	345.44
Ostracoda	N	2,540	—	—	—	5,080	10,160	—	35,560	—
	B	16.51	—	—	—	33.02	66.04	—	231.14	—
Halacarida	N	—	—	—	—	5,080	—	5,080	5,080	—
	B	—	—	—	—	345.44	—	345.44	345.44	—
Turbellaria	N	22,860	—	—	—	132,080	—	5,080	15,240	—
	B	914.40	—	—	—	5,283.20	—	203.20	203.20	—
Eumeiobenthos	N	386,080	1,976,120	4,033,520	2,438,400	756,920	1,285,240	398,780	863,600	528,320
	B	1,540.25	1,231.29	1,363.27	1,256.08	6,237.73	1,834.65	1,407.01	2,437.16	413.36
Oligochaeta	N	60,960	45,720	—	147,320	60,960	40,640	2,540	40,640	22,860
	B	670.56	502.92	—	1,620.52	670.56	446.60	27.94	446.60	251.46
Polychaeta	N	2,540	—	—	2,540	—	—	—	—	—
	B	129.54	—	—	129.54	—	—	—	—	—
Bivalvia	N	12,700	5,080	15,240	—	5,080	15,240	60,960	25,400	20,320
	B	5,080.00	2,032.00	6,096.00	—	2,032.00	6,096.00	24,384.00	10,160.00	8,128.00
Gastropoda	N	38,100	—	10,160	2,540	20,320	—	104,140	20,320	5,080
	B	24,003.00	—	6,400.80	1,600.20	12,801.60	—	65,608.20	12,801.60	3,200.40

Pseudomeio-benthos	N	114,300	50,800	25,400	152,400	86,360	55,880	167,640	86,360	48,260
	B	29,883.10	2,534.92	12,496.80	3,350.26	15,504.16	6,542.26	90,020.14	23,408.20	11,579.86
Meiobenthos (total)	N	500,380	2,026,920	4,058,920	2,590,800	843,280	1,341,120	566,420	949,950	576,580
	B	31,423.35	3,766.21	13,860.07	4,606.34	21,741.89	8,377.25	91,427.15	25,845.36	11,993.22
October 9th										
Foraminifera	N	1,524	—	5,080	10,160	—	5,080	12,700	7,620	15,240
	B	19.81	—	66.04	132.08	—	66.04	165.10	99.06	198.12
Nematoda	N	103,124	645,160	5,831,840	2,560,320	955,680	772,160	276,860	469,900	82,804
	B	14.43	90.32	816.46	358.44	139.40	108.10	38.76	65.79	1.59
Harpacticoida	N	49,276	147,320	30,480	96,520	66,040	30,480	96,520	134,620	64,516
	B	394.21	1,178.56	243.84	772.10	528.32	243.84	772.16	1,076.96	516.13
Ostracoda	N	—	—	—	—	—	—	2,540	—	1,524
	B	—	—	—	—	—	—	16.51	—	9.91
Halacarida	N	—	—	—	—	—	—	2,540	—	—
	B	—	—	—	—	—	—	172.72	—	—
Turbellaria	N	3,556	10,160	15,240	10,160	60,960	5,080	5,080	—	—
	B	146.24	406.40	609.60	406.40	2,438.40	203.20	203.20	—	—
Eumeiobenthos	N	157,480	802,640	5,882,640	2,677,160	1,122,680	812,800	396,240	612,140	164,084
	B	574.69	1,675.28	1,735.94	1,669.02	3,106.12	648.18	1,368.45	1,241.81	735.75
Oligochaeta	N	40,640	15,240	10,160	35,560	40,640	60,960	2,540	5,080	—
	B	447.04	167.64	111.76	391.16	447.04	670.56	27.94	55.88	—
Bivalvia	N	3,556	55,880	—	—	—	5,080	—	35,560	42,164
	B	1,442.40	22,360.00	—	—	—	2,032.00	—	14,224.00	16,865.60
Gastropoda	N	—	45,720	10,160	5,080	20,320	20,320	2,540	43,180	11,684
	B	—	28,803.60	6,400.80	3,200.00	12,801.60	12,801.60	1,600.20	27,203.40	7,360.92
Pseudomeio-benthos	N	44,196	116,840	20,320	40,640	60,960	86,360	5,080	83,820	53,848
	B	1,869.44	22,527.64	6,512.56	3,591.56	13,248.64	15,504.16	1,628.14	41,483.28	24,226.52
Meiobenthos (total)	N	201,676	919,480	5,902,960	2,777,800	1,183,640	899,160	401,320	695,960	217,932
	B	2,444.13	24,202.92	8,248.50	5,260.58	16,354.72	16,152.34	2,996.59	42,725.09	24,962.27



192 Figure 5. Dynamics of the total population of marine nematodes in the littoral zone of Kruglo'e Bay in autumn of 1971

The density of pseudomeiobenthos was lower in autumn than in summer, comprising 5,080 to 277,520 specimens/m^2. As in summer, the bulk of pseudomeiofauna constituted bivalves and gastropods.

Oligochaetes constituted 1.0 to 5.0% of the total population of meiofauna (2,540 to 215,360 specimens/m^2), and were found throughout the entire section. The maximum density was observed during the middle of September (150,000 to 200,000) and the maximum concentration in the middle horizon of the littoral zone.

Polychaetes constituted less than 1.0% or 1,000 to 2,000 specimens/m^2. They were found in small numbers in different probes.

The young of bivalves constituted 1.0 to 7.0% of the meiobenthos population (2,540 to 83,820 specimens/m^2). Their population gradually declined from the beginning of September toward mid-October, indicating that the growth of mollusks to 2.0 to 3.0 mm had taken place, i.e., beyond the limits of meiobenthos.

The young of gastropods constituted 1.0 to 10.0% of the total population of meiofauna (1,520 to 162,560 specimens/m^2). The same tendency seen in bivalves was observed in the population dynamics of gastropods.

During the autumn season the biomass of meiobenthos constituted 3.1 to 115.7 g/m^2 and that of eumeiobenthos 0.4 to 6.2 g/m^2.

Biomass of foraminiferans was 19 to 429 (maximum on September 28, 1971), harpacticoids 40 to 1,727 (maximum on September 8, 1971), ostracods 9.0 to 23.1, halacarids 172 to 1,727, turbellarians 60 to 5,213, and nematodes 10 to 761 mg/m^2 (a few times higher than that in summer, with the maximum observed in the first half of September).

The biomass of pseudomeiobenthos constituted only 1.8 to 114.6 g/m^2 (five to six times less than the summer values). This was due to a significant reduction in population of young mollusks.

Having analyzed the distribution of meiofauna during both summer and autumn seasons, its irregularity in the horizons of the littoral zone could be recorded. The middle horizon was the most richly populated during both seasons. During summer a peak was recorded in the lower horizon and during autumn in the upper. The distribution of meiofauna was irregular in character even within the limits of a single horizon. For example, if the change in meiobenthos population at any station of the section is examined, it will be seen that during one season the density of organisms at a given station considerably changed after seven to ten days. That is why one sample from one horizon cannot reflect the population dynamics of a given area. According to my data an analysis of at least three samples is essential in order to characterize the density of a more or less homogeneous region. It is desirable that the distance between stations should not exceed 2.0 to 3.0 m. A steady pattern of distribution of meiofauna was found during autumn, when the population peak in the upper horizon of the littoral zone remained constant throughout the entire month.

Of the two components of meiofauna, eumeiobenthos occupied a predominant position with respect to population. But pseudomeiobenthos occupied the leading position with respect to biomass due to the high average weight of young mollusks.

Considering both seasons, a higher population of meiofauna was observed in autumn and a higher biomass in summer.

Marine nematodes constituted the leading group, comprising half of the meiofauna population; as such their contribution played a main role in the pattern of distribution of the entire meiofauna in the littoral zone.

List of Species of Nematodes of the White Sea

194 Class NEMATODA

Subclass *ADENOPHOREA*

1. Order **ENOPLIDA**

1. Family ENOPLIDAE

1. Genus *Enoplus* Dujardin, 1845

1. *E. demani* nom. nov.................................. 260

2. Genus *Mesacanthion* Filipjev, 1927

2. *M. marisalbi* sp. n.................................. 261

3. Genus *Chaetonema* Filipjev, 1927

3. *C. longisetum* (Steiner, 1916).......................... 263

2. Family ONCHOLAIMIDAE

4. Genus *Anoplostoma* Buetschli, 1874

4. *A. rectospiculum* sp. n................................ 264

5. Genus *Metoncholaimoides* Wieser, 1953

5. *M. filicauda* sp. n.................................. 265

6. Genus *Metaparoncholaimus* de Coninck and Schuurmans-Stekhoven, 1933

6. *M. longispicula* sp. n................................ 267

3. Family OXYSTOMINIDAE

7. Genus *Halalaimus* de Man, 1888

4. Family IRONIDAE

8. Genus *Parironus* Micoletzky and Kreis, 1930

5. Family CRENOPHARYNGIDAE

9. Genus *Crenopharynx* Filipjev, 1934

2. Order **CHROMADORIDA**

6. Family CHROMADORIDAE

10. Genus *Hypodontolaimus* de Man, 1886

11. Genus *Chromadora* Bastian, 1865

12. Genus *Spiliphorella* Filipjev, 1918

195 13. Genus *Timmia* Hopper, 1961

14. Genus *Prochromadorella* Micoletzky, 1924

15. Genus *Prochromadora* Filipjev, 1922

7. Family CYATHOLAIMIDAE

16. Genus *Paracanthonchus* Micoletzky, 1924

8. Family COMESOMATIDAE

17. Genus *Sabatieria* de Rouville, 1904

9. Family CHOANOLAIMIDAE

18. Genus *Halichoanolaimus* (Bastian, 1865)

3. Order **MONHYSTERIDA**

10. Family SPHAEROLAIMIDAE

19. Genus *Sphaerolaimus* Filipjev, 1918

11. Family MONHYSTERIDAE

20. Genus *Theristus* Bastian, 1865

1. Subgenus *Mesotheristus* Wieser, 1956

2. Subgenus *Pseudosteineria* Wieser, 1956

3. Subgenus *Daptonema* Cobb, 1920

4. Subgenus *Penzancia* de Man, 1922

12. Family LINHOMOEIDAE

21. Genus *Terschellingia* de Man, 1888

22. Genus *Metalinhomoeus* de Man, 1907

4. Order **ARAEOLAIMIDA** 196

13. Family TRIPYLOIDIDAE

23. Genus *Tripyloides* Filipjev, 1918

14. Family AXONOLAIMIDAE

24. Genus *Axonolaimus* de Man, 1889

25. Genus *Odontophora* Buetschli, 1874

5. Order **DESMODORIDA**

15. Family MONOPOSTHIIDAE

26. Genus *Monoposthia* de Man, 1889

16. Family SPIRINIIDAE

27. Genus *Chromodoropsis* Filipjev, 1918

28. Genus *Spirinia* Gerlach, 1963

Taxonomic Review of Species

The nematode fauna of the White Sea has hardly been studied to date. Filip'ev (1927) described a few species of enoplids from the isthmus of the White Sea, and Frolov (1972) has published a list of nematode species from the sandy littoral zone of the strait of Velikaya Salma. In describing nematodes from the inlets of Chupinskaya River I am simply supplementing the list of already known nematodes of the White Sea.

As many as 76 species of nematodes were recorded by me during investigations of material from the White Sea; 35 species were found in large numbers in silted sand in the littoral zone.

The nematode species detected belong to 5 orders, 16 families, and 28 genera. For species already known only a brief description has been given, while 13 new species are described in greater detail.

Cobb's formula (Cobb, 1891), modified by Filip'ev (1916), has been used in describing the new species, along with indices according to de Man (a, b, c). Cobb's formula is represented by a fraction with numerical figures in microns. The numerator indicates distances from the anterior end to: 1. end of oral cavity, 2. nerve ring, 3. end of esophagus, 4. vulva (in the case of females), and 5. anus. The denominator gives the width of the corresponding body region. Total length of the nematode (also in microns) is indicated at the end of the fraction.

197

1. Order ENOPLIDA

1. Family ENOPLIDAE Baird, 1853

1. Genus *Enoplus* Dujardin, 1845

Synonym: *Enoplostoma* Marion, 1870.

1. *Enoplus demani* nom. nov. (Figure 6)
de Man 1886 (*brevis*) non Bastian, 1865.

4 ♂: L = 4,103.0–5,511.0 μm; a = 26.6–32.4; b = 4.9–6.4; c = 20.6–29.0.
4 ♀: L = 4,696.0–5,247.0 μm; a = 26.6–32.5; b = 5.5–6.2; c = 19.1–24.5; V = 49.2–53.3%.

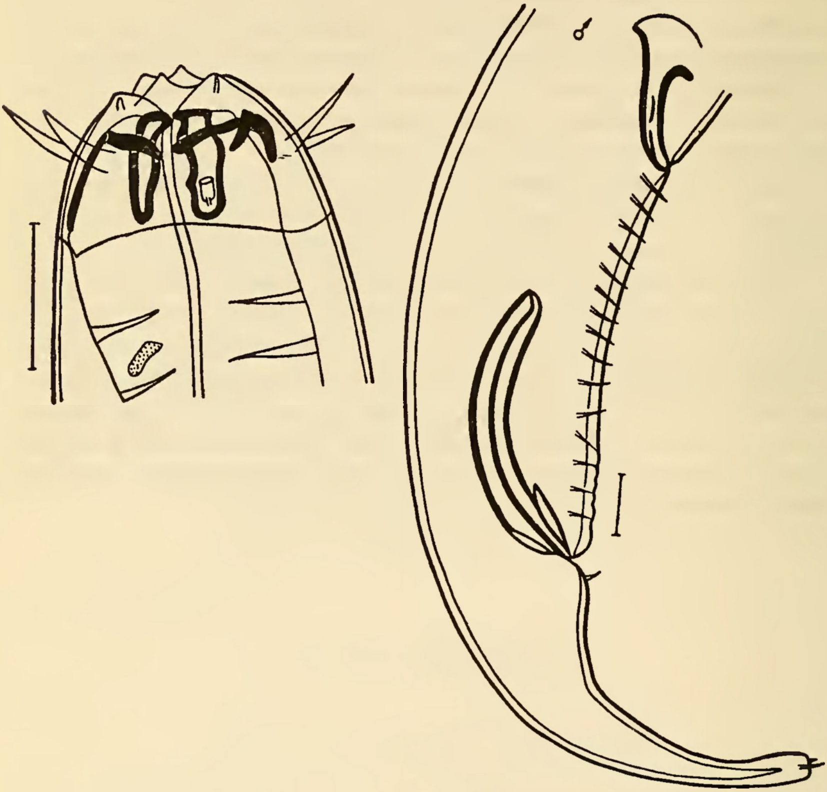


Figure 6. *Enoplus demani* nom. nov.[3]

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[3] In Figures 6 to 40 the line corresponds to 20 μm. Tentative insertions in the figures: bb. e = bulbus of esophagus; ba. e = base of esophagus; sp = spicules; and t. o = tubular organ.

The White Sea form collected by me and that described by de Man (1886) from the coast of the North Sea seem identical. Bastian (1865) described a new species, *E. brevis*, on the basis of a female specimen. Subsequently, de Man (1886) described this species, also recorded from the North Sea, on the basis of a male and a female. After carefully studying the works of these authors, I concluded that these are two different species, distinguished from each other in indices *a* and *c*. The species of Bastian is devoid of cephalic papillae, which are present in the species of de Man. The former species has short jaws (15.4 μm), which in the species of de Man are 1.5 to 1.7 times longer. This enables one to consider the two species independent. I have proposed a new name, *E. demani*, for species *E. brevis* described by de Man (1886), and retained the name *E. brevis* for the species described by Bastian (1865).

198 In the White Sea specimens of *E. demani* longitudinal striations on the labia are discernible. Amphids oval, with large openings, and 9.6 μm × 3.6 μm in size. Genital armature of male represented by spicules, accessory organ, and setae. Spicules thin, long, almost uniform in width throughout, and 124.2 to 164.7 μm long. Gubernaculum simple, small, and 48.6 to 51.3 μm long. Accessory organ funnel-shaped and situated 176.0 to 199.8 μm from anus. Anal setae 14 to 15 pairs; situated between anus and accessory organ.

Geographic distribution. Found in the North and White Seas, mainly in slightly silted sand.

2. Genus *Mesacanthion* Filipjev, 1927

2. *Mesacanthion marisalbi* sp. n. (Figure 7)

Holotype ♂. Institute of Zoology, Academy of Sciences, USSR. Collection No. 3.

$$\frac{-\qquad 202.5\qquad 759.0\qquad -\qquad 3{,}859.0}{24.3\qquad 51.3\qquad 51.3\qquad 72.9\qquad 40.5}\ 4{,}037\,\mu\text{m};\ a=52.4;\ b=5.5;\ c=19.3.$$

Paratypes.

$$2\,♂\!:\ \frac{-\qquad 198.0\text{–}209.0\qquad -\qquad 2{,}805.0\text{–}3{,}773.0}{25.0\text{–}28.0\qquad 54.0\text{–}55.0\qquad 74.0\text{–}77.0\qquad 40.5\text{–}43.6}$$

$$\times\, 2{,}992.0\text{–}3{,}971.0\,\mu\text{m};\ a=45.4\text{–}51.6;\ b=4.3\text{–}5.1;\ c=16.0\text{–}20.1.$$

$$1\,♀\!:\ \frac{-\qquad 231.0\qquad 682.0\qquad 1{,}837.0\qquad 3{,}311.0}{29.0\qquad 55.0\qquad 66.0\qquad 88.0\qquad 44.0}\ 3{,}509\,\mu\text{m};\ a=45.6;\ b=5.2;\ c=17.7;\ V=54.6\%.$$

$$1\ \text{juv.}\!:\ \frac{-\qquad 220.0\qquad 660.0\qquad -\qquad 2{,}915.0}{28.0\qquad 44.0\qquad 66.0\qquad 77.0\qquad 43.2}\ 3{,}333.0\,\mu\text{m};\ a=46.7;\ b=5.1;\ c=16.8.$$

Figure 7. *Mesacanthion marisalbi* n. sp.

Body elongated; tapers to 1/3 midbody diameter at anterior end and 5/9 at posterior end. Head demarcated from body. Tail long and tapers gradually toward end; length 5.5 diameter at anus. Lips well developed and armed with setae 6.0 to 8.0 μm long. Length of cephalic setae 61.2
199 to 64.0 μm; cervical setae rather short, 16.2 μm. Setae absent on tail. Cuticle smooth. Amphids not discernible. Photosensitive pigment absent. Oral cavity 26.4 μm × 15.6 μm, cylindrical changing to conical near base, armed with three equal-sized teeth 12 μm long, and with a ring that extends approximately along the middle. Esophagus almost uniform in width throughout its length. Reproductive system of female represented by unflexed paired tubules. Sexual armature of male consists of accessory organ and spicules. Accessory organ tubular and situated 126.9 μm from anus. Spicules curved, almost uniform in width throughout their length, and 56.7 μm long. Gubernaculum with dorsal appendage closely attached to spicules; length 21.6 μm.

This species comes close to the description of *M. longissimesetosus* Wieser, 1953, recorded from the coast of Chile, but can be distinguished from it by indices *a* and *c*, smaller size of cephalic setae, teeth, and spicules. In *M. marisalbi* the accessory organ is situated closer to the anus than in *M. longissimesetosus*. These distinguishing characters permit one to consider *M. marisalbi* a new species.

Geographic distribution. Found in the White Sea, mainly in the middle and lower horizons of the littoral zone in slightly silted sand.

Genus *Chaetonema* Filipjev, 1927

3. *Chaetonema longisetum* (Steiner, 1916) (Figure 8)

Steiner, 1916; 600–602, tab. 25, fig. 16a–c (*Anoplostoma*); Filip'ev, 1925: 182.

1♀: L = 1,269.0 μm; a = 29.4; b = 4.9; c = 10.7; V = 49%.
4 juv.: L = 837.0–1,104.3 μm; a = 29.4–34.0; b = 3.5–4.8; c = 7.7–10.8.

White Sea specimens distinguishable from those described by Steiner from the coast of the Barents Sea and by Filip'ev from the Kara Sea by larger size of cephalic setae (35.1 to 40.5 versus 21.0 to 27.0 μm). The White Sea population fully coincides with those specimens described earlier in all remaining features. To my regret males were lacking in my material. In the specimens examined amphids could not be detected.

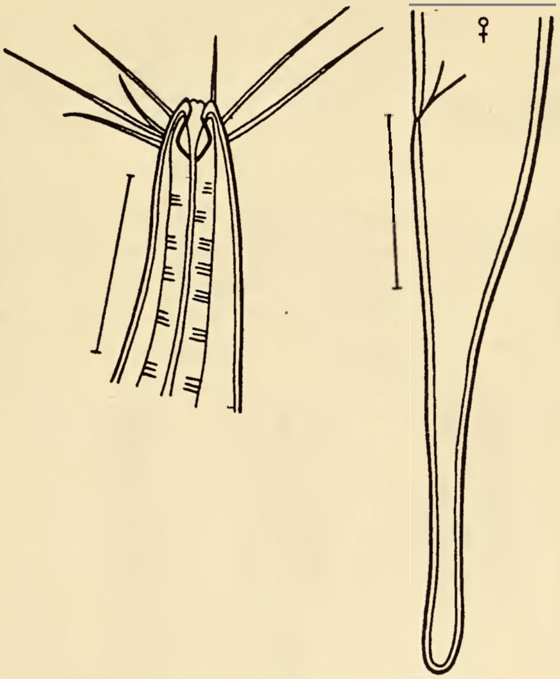


Figure 8. *Chaetonema longisetum.*

200 **Geographic distribution.** Recorded from the White, Barents and Kara Seas in small numbers in the lower, slightly silted horizons of the littoral zone.

2. Family ONCHOLAIMIDAE Perrier, 1897

4. Genus *Anoplostoma* Buetschli, 1874

4. *Anoplostoma rectospiculum* sp. n. (Figure 9)

Holotype ♂: Institute of Zoology, Academy of Sciences, USSR. Collection No. 7.

$$\frac{\begin{array}{ccccc}14.8 & 145.8 & 286.0 & — & 1{,}364.0\end{array}}{\begin{array}{ccccc}8.1 & 32.4 & 39.0 & 44.0 & 22.0\end{array}}\ 1{,}496.0\ \mu\text{m};\ a=34.0;\ b=5.2;\ c=11.4.$$

Paratypes.

$$3\,♀\text{:}\ \frac{\begin{array}{cccc}13.5\text{–}16.2 & 162.0\text{–}172.8 & 330.0\text{–}352.0 & 935.0\text{–}1{,}144.0\end{array}}{\begin{array}{cccc}8.1\text{–}9.4 & 35.0\text{–}35.1 & 44.0\text{–}55.0 & 55.0\text{–}66.0\end{array}}$$

$$\times\frac{1{,}694.0\text{–}2{,}024.0}{24.0\text{–}33.0}\ 1{,}837\text{–}2{,}178\ \mu\text{m};\ a=32.4\text{–}39.6;\ b=5.5\text{–}6.2;\ c=12.8\text{–}15.6;\ V=47.9\text{–}55.0\%.$$

$$3\,♂\text{:}\ \frac{\begin{array}{cccc}13.5\text{–}16.1 & 148.5\text{–}159.3 & 319.0\text{–}341.0 & —\end{array}}{\begin{array}{cccc}8.0\text{–}9.3 & 29.7\text{–}32.4 & 38.0\text{–}49.0 & 54.0\text{–}55.0\end{array}}$$

$$\times\frac{1{,}540.0\text{–}1{,}705.0}{22.0\text{–}27.0}\ 1{,}815.0\text{–}1{,}837.0\ \mu\text{m};\ a=30.6\text{–}41.0;\ b=5.3\text{–}5.7;\ c=11.7\text{–}13.9.$$

Body thin, long, and tapers to 1/5 to 2/11 midbody diameter at anterior end and 1/2 to 10/23 at posterior end. Head demarcated from body. Tail long (4.5 anal body diameters), initially conical, then narrows into a cylinder for three-fourths its length. Labia well developed and armed with papillae. Length of cephalic setae 9.2 to 9.6 µm. Setae also present

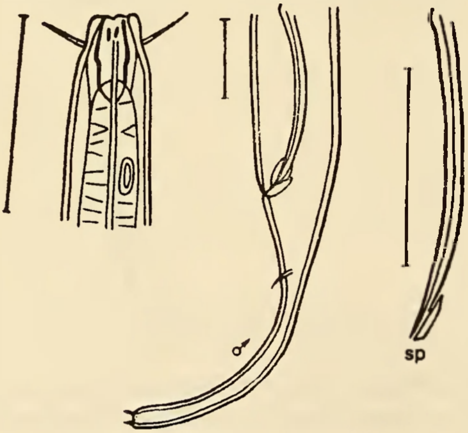


Figure 9. *Anoplostoma rectospiculum*

on tail, 1.2 to 1.3 μm long. Cuticle smooth. Amphids saccate and longitudinally elongated, thick-walled, and situated 2.5 cephalic diameters from anterior end. Amphids 7.2 μm × 3.6 μm; width 1/4 corresponding body diameter. Oral cavity large, prismatic; length exceeds width about 2.5 times. Esophagus initially uniform in width, broadens gradually toward base. Reproductive system of female consists of pair of unflexed tubules, containing seven to eight eggs each. Diameter of eggs 65 to 70 μm. Spicules thin, long (54 to 60 μm) and slightly curved. Gubernaculum simple and small (8.5 to 9.6 μm).

This species comes close to *A. blanchardi* de Man, 1888 but can be distinguished from it by larger body size, oral cavity, apparently the size and shape of amphids (de Man was not able to observe the amphids distinctly), and longer, thinner, and weakly curved spicules. All these characters permit one to consider *A. rectospiculum* a new species.

Geographic distribution. Found in large numbers in the White Sea in all horizons of the littoral zone in silted sand.

5. Genus *Metoncholaimoides* Wieser, 1953

5. *Metoncholaimoides filicauda* sp. n. (Figure 10)

Holotype ♀: Institute of Zoology, Academy of Sciences, USSR. Collection No. 10.

$$\frac{43.2 \quad 216.0 \quad 451.0 \quad 1{,}232.0 \quad 2{,}310.0}{35.1 \quad 56.7 \quad 77.0 \quad 88.0 \quad 44.0}\ 2{,}431.0\ \mu\text{m};\ a=27.6;\ b=5.4;$$
$$c=20.0;\ V=50.6\%.$$

201 **Paratypes.**

$$2\,♂\!:\ \frac{32.4\text{–}37.8 \quad 292.5\text{–}313.3 \quad 374.8\text{–}385.0 \quad \text{—}}{27.0\text{–}29.7 \quad 56.7\text{–}59.4 \quad 55.0\text{–}66.0 \quad 66.0\text{–}71.0}$$
$$\times\,\frac{1{,}947.0\text{–}2{,}057.0}{43.0\text{–}44.0}\ 2{,}057.0\text{–}2{,}156.0\ \mu\text{m};\ a=30.1\text{–}30.8;$$
$$b=5.3\text{–}5.8;\ c=18.1\text{–}21.8.$$

$$1\,♀\!:\ \frac{40.5 \quad 202.5 \quad 473.0 \quad 1{,}452.0 \quad 2{,}618.0}{29.7 \quad 54.0 \quad 55.0 \quad 88.0 \quad 44.0}\ 2{,}750\ \mu\text{m};\ a=29.7;$$
$$b=4.3;\ c=20.4;\ V=52.8\%.$$

$$2\ \text{juv.}\!:\ \frac{32.4\text{–}35.1 \quad 180.9\text{–}199.8 \quad 341.0\text{–}374.0 \quad \text{—}}{22.9\text{–}24.3 \quad 44.0\text{–}40.5 \quad 38.0\text{–}44.0 \quad 44.0\text{–}55.0}$$
$$\times\,\frac{1{,}463.0\text{–}1{,}749.0}{30.0\text{–}33.0}\ 1{,}501.0\text{–}1{,}848.0\ \mu\text{m};\ a=32.6\text{–}35.3;$$
$$b=4.6\text{–}4.9;\ c=17.6\text{–}18.7.$$

Body rather thick; tapers to 2/5 midbody diameter at anterior end and to 1/2 at posterior end. Head rounded and almost not demarcated from body as cervical constriction absent. Tail conical; length 2.0 to 2.5 anal diameters. Lips well developed and armed with papillae. Cephalic setae small, 1.4 to 1.5 μm. Extremely short setae (1.2 to 1.4 μm) present on tail. Cuticle smooth. Amphids cyathiform and situated almost at mid-level of oral cavity. Amphids 3.6 μm × 8.4 μm; width 1/4 corresponding body diameter. Oral cavity large, almost cylindrical, its length twice its width, and armed with teeth of unequal length. Dorsal tooth 29.7 μm, ventral 24.3 μm. Esophagus almost equal in width up to 3/4 its length, then gradually dilates toward base. Rectum unusually thick-walled.

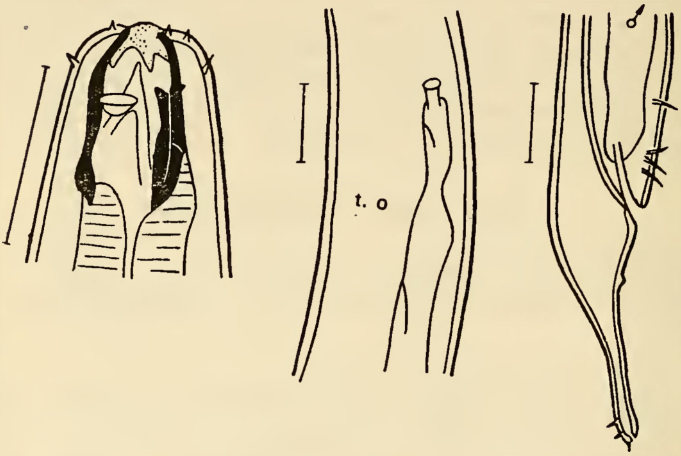


Figure 10. *Metoncholaimoides filicauda* sp. n.

Females with tubular organ 251.0 μm long opening through pore situated 170.1 μm anterior to anus. Reproductive system of female with paired unflexed tubes, containing seven eggs each. Diameter of eggs 77.0 to 80.0 μm. Spicules thin, very long (102.6 μm), and weakly curved. Gubernaculum absent. Preanal setae present.

M. filicauda must be compared with the only other species of this genus, *M. squalus* Wieser, 1953, recorded from the coast of Chile. The White Sea form is much smaller than *M. squalus*. *M. filicauda* can also be distinguished from *M. squalus* in indices *a* and *c* and spicules five to six times shorter. Females with smaller number of eggs than in *M. squalus*. These characters permit one to consider *M. filicauda* an independent species.

Geographic distribution. Found in the White Sea in silted sand, mainly in the upper and middle horizons of the littoral zone.

202
6. Genus *Metaparoncholaimus* de Coninck and Schuurmans-Stekhoven, 1933

6. *Metaparoncholaimus longispicula* sp. n. (Figure 11)

Holotype ♀. Institute of Zoology, Academy of Sciences, USSR. Collection No. 13.

$$\text{♀}\ \frac{50.4 \quad 347.2 \quad 649.0 \quad 4{,}411.0 \quad 6{,}027.0}{39.2 \quad 78.6 \quad 88.0 \quad 110.0 \quad 49.0}\ 6{,}215.0\ \mu\text{m};\ a=56.5;\ b=9.6;\ c=70.6;\ V=71.2\%.$$

Paratypes.

$$3\,\text{♀}:\ \frac{37.8\text{–}56.7 \quad 189.0\text{–}272.7 \quad 585.0\text{–}583.0 \quad [\textit{sic}] \quad 1{,}705.0\text{–}4{,}290.0}{32.4\text{–}39.0 \quad 75.6\text{–}81.0 \quad 66.0\text{–}82.0 \quad 77.0\text{–}121.0}$$

$$\times \frac{2{,}277.0\text{–}5{,}709.0}{44.0\text{–}55.0}\ 2{,}332.0\text{–}5{,}808.0\ \mu\text{m};\ a=30.5\text{–}49.0;$$

$$b=6.0\text{–}9.9;\ c=42.5\text{–}58.6;\ V=72.5\text{–}74.0\%.$$

$$2\,\text{♂}:\ \frac{40.5\text{–}43.2 \quad 286.2\text{–}313.2 \quad 561.0\text{–}660.0 \quad \text{—}}{32.4\text{–}37.8 \quad 56.7\text{–}72.9 \quad 55.0\text{–}99.0 \quad 77.0\text{–}110.0}$$

$$\times \frac{3{,}432.0\text{–}5{,}016.0}{44.0\text{–}55.0}\ 3{,}520.0\text{–}5{,}104.0\ \mu\text{m};\ a=45.7\text{–}46.4;$$

$$b=6.3\text{–}7.7;\ c=40.0\text{–}57.9.$$

Body thick, long, and tapers to 2/5 to 1/3 midbody diameter at anterior end and 1/2 at posterior end. Head rounded and almost not demarcated from body. Tail blunt, short; length approximately 1.5 times anal body diameter. Labia well developed and armed with papillae. Cephalic setae 10.8 μm long. Short setae (1.2 to 1.3 μm) present on tail. Cuticle smooth. Amphids cyathiform and situated at midlevel of oral cavity. Amphid size 4.8 μm × 12.0 μm; width 1/4 to 1/5 corresponding cephalic diameter. Oral cavity large, almost cylindrical, its length twice greater than width, and armed with three teeth of unequal size. Two ventral teeth large (27.0 μm) and dorsal one smaller (21.6 μm). Esophagus almost
203 uniform throughout its length.

Females with tubular organ 693.0 μm long with numerous pores on dorsal, ventral and lateral surfaces. Reproductive system of female consists of unpaired curved tubes, containing four large eggs. Diameter of eggs 165.0 μm. Spicules rather thick and long (45.9 μm). Gubernaculum absent. Six to seven preanal setae present.

This species can be compared with one of the two known species of this genus—*M. campylocercus* (de Man) de Coninck and Stekhoven (1933)—found along the Belgium coast. It differs from the latter in larger body size, index *a*, and shorter tail [1.5 times anal body diameter versus 3.5 times in *M. campylocercus* (de Man)]. Females of *M. longispicula* can

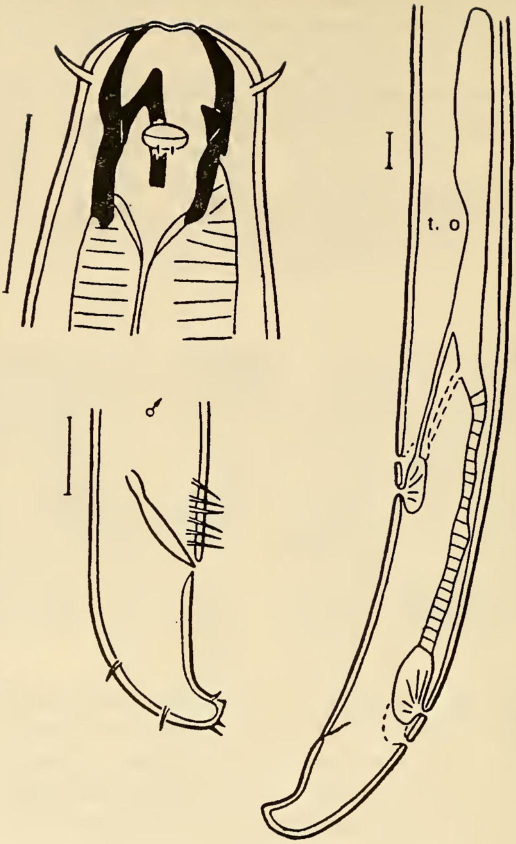


Figure 11. *Metaparoncholaimus longispicula* sp. n.

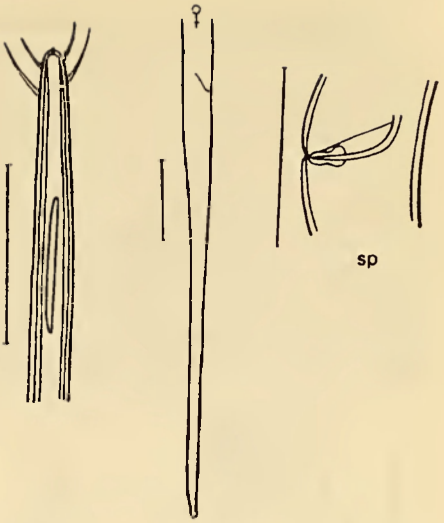
be distinguished from those of *M. campylocercus* by the presence of a tubular organ opening into a large number of excretory pores (in *M. campylocercus* there are only two pores) and more posteriorly displaced vulva. All these features permit one to consider *M. longispicula* a new species.

Geographic distribution. Found in large numbers in the White Sea, mainly in the upper and middle horizons of the littoral zone in silted sand.

3. Family OXYSTOMINIDAE Chitwood, 1935

7. Genus *Halalaimus* de Man, 1888

Synonyms: *Halalaimoides* Cobb, 1933 and *Nuada* Southern, 1914.



202 Figure 12. *Halalaimus zenkevitchi.*

7. *Halalaimus zenkevitchi* Filipjev, 1927 (Figure 12)

4 ♂: L = 1,353.0–1,419.0 μm; a = 62.0–71.0; b = 4.0–5.1; c = 7.0–10.4.
1 ♀: L = 1,331.0 μm; a = 60.5; b = 4.1; c = 6.4; V = 48.6%.
1 juv.: L = 1,166.0 μm; a = 42.5; b = 3.9; c = 8.8.

White Sea specimens can be distinguished from those described by Filip'ev by smaller size and proportionately smaller length of spicules and amphids. Judging from the diagram of Filip'ev the White Sea specimens have longer cephalic setae (5.0 to 5.4 μm). The lateral membrane mentioned by Filip'ev was not found in my specimens.

Geographic distribution. Found in small numbers in the White, Barents and Kara Seas in all horizons of the littoral zone.

4. Family IRONIDAE

8. Genus *Parironus* Micoletzky and Kreis, 1930

8. *Parironus tubulilaimus* sp. n. (Figure 13)

Holotype ♀: Institute of Zoology, Academy of Sciences, USSR, Collection No. 17.

$$\frac{88.0\quad 242.0\quad 473.0\quad 1{,}694.0\quad 3{,}069.0}{22.0\quad 88.0\quad 99.0\quad 115.0\quad 66.0}\ 3{,}289.0\ \mu\text{m};\ a = 28.4;\ b = 6.9;$$

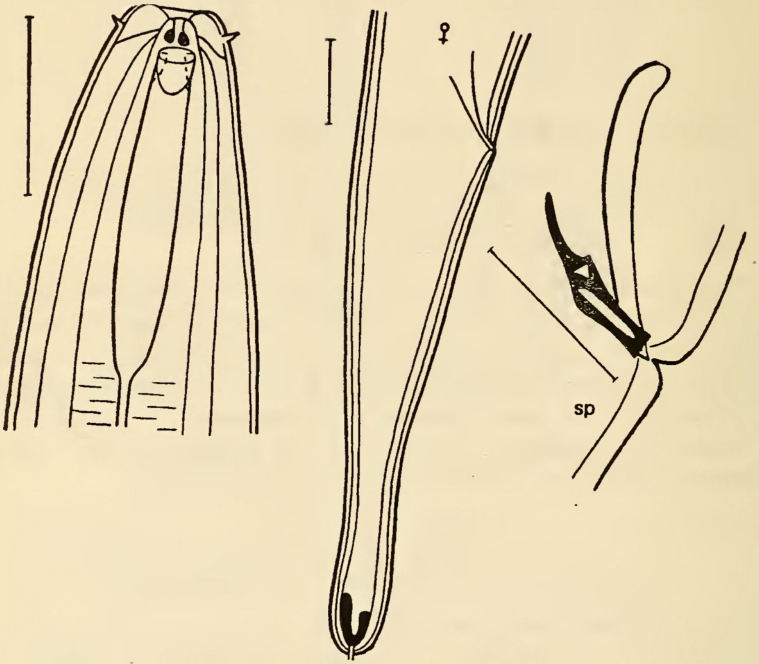
c = 14.9; V = 51.5%.

Paratype.

$$1\ ♂\text{:}\ \frac{88.0\quad 275.0\quad 539.0\quad —\quad 2{,}871.0}{25.0\quad 77.0\quad 88.0\quad 110.0\quad 77.0}\ 3{,}058.0\ \mu\text{m};\ a = 27.8;$$

b = 5.7; c = 16.3.

Body elongated, thick, and tapers to 1/5 midbody diameter at anterior end and 2/3 to 10/17 at posterior end. Head poorly demarcated from body. Tail conical and length equal to 3.5 to 4.0 anal body diameters. Labia well developed and with papillae. Cephalic setae extremely short (1.1 to 1.2 μm). Setae absent on tail. Amphids slightly elongated longitudinally, 6.7 × 5.4 μm, width 1/3 corresponding head diameter. Oral cavity cylindrical and large (59.4 × 8.1 μm); length 13.7% of esophageal length; cavity armed with three teeth of equal size, 4.0 μm. Esophagus widens
205 gradually toward base. Genital tubes of female paired and reflexed. Spicules almost straight but their proximal ends curve ventrally at an angle of 90°; length of spicules 51.3 μm. Gubernaculum large, wide at distal end, and narrows sharply in proximal part.



204 Figure 13. *Parironus tubulilaimus* sp. n.

Readily distinguishable from the three species of the genus *Parironus* described earlier, and hence a comparison is not necessary. The distinguishing features of this species are: short cephalic setae, broad amphids, large oral cavity, and characteristic structure of spicules.

Geographic distribution. Found singly in the White Sea, in the middle horizon of the littoral zone in slightly silted sand.

5. Family CRENOPHARYNGIDAE Platonova, 1976

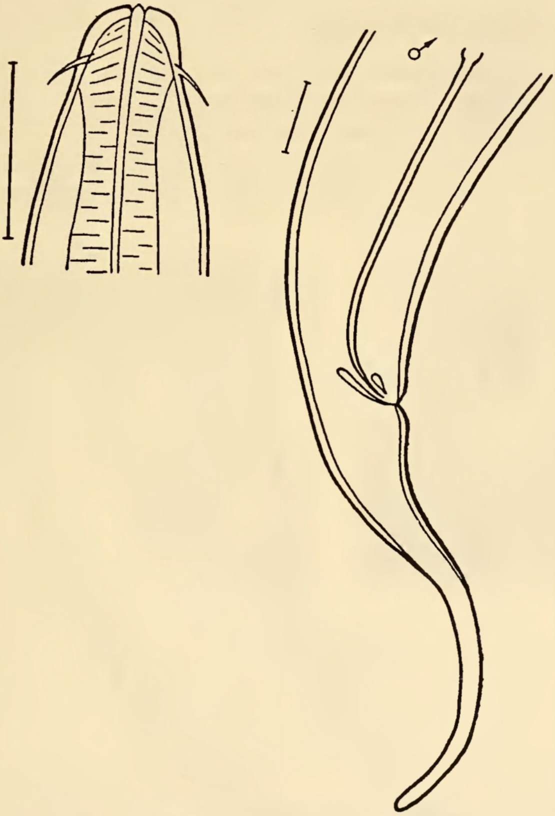
9. Genus *Crenopharynx* Filipjev, 1934

Synonyms: *Anoplostoma* Linstow, 1900 non Bütschli, 1874; *Stenolaimus* Southern, 1914 et auctrium non Marion, 1870.

9. *Crenopharynx gracilis* (Linstow, 1900) (Figure 14)
Filip'ev, 1927: 119–122, tab. 1, fig. 29a–3 (*Stenolaimus*); 1934: 9.

1 ♂: L = 6,060.0 μm; a = 23.3; b = 3.9; c = 13.7.

My specimen of *Crenopharynx gracilis* fully coincides with the description given by Filip'ev (1927) with respect to all measurements and characters. However, I could detect neither amphids nor renette.



204 Figure 14. *Crenopharynx gracilis.*

Geographic distribution. Found singly in the White, Barents, and Kara Seas in the upper and middle horizons of the littoral zone in silted sand.

2. Order **CHROMADORIDA**

6. Family CHROMADORIDAE

10. Genus *Hypodontolaimus* de Man, 1886

Synonyms: *Iotadorus* Cobb, 1920 and *Ptycholaimellus* Cobb, 1920.

10. *Hypodontolaimus inaequalis* (Bastian, 1865) (Figure 15)
Bastian, 1865; (*Spilophora*) non Bütschli, 1874; de Man, 1888.

5 ♂: L = 869.0–1,430.0 μm; a = 14.5–17.2; b = 4.9–6.6; c = 8.6–14.5.
2 ♀: L = 1,221.0–1,364.0 μm; a = 17.1–17.7; b = 5.3–6.2; c = 10.1–11.3; V = 50.0–52.2%.
2 juv.: L = 759.0–847.0 μm; a = 11.5–15.4; b = 4.6–4.8; c = 8.1–8.6.

The White Sea population coincides very well with the description given by de Man (1888) with respect to all measurements and characters. However, de Man did not succeed in observing amphids in his material. My specimens had amphids. Width of amphids 10.8 μm, greater than length, and about 1/3 corresponding cephalic width. Amphids situated

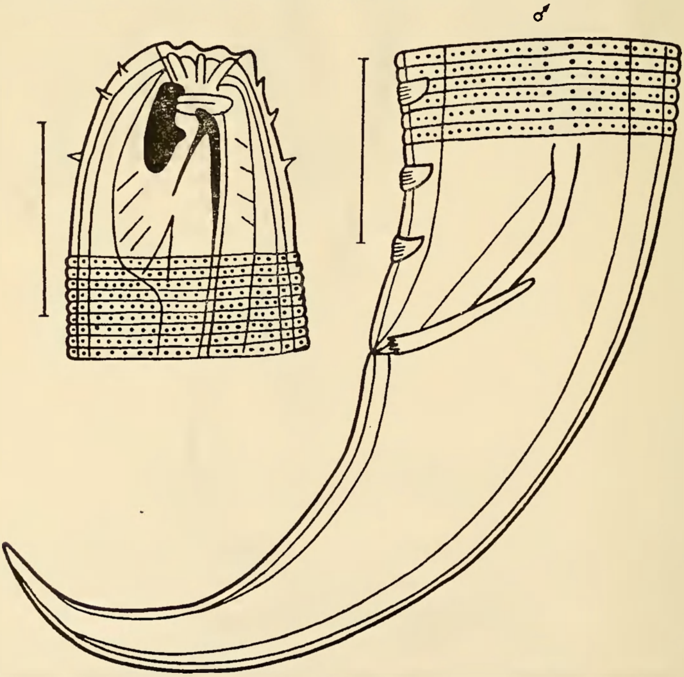


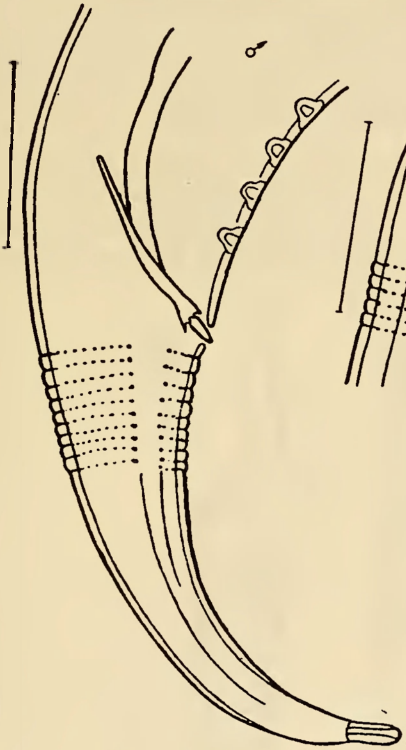
Figure 15. *Hypodontolaimus inaequalis*.

6.0 μm from anterior end. Spicules 59.4 μm long or 1.5 anal body diameters.

Geographic distribution. Found in the White, Baltic, Norwegian, and North Seas in all horizons of the littoral zone in slightly silted sand.

11. *Hypodontolaimus buetschlii* (Buetschli, 1874) (Figure 16)
Bütschli, 1874: 44, pls. 5, 6, fig. 23, non Bastian, 1865 (*Spiliphera*); Ditlevsen, 1919: 194, tab. 10, fig. 2 (*striatus*); Filip'ev, 1918: 211.

4 ♂: L=825.0–1,419.0 μm; a=12.7–16.2; b=5.0–6.5; c=9.4–12.9.
1 ♀: L=1,133.0 μm; a=14.9; b=6.5; c=13.0; V=47.6%.



206 Figure 16. *Hypodontolaimus buetschlii.*

Most of the characters of the White Sea specimens coincide with the brief description given by Bütschli (1874). The following may be added
207 to this description on the basis of my material: cephalic setae 5.4 μm long. Spicules long, slightly curved, and 70.4 μm long, or about 1.5 anal body diameters. Gubernaculum massive, slightly dilated at its distal end,

and 25.1 μm long. Accessory organs 23 in males and situated anterior to anus.

Geographic distribution. Found in the White, Baltic, Norwegian, and North Seas, mainly in the middle and lower horizons of the littoral zone in slightly silted sand.

11. Genus *Chromadora* Bastian, 1865

Synonyms: *Tridontolaimus* Micoletzky, 1913 and *Parachromadora*, Micoletzky, 1914.

12. *Chromadora macrolaima* de Man, 1889 (Figure 17)
Allgen, 1933; 69 (var. *pigmentata*).

4 ♂: L = 543.0–704.0 μm; a = 21.1–23.3; b = 5.1–6.0; c = 6.2–7.1.
1 juv.: L = 616.0 μm; a = 28.0; b = 5.6; c = 7.0.

My specimens conform very well to the description given by de Man with respect to characters and measurements. Peculiarities of the White Sea specimens are: smaller size than those described by de Man and 10 to 11 accessory organs. To the description of de Man the following may be

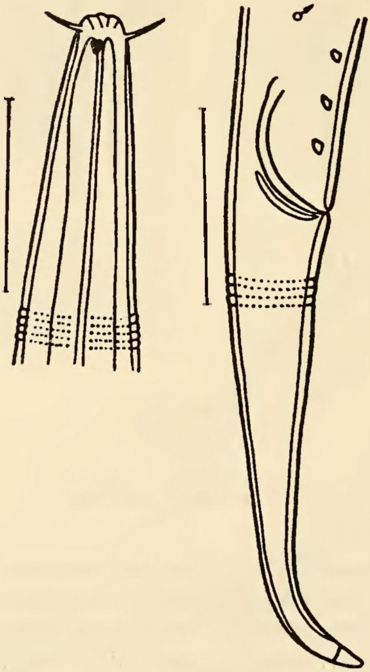


Figure 17. *Chromadora macrolaima.*

added: cephalic setae 5.5 to 6.0 μm long. Spicule length approximately 1.2 anal body diameters.

Geographic distribution. Found in the White, Barents, and North Seas in all horizons of the littoral zone in slightly silted sand.

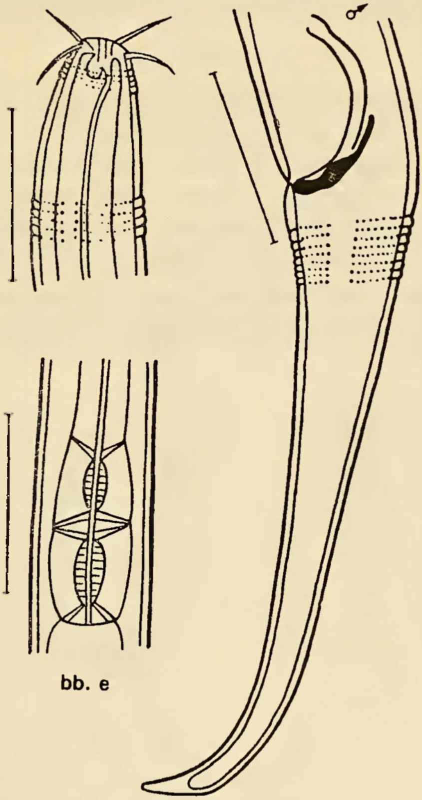
208 12. Genus *Spilophorella* Filipjev, 1918

13. *Spilophorella candida* Gerlach, 1951 (Figure 18)

1 ♂: L = 1,007.0 μm; a = 22.0; b = 5.6; c = 8.5.
1 juv.: L = 821.0 μm; a = 23.0; b = 5.9; c = 7.0.

This species conforms to the description given by Gerlach (1951) with respect to all characters and measurements, except that in my specimen the spicules were more curved than in the North Sea form.

Geographic distribution. Found in the White and North Seas in all horizons of the littoral zone in slightly silted sand.



207 Figure 18. *Spilophorella candida.*

13. Genus *Timmia* Hopper, 1961

Synonym: *Parachromadora* Timm., 1952.

14. *Timmia acuticauda* sp. n. (Figure 19)

Holotype ♂: Institute of Zoology, Academy of Sciences, USSR. Collection No. 25.

$$\frac{-\quad 67.5\quad 110.7\quad -\quad 486.0}{10.8\quad 18.9\quad 21.6\quad 27.0\quad 21.6}\ 564.3\ \mu m;\ a=20.9;\ b=5.1;\ c=7.2.$$

Paratypes.

$$3\ ♂:\ \frac{-\qquad 70.2\text{–}72.9\qquad 110.7\text{–}118.8\qquad -}{10.8\text{–}14.7\qquad 22.8\text{–}24.3\qquad 24.3\text{–}27.0\qquad 29.7\text{–}35.1}\times\frac{634.5\text{–}658.8}{24.3\text{–}27.0}$$

$$726.3\text{–}731.7\ \mu m;\ a=20.7\text{–}27.0;\ b=6.2\text{–}6.6;\ c=7.9\text{–}11.9.$$

$$2\ ♀:\ \frac{-\qquad 67.5\text{–}70.2\qquad 110.7\text{–}118.8\qquad 313.2\text{–}342.9}{13.3\text{–}13.5\qquad 16.2\text{–}24.3\qquad 26.0\text{–}27.0\qquad 32.4\text{–}37.8}$$

$$\times\frac{556.2\text{–}648.0}{21.6\text{–}27.0}\ 656.1\text{–}750.6\ \mu m;\ a=19.8\text{–}20.2;\ b=5.9\text{–}6.3;$$

$$c=6.3\text{–}6.4;\ V=47.5\text{–}47.7\%.$$

Body elongated, tapers to 1/2 midbody diameter at anterior end and 2/3 at posterior end. Head not demarcated from body. Tail acicular and length three anal body diameters. Four cephalic setae present, 6.0 μm long, or more than 1/2 cephalic diameter. Setae absent on tail. Cuticle ornamented with dots of almost equal size; lateral differentiation absent. Amphids not detected. Saccate photosensitive pigment spots situated 22 μm from anterior end. Oral cavity (5.0 μm × 10.0 μm) armed with three small teeth almost uniform in length (2.8 μm). Esophagus with bulb 24.3 μm × 27.0 μm in size.

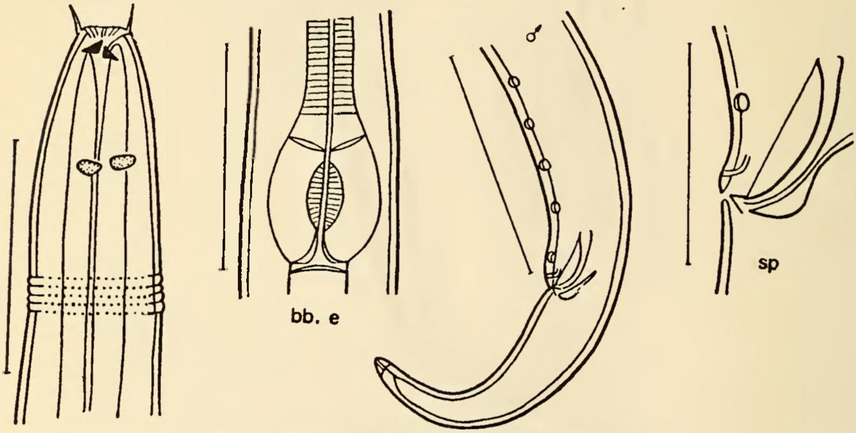


Figure 19. *Timmia acuticauda* sp. n.

Reproductive system of female consists of paired and reflexed tubes. Male with five pairs of accessory organs and one unpaired in shape of
209 tube situated 3.0 to 4.0 μm anterior to anus. Spicules curved, slightly wider in distal part, and 30 μm long, or 1.2 anal body diameters. Gubernaculum simple and 18.0 μm long (0.6 spicular lengths).

Of the two species of *Timmia* described to date, this species is more similar in description to *Timmia parva* (Timm, 1952), but can be distinguished from it by smaller cephalic setae, shape and situation of pigment spots, larger number of accessory organs, absence of velum in spicules, and terminal tooth on gubernaculum. This enables one to consider the White Sea population a new species.

Geographic distribution. Found in the White Sea in all horizons of the littoral zone in slightly silted sand.

14. Genus *Prochromadorella* Micoletzky, 1924

15. *Prochromadorella crassispicula* sp. n. (Figure 20)

Holotype ♂: Institute of Zoology, Academy of Sciences, USSR. Collection No. 27.

$$\frac{\begin{array}{ccccc} \text{—} & 110.0 & 231.0 & \text{—} & 1{,}584.0 \end{array}}{\begin{array}{ccccc} 22.0 & 33.0 & 44.0 & 77.0 & 55.0 \end{array}}\ 1{,}749.0\ \mu\text{m};\ a=22.7;\ b=7.6;\ c=10.6.$$

Paratypes.

$$1\ ♂\text{:}\ \frac{\begin{array}{ccccc} \text{—} & 121.0 & 209.0 & \text{—} & 1{,}199.0 \end{array}}{\begin{array}{ccccc} 22.2 & 33.1 & 44.1 & 66.0 & 44.0 \end{array}}\ 1{,}342.0\ \mu\text{m};\ a=20.3;\ b=6.4;\ c=9.4.$$

$$1\ ♀\text{:}\ \frac{\begin{array}{ccccc} \text{—} & 104.0 & 181.0 & 858.0 & 1{,}276.0 \end{array}}{\begin{array}{ccccc} 22.4 & 33.0 & 38.0 & 71.0 & 33.0 \end{array}}\ 1{,}441.0\ \mu\text{m};\ a=20.1;\ b=7.9;\ c=8.8;\ V=44.3\%.$$

Body rather long and tapers to 1/3 to 2/7 midbody diameter at anterior end and 3/4 to 1/2 at posterior end. Head poorly demarcated from body. Tail conical, acicular at end; length 4.5 anal body diameters. Cephalic setae long (10.8 μm); setae sparsely scattered throughout body. Setae 5.4 to 8.1 μm long also present on tail. Cuticle smooth in cephalic region, but becomes annulate approximately at level of cephalic setae; ornamentation at anterior margin in form of minute punctation; posteriorly replaced by oval and then virgate sclerites. In anal region sclerites again round. Lateral differentiation lacking. Amphids not detected. Oral cavity small and armed with three teeth of unequal size; larger dorsal
210 tooth 3.6 μm long and two subventral ones 2.4 μm long. Esophagus with elongated bulb 32.4 μm × 24.3 μm.

Reproductive system of female consists of paired reflexed tubes.

Large egg, 62.1 μm in diameter, found in one genital tube. Sexual armature of male represented by nine accessory organs, spicules, and gubernaculum. Spicules curved, 61.2 μm long, or 1.1 to 1.2 anal body diameters. Gubernaculum simple and 34.8 μm long.

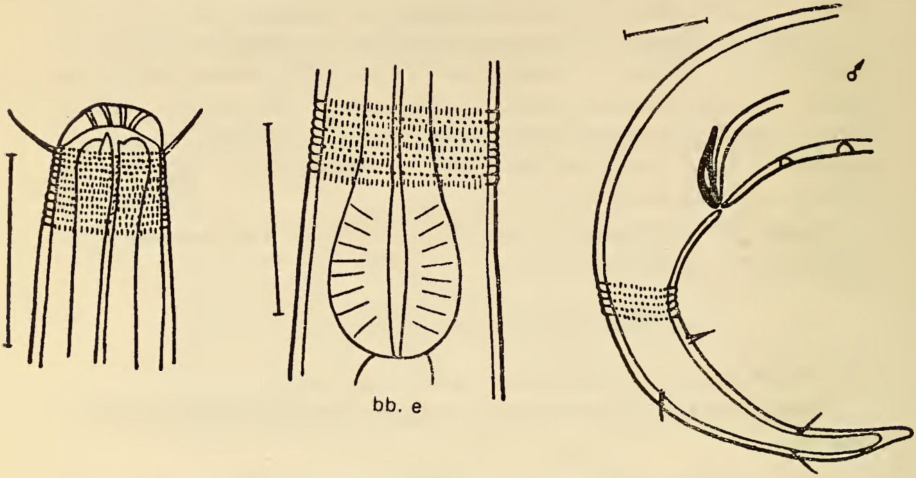


Figure 20. *Prochromadorella crassispicula* sp. n.

Of all the known species of the genus, the White Sea species may be compared with *P. obtusidens* (Stekhoven and Adam, 1931) from the Belgian coast, which has been described on the basis of only males. *P. crassispicula* can be distinguished from *P. obtusidens* by the much longer cephalic setae, presence of setae throughout body, and shape of large dorsal tooth (in the White Sea species absolutely straight). On the basis of these characters it seems feasible to isolate *P. crassispicula* as a new species. It should be noted that had it been possible to compare males the distinguishing features would undoubtedly be more.

Geographic distribution. Found in the White Sea in all horizons of the littoral zone in slightly silted sand.

15. Genus *Prochromadora* Filipjev, 1922

16. *Prochromadora bulbosa* sp. n. (Figure 21)

Holotype ♂: Institute of Zoology, Academy of Sciences, USSR. Collection No. 30.

$$\frac{\text{—}\quad 59.4\quad 90.4\quad \text{—}\quad 332.1}{13.5\quad 21.6\quad 24.3\quad 27.0\quad 24.3}\ 413.1\ \mu\text{m};\ a=15.3;\ b=4.6;\ c=5.1.$$

Paratypes.

$$3\,♂\!:\ \frac{\text{—}\qquad 48.6\text{–}64.8\qquad 64.8\text{–}97.2\qquad \text{—}\qquad 386.1\text{–}440.1}{13.5\text{–}18.9\qquad 18.9\text{–}21.6\qquad 22.9\text{–}24.3\qquad 27.0\text{–}29.7\qquad 24.3\text{–}27.0}$$

× 469.8–523.8 μm; a = 17.4–18.2; b = 5.4–8.3; c = 5.5–6.2.

$1\ \text{juv.:}\ \dfrac{-\qquad 54.0\qquad 91.8\qquad -\qquad 351.0}{16.2\qquad 20.2\qquad 21.6\qquad 24.3\qquad 18.9}\ 431.2\ \mu\text{m};\ a = 17.3;\ b = 4.6;\ c = 6.0.$

Body short and tapers to 2/3 midbody diameter at anterior end and
10/11 to 5/6 at posterior end. Head not demarcated from body. Tail
conical but acicular at end. Cephalic setae 7.2 μm, equal to 0.5 cephalic
diameter. Setae absent on rest of body. Cuticle annulate, and ornamented
with round sclerites; latter smaller on head than on rest of body.
Lateral differentiation absent. Amphids not detected. Oral cavity small
211 and armed with tooth 3.6 μm long. Esophagus with bulb 22.8 μm × 18.0
μm. Spicules curved, large, 33.6 μm long, or 1.5 anal body diameters.
Gubernaculum small (12.0 μm) and resembles a walking stick with the
handle turned upward.

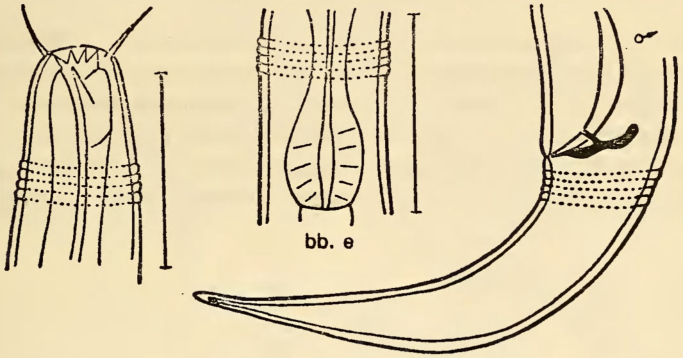


Figure 21. *Prochromadora bulbosa* sp. n.

P. bulbosa may be compared with one of the closest species of the genus—*P. oerlayi* (de Man)—from which the White Sea species differs in index *c*, absence of setae throughout body (except for head), absence of eye pigment spots, shape of spicules and gubernaculum, larger size, and absence of accessory organ. This enables one to consider the species from the White Sea new.

Geographic distribution. Found in the White Sea, mainly at the upper and lower horizons of the littoral zone in slightly silted sand.

7. Family CYATHOLAIMIDAE Filipjev, 1918

16. Genus *Paracanthonchus* Micoletzky, 1924

Synonyms: *Harveyjohnstonia* Mawson, 1953; *Metacanthonchus* Wieser, 1954; *Paraseuratiella* Stekhoven, 1950.

17. *Paracanthonchus medius* sp. n. (Figure 22)

Holotype ♂: Institute of Zoology, Academy of Sciences, USSR. Collection No. 31.

$$\frac{\begin{array}{ccccc} - & 99.0 & 198.0 & - & 990.0 \end{array}}{\begin{array}{ccccc} 22.0 & 33.0 & 38.0 & 44.0 & 34.0 \end{array}}\ 1{,}089.0\ \mu\text{m};\ a=24.8;\ b=5.5;\ c=11.0.$$

Paratypes.

$$2\,♂\!:\ \frac{\begin{array}{cccc} - & 104.0\text{–}121.0 & 187.0\text{–}220.0 & - \end{array}}{\begin{array}{cccc} 16.0\text{–}20.0 & 24.0\text{–}35.0 & 33.0\text{–}44.0 & 39.0\text{–}49.0 \end{array}} \times \frac{814.0\text{–}1{,}155.0}{31.0\text{–}44.0}\ 913.0\text{–}1{,}254.0\ \mu\text{m};\ a=23.7\text{–}25.3;$$

$$b=4.9\text{–}5.7;\ c=9.2\text{–}12.7.$$

$$1\,♀\!:\ \frac{\begin{array}{cccccc} - & 110.0 & 231.0 & 671.0 & 1{,}122.0 \end{array}}{\begin{array}{cccccc} 22.1 & 33.0 & 41.0 & 55.0 & 30.0 \end{array}}\ 1{,}232.0\ \mu\text{m};\ a=22.4;$$

$$b=5.3;\ c=11.2;\ V=54.3\%$$

Body rather long and tapers to 1/2 midbody diameter at anterior end and 5/6 to 10/13 at posterior end. Head anteriorly truncated; not demarcated from body. Tail conical and length 3.5 anal body diameters. Cephalic setae situated in two circles (Figure 22) and 10.8 μm long, i.e., approximately 1/2 cephalic diameter. Setae absent on tail. Cuticle annulate and ornamented with round, punctate sclerites, larger in cephalic

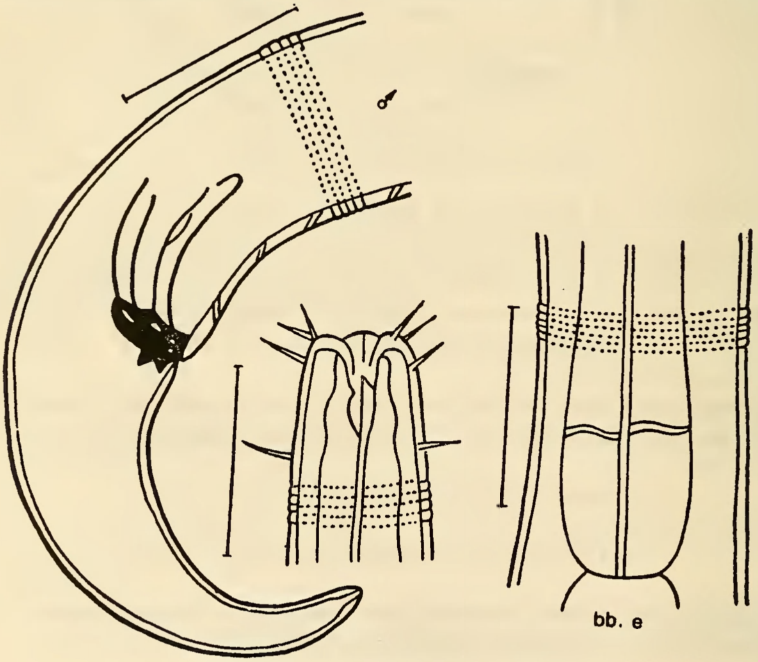


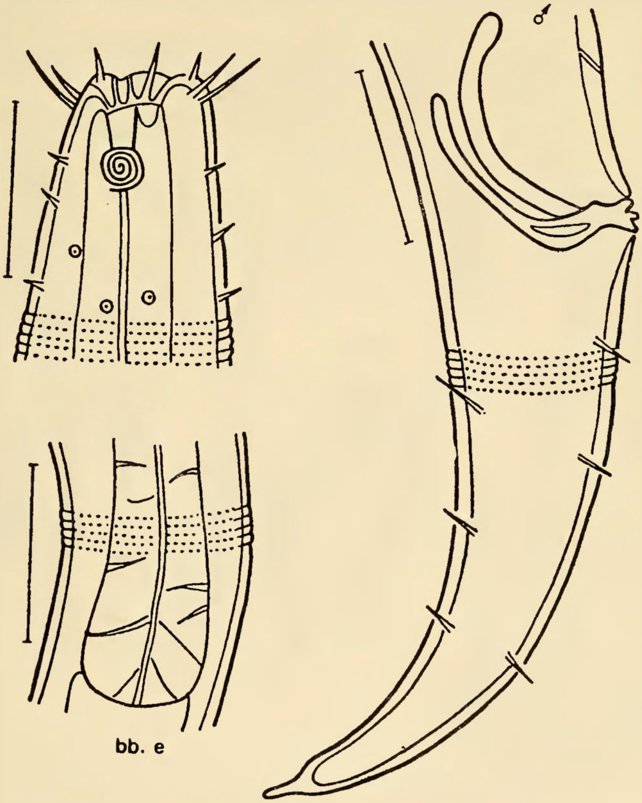
Figure 22. *Paracanthonchus medius* sp. n.

region than on rest of body. Amphids not detected. Oral cavity large, 15.6 μm × 8.4 μm, and armed with single tooth 4.8 μm long. Esophagus without bulb and dilates gradually toward base.

Reproductive system of female consists of paired unflexed tubes. Genital armature of male represented by four tubular accessory organs, spicules, and gubernaculum. Spicules curved, rather long (48.0 μm), and slightly broader in distal part. Gubernaculum well developed, length almost equal to spicular length (44.4 μm), and armed with several small denticles at distal end.

This White Sea species is very close to *P. uniformis* (Stekhoven, 1950), described from the coast of the Mediterranean Sea, but can be distinguished from it by indices *a* and *b*, longer cephalic setae, absence of pigmented eyes, and shape and size of gubernaculum and spicules. These characters enable one to consider *P. medius* a new species.

Geographic distribution. Found in the White Sea in all horizons of the littoral zone in slightly silted sand.



212 Figure 23. *Paracanthonchus macrodon.*

18. *Paracanthonchus macrodon* (Ditlevsen, 1910) (Figure 23)

Ditlevsen, 1919: 200, pls. 11, 12, figs 6–8 (*Cyatholaimus*); Micoletzky, 1924: 138.

213 4 ♂: L=990.0–1,320.0 μm; a=19.5–29.4; b=5.3–6.3; c=9.1–12.9.
1 ♀: L=902.0 μm; a=23.4; b=5.6; c=10.2; V=51.1%.

The White Sea population coincides with those specimens described earlier with respect to major characters and measurements, but is slightly smaller in size than species described from the coast of the North Sea.

Geographic distribution. Found in the White, Norwegian, Baltic and North Seas in all horizons of the littoral zone in slightly silted sand.

8. Family COMESOMATIDAE Filipjev, 1918

17. Genus *Sabatieria* de Rouville, 1904

19. *Sabatieria vulgaris* (de Man, 1907) (Figure 24)

de Man, 1907: 66–67, fig. 12a–i (*Parasabatieria*); Filip'ev, 1934: 27.

2 ♂: L=2,167.0–2,299.0 μm; a=49.4–52.3; b=7.2–8.6; c=16.1–16.4.
2 ♀: L=1,815.0–2,035.5 μm; a=37.0–39.3; b=10.2–10.3; c=14.8–16.5; V=50.6–53.0%.
1 juv.: L=1,133.0–1,166.0 μm; a=34.3–35.4; b=5.6–6.9; c=8.6–9.1.

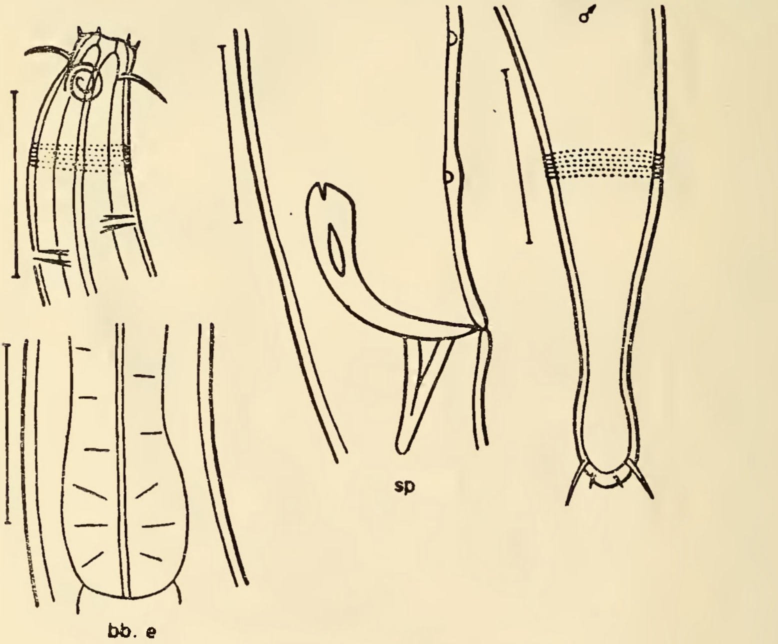


Figure 24. *Sabatieria vulgaris.*

The White Sea population coincides very well with that described earlier by de Man, but individuals are smaller in size than those of the species described from the coast of the North Sea. Judging from the drawing given by de Man, the White Sea species also has longer cephalic setae (3.6 μm).

Geographic distribution. Found in the White, Baltic, and North Seas, mainly at the middle and lower horizons of the littoral zone in slightly silted sand.

9. Family CHOANOLAIMIDAE Schuurmans-Stekhoven and Adam, 1931

18. Genus *Halichoanolaimus* de Man, 1886

20. *Halichoanolaimus robustus* (Bastian, 1865) (Figure 25)

Bastian, 1865; 166, pl. 13, fig. 226 (*Spilophora*); de Man, 1888; 38, pl. 4, fig. 17; Allgen, 1929; 454, fig. 16a, b (*Smalsundia punctata*).

1♂: L = 2,112.0 μm; a = 27.4; b = 6.7; c = 19.2.
1♀: L = 1,419.0 μm; a = 16.2; b = 5.9; c = 18.1; V = 45.0%.
1 juv.: L = 1,529.0 μm; a = 27.8; b = 5.4; c = 17.4.

214 The White Sea population conforms very well to the description given by de Man (1888), but individuals are somewhat smaller than those of the species described earlier from the coast of the North Sea.

Geographic distribution. Found in the White, Baltic, Irish, Norwegian, and North Seas, mainly in the middle and lower horizons of the littoral zone in slightly silted sand.

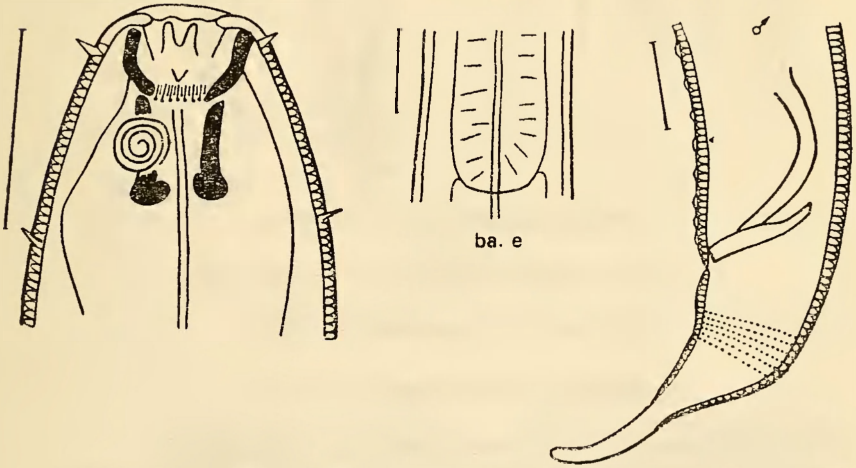


Figure 25. *Halichoanolaimus robustus.*

3. Order **MONHYSTERIDA**

10. Family SPHAEROLAIMIDAE Filipjev, 1918

19. Genus *Sphaerolaimus* Bastian, 1865

Synonym: *Parasphaerolaimus* Ditlevsen, 1919.

21. *Spharolaimus macrolasius* Schulz, 1932 (Figure 26)

1 ♂: L = 1,859.0 μm; a = 16.9; b = 4.5; c = 9.9.
3 ♀: L = 1,639.0–1,947.0 μm; a = 14.8–19.2; b = 4.8–5.4; c = 8.8–9.1; V = 69.9–73.5%.
1 juv.: L = 1,276.0 μm; a = 16.6; b = 4.5; c = 7.2.

The White Sea population conforms completely to the description given by Schulz with respect to characters and measurements, but individuals are smaller than those from the North Sea.

215 **Geographic distribution.** Found in the White and North Seas in all horizons of the littoral zone in slightly silted sand.

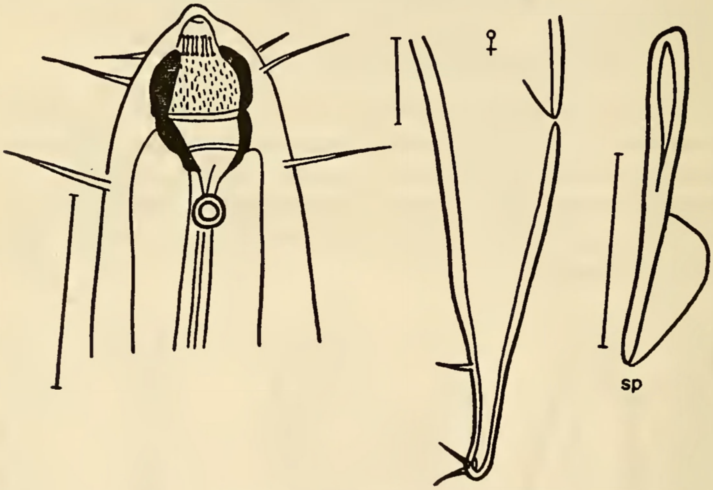


Figure 26. *Sphaerolaimus macrolasius.*

11. Family MONHYSTERIDAE de Man, 1867

20. Genus *Theristus* Bastian, 1865

1. Subgenus *Mesotheristus* Wieser, 1956

22. *Theristus* (*Mesotheristus*) *setosus* (Buetschli, 1874) Figure 27

Bütschli, 1874; 29, pls. 5, 6, fig. 4 (*Monhystera setosa*); Filip'ev, 1918: 277.

4 ♂: L = 1,227.0–1,496.0 μm; a = 17.5–20.8; b = 3.4–3.7; c = 5.8–6.4.
2 ♀: L = 1,914.0–2,200.0 μm; a = 16.6–17.4; b = 3.6–4.1; c = 7.0–7.4; V = 68.0–74.2%.

This White Sea species fully conforms to the earlier description by Bütschli (1874) with respect to all characters and measurements.

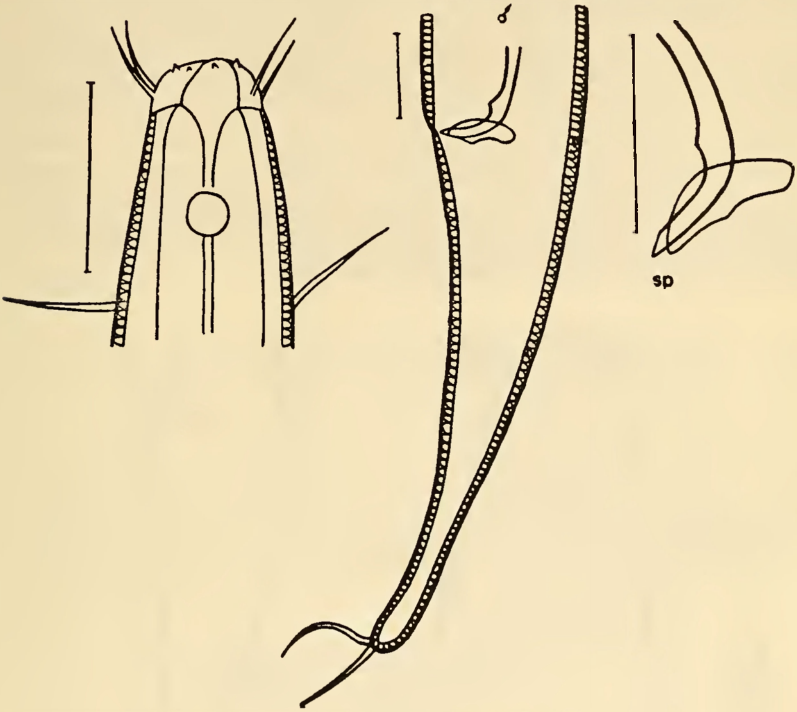


Figure 27. *Theristus setosus.*

Geographic distribution. Found in the White, Baltic and North Seas in all horizons of the littoral zone in slightly silted sand.

23. *Theristus* (*Mesotheristus*) *platonovae* sp. n. (Figure 28)

Holotype ♂: Institute of Zoology, Academy of Sciences, USSR. Collection No. 50.

$$\frac{11.1 \quad 165.0 \quad 473.0 \quad - \quad 1{,}485.0}{27.0 \quad 66.0 \quad 88.0 \quad 99.0 \quad 66.0}\ 1{,}782\ \mu\text{m};\ a = 18.0;\ b = 3.8;\ c = 6.2.$$

Paratypes.

$$2\,♂\!:\ \frac{12.0\text{–}13.0 \quad 165.0\text{–}176.0 \quad 482.0\text{–}484.0 \quad -}{27.0\text{–}34.0 \quad 71.0\text{–}73.0 \quad 82.0\text{–}94.0 \quad 93.0\text{–}104.0}$$

$$\times \frac{1{,}529.0\text{–}1{,}562.0}{60.0\text{–}66.0}\ 1{,}782.0\text{–}1{,}859.0\ \mu\text{m};\ a = 17.1\text{–}19.8;\ b = 3.7\text{–}3.8;$$

$$c = 6.3\text{–}7.0.$$

1 ♀: $$\frac{11.0 \quad 187.0 \quad 495.0 \quad 1{,}408.0 \quad 1{,}620.0}{33.0 \quad 77.0 \quad 99.0 \quad 115.0 \quad 66.0}\ 1{,}892.0\ \mu\text{m};\ a=16.4;$$
$$b=3.8;\ c=7.2;\ V=74.4\%.$$

216 Body long and wide; tapers to 2/7 midbody diameter at anterior end and 2/3 at posterior end. Tail long and divided into two parts: conical part 2/3 caudal length and cylindrical 1/3. Cephalic setae unequal in size; one seta in each pair much thicker and rather longer (13.5 μm) and the other one thinner and shorter (10.1 μm). Cervical setae thin and long (38.0 μm). Some setae present on tail and 10.0 to 12.0 μm long. Cuticle annulate. Amphids round, thin-walled, 7.8 μm in diameter (1/5 corresponding head diameter), and located 43.2 μm from anterior end. Oral cavity well developed, 18.9 μm × 10.8 μm, and internally supported by sclerotized ring. Labia with rough folds on inner side. Esophagus cylindrical and uniform in width throughout its length.

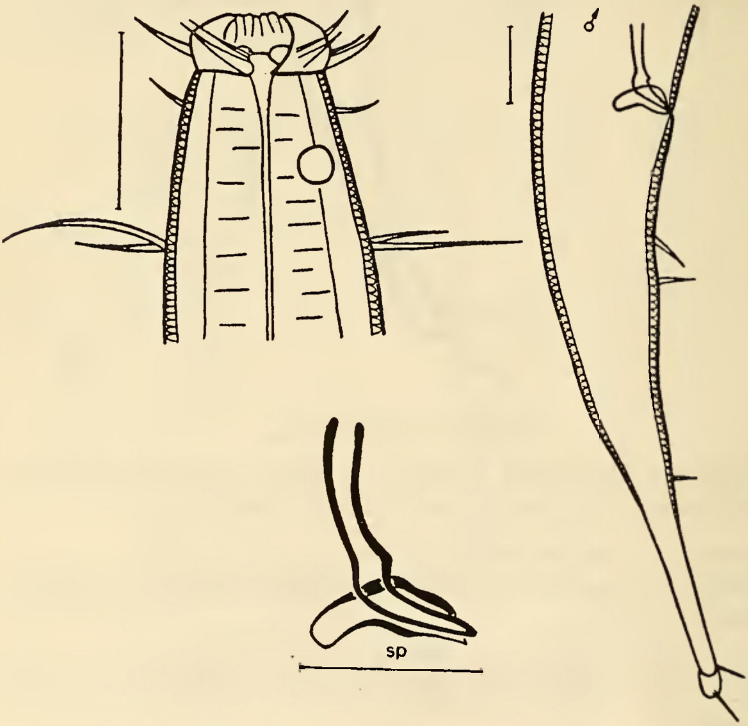


Figure 28. *Theristus platonovae* sp. n.

Reproductive system of females consists of paired (anterior) unflexed tubes. Spicules of male slightly curved and 56.7 μm long. Gubernaculum large (45.9 μm), with an appendage 13.5 μm long.

Of all the known species of this subgenus, this species is comparable to *T.* (*M.*) *hirtus* Gerlach, 1951, described from the coast of the North Sea. It can be distinguished from the remaining species by its much larger size and width of body (index *a*), different structure of the gubernaculum, characteristic structure of the cephalic setae, small number of setae on the body, and labia with rough folds. All this enables one to consider *T. platonovae* an independent species.

Geographic distribution. Found in the White Sea, mainly in the lower and middle horizons in slightly silted sand.

217 2. Subgenus *Pseudosteineria* Wieser, 1956

24. *Theristus* (*Pseudosteineria*) *horridus* (Steiner, 1916) (Figure 29)

Steiner, 1916b: 643, tab. 33, fig. 40a–c (*Monhystera horrida*); Filip'ev, 1918: 278.

1 ♂: L = 1,101.0 μm; a = 21.4; b = 3.7; c = 6.6.
2 ♀: L = 1,412.0–1,584.0 μm; a = 17.4–18.1; b = 4.3–4.5; c = 6.8–7.8; V = 66.0–68.0%.
3 juv.: L = 902.0–1,485.0 μm; a = 16.4–18.0; b = 3.4–4.0; c = 5.9–7.1.

The White Sea population conforms to the description given earlier by Steiner, but certain supplementary characters need to be added as the previous description was based only on a female. Spicules of male somewhat curved and almost uniform in width throughout their length

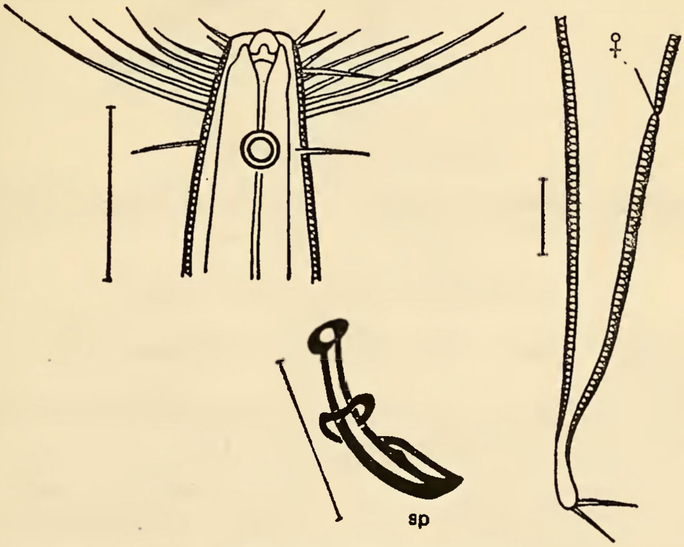


Figure 29. *Theristus horridus.*

(43.2 µm). Capitulum distinctly present at proximal end of spicule. Gubernaculum closely apposed to spicules, with proximal part terminating in dilatation, length 27.0 µm (about 2/3 spicular length).

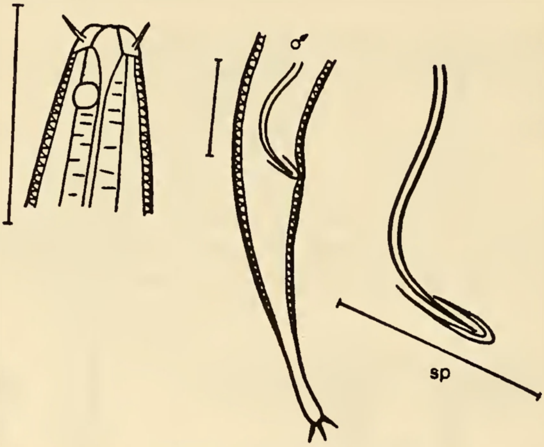
Geographic distribution. Found in the White and Barents Seas in all horizons of the littoral zone in slightly silted sand.

3. Subgenus *Daptonema* Cobb, 1920

25. *Theristus* (*Daptonema*) *procerus* Gerlach, 1951 (Figure 30)

3 ♂: L = 677.0–803.0 µm; a = 17.9–20.6; b = 3.3–4.6; c = 6.1–6.9.
1♀: L = 675.0 µm; a = 22.8; b = 3.1; c = 6.8; V = 64.6%.

The White Sea population conforms very well to the earlier description with respect to all characters and measurements given by Gerlach (1951b).



218 Figure 30. *Theristus procerus.*

Geographic distribution: Found in the White and North Seas in all horizons of the littoral zone in slightly silted sand.

4. Subgenus *Penzancia* de Man, 1922

26. *Theristus* (*Penzancia*) *flevensis* Schuurmans-Stekhoven, 1935 (Figure 31)

de Man 1922: 221, fig. 6a–e [*Monhystera* (*Penzancia*) *velox*] *et auctorum* non Bastian, 1865 (synonyms: see Wieser, 1956).

4 ♂: L = 913.0–1,071.0 µm; a = 33.2–44.0; b = 4.4–5.5; c = 5.9–6.9.
2 juv.: L = 990.0–1,034.0 µm; a = 31.4–42.4; b = 4.7–4.9; c = 6.9–7.2.

The White Sea population conforms to the earlier description and

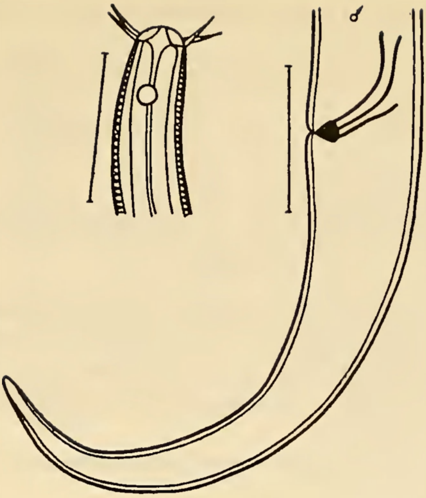


Figure 31. *Theristus flevensis.*

measurements given by de Man. Gerlach (1951b) has described this species in greater detail.

Geographic distribution. Found in the White, Baltic, and North Seas in all horizons of the littoral zone in slightly silted sand.

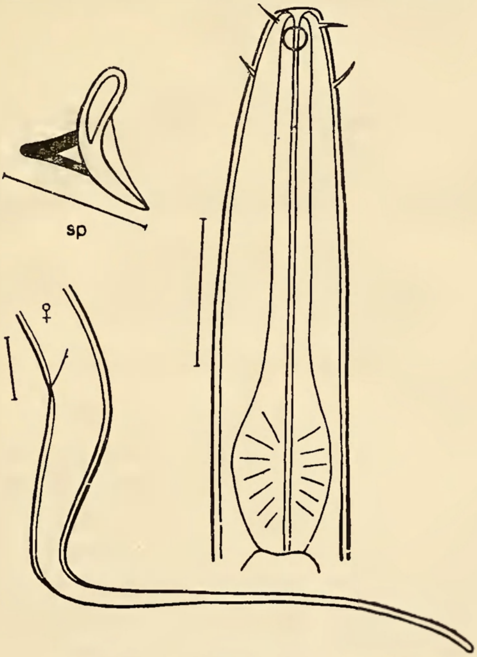


Figure 32. *Terschellingia longicaudata.*

12. Family LINHOMOEIDAE Filipjev, 1922

21. Genus *Terschellingia* de Man, 1888

27. *Terschellingia longicaudata* de Man, 1907 (Figure 32)

1 ♂: L = 1,804.0 µm; a = 41.0; b = 10.8; c = 4.1.
1 ♀: L = 1,593.0 µm; a = 37.0; b = 11.6; c = 4.3; V = 44.1%.
2 juv.: L = 1,342.0–1,430.0 µm; a = 38.1–40.6; b = 10.1–11.8; c = 3.5–3.6.

The White Sea population conforms entirely to the earlier description given by de Man with respect to all characters and measurements.

219 **Geographic distribution.** Found in the White, Baltic, Norwegian and North Seas in all horizons of the littoral zone in slightly silted sand.

22. Genus *Metalinhomoeus* de Man, 1907

Synonym: *Deltanema* Kreis, 1929.

28. *Metalinhomoeus obtusiceps* sp. n. (Figure 33)

Holotype ♂: Institute of Zoology, Academy of Sciences, USSR. Collection No. 56.

$$\frac{\text{—}\quad 99.0\quad 187.0\quad \text{—}\quad 1{,}595.0}{22.0\quad 38.0\quad 44.0\quad 55.0\quad 44.0}\ 1{,}782.0\ \mu\text{m};\ a=32.4;\ b=9.5;\ c=9.5.$$

Paratypes.

$$2\,♂:\ \frac{\text{—}\qquad 77.0\text{–}104.0\qquad 143.0\text{–}170.0\qquad \text{—}}{22.0\text{–}23.0\qquad 27.0\text{–}33.0\qquad 33.0\text{–}37.0\qquad 38.0\text{–}44.0}\times\frac{1{,}100.0\text{–}1{,}540.0}{34.0\text{–}41.0}\ 1{,}232.0\text{–}1{,}727.0\ \mu\text{m};\ a=28.0\text{–}34.9;\ b=8.6\text{–}9.5;\ c=9.2\text{–}9.4.$$

$$2\,♀:\ \frac{\text{—}\qquad 110.0\text{–}111.0\qquad 176.0\text{–}181.0\qquad 1{,}034.0\text{–}1{,}133.0}{21.0\text{–}22.0\qquad 33.0\text{–}34.0\qquad 43.0\text{–}44.0\qquad 54.0\text{–}55.0}\times\frac{2{,}013.0\text{–}2{,}090.0}{32.0\text{–}33.0}\ 2{,}178.0\text{–}2{,}266.0\ \mu\text{m};\ a=40.5\text{–}41.4;\ b=12.0\text{–}12.2;\ c=12.2\text{–}13.2;\ V=47.5\text{–}49.5\%.$$

Body long and tapers to 2/5 midbody diameter at anterior end and 10/13 at posterior end. Head flat and not demarcated from body. Tail conical and length equal to four anal body diameters. Cephalic setae long (7.2 µm) and situated in one circle. Setae absent on tail. Cuticle smooth. Amphids resemble an incomplete spiral, 7.1 µm in diameter, situated 12.0 µm from anterior end. Oral cavity small with supporting internal sclerotized ring. Esophagus with bulb 16.5 µm × 14.3 µm.

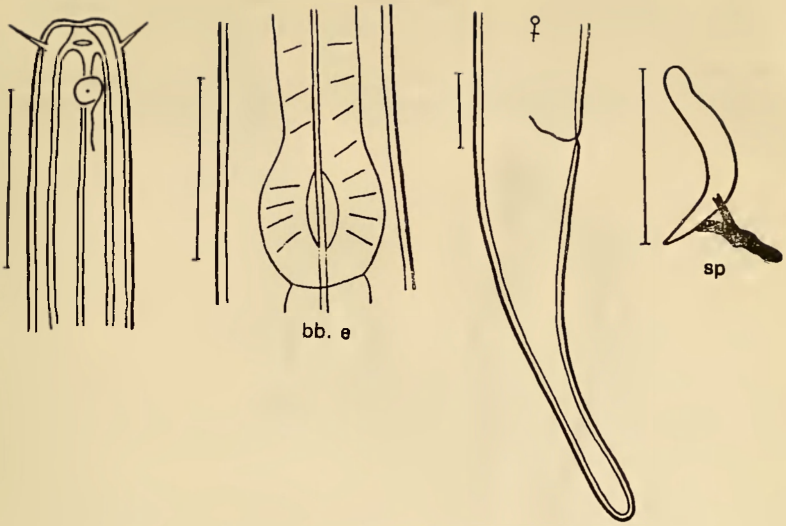


Figure 33. *Metalinhomoeus obtusiceps* sp. n.

Reproductive system of female consists of paired unflexed tubes. Spicules arcuate, taper in distal part, and 44.4 µm long. Gubernaculum 13.2 µm long, with an appendage with a bifurcate base.

Of all the known species of this genus, this species is comparable to *M. zosterae* Filipjev, 1918, but differs in much smaller body size (index *a*), smooth cuticle, shape of amphids, and spicules and gubernaculum twice as large.

Geographic distribution. Found in the White Sea in all horizons of the littoral zone in slightly silted sand.

220 4. Order ARAEOLAIMIDA

13. Family TRIPYLOIDAE Filipjev, 1918

23. Genus *Tripyloides* de Man, 1886

Synonym: *Nannonchus* Cobb, 1913.

29. *Tripyloides septentrionalis* de Coninck and Schuurmans-Stekhoven,1933 (Figure 34)

de Man 1922: 229, fig. 18 (*T. marinus*); Ditlevsen, 1919: 190, tabs. 9, 10, figs. 3, 4 (*Cothonolaimus gracilis*).

3 ♂: L = 1,133.0–1,617.0 μm; a = 34.4–37.7; b = 4.0–5.8; c = 11.4–14.7.
1 juv.: L = 913.0 μm; a = 29.7; b = 4.6–6.9; c = 10.4.

The White Sea population conforms well to the description given by de Coninck and Stekhoven with respect to all characters and measurements.

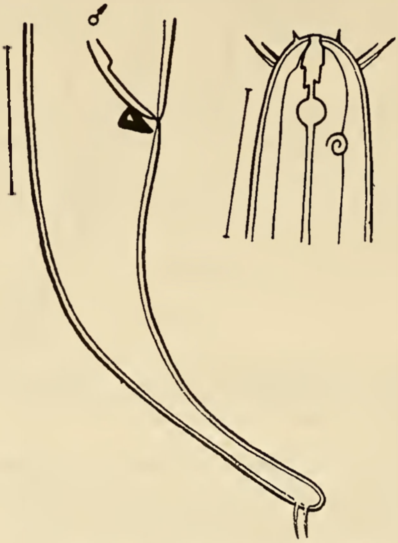


Figure 34. *Tripyloides septentrionalis.*

Geographic distribution. Found in the White, Norwegian, Baltic and North Seas, mainly in the upper horizon of the littoral zone in slightly silted sand.

14. Family AXONOLAIMIDAE Filipjev, 1918

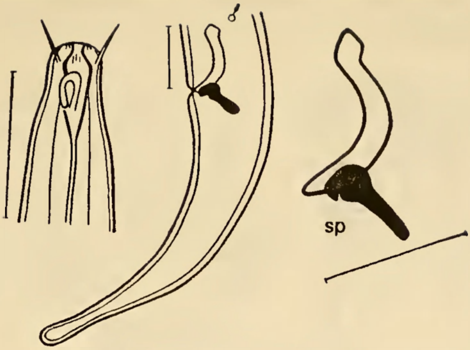
24. Genus *Axonolaimus* de Man, 1889

30. *Axonolaimus paraspinosus* Schuurmans-Stekhoven and Adam, 1931 (Figure 35)
de Man, 1888: 19, pl. 19, fig. 11 (*Anoplostoma spinosum*).

2 ♂: L = 1,566.0–1,925.0 μm; a = 35.0–38.6; b = 6.7–7.6; c = 10.4–10.6.
3 juv.: L = 1,133.0–1,551.0 μm; a = 29.5–40.9; b = 5.7–6.7; c = 8.2–10.1.

The White Sea specimens conform entirely to the earlier description given by de Man.

Geographic distribution. Found in the White, Baltic, and North Seas in all horizons of the littoral zone in slightly silted sand.



221 Figure 35. *Axonolaimus paraspinosus.*

25. Genus *Odontophora* Buetschli, 1874

Synonyms: *Conolaimus* Filipjev, 1918 and *Trigonolaimus* Ditlevsen, 1919.

31. *Odontophora deconincki* nom. nov. (Figure 36)
de Coninck and Schuurmans-Stekhoven, 1933: 108, figs. 89–95 (*armata*), non *Trigonolaimus armatus*; Ditlevsen, 1919: 178, figs. 1, 4, 6, 7.

2 ♀: L = 3,102.0–3,278.0 μm; a = 59.6–70.0; b = 17.6–18.6; c = 18.8–24.8; V = 51.5–54.2%.

The White Sea specimens conform well to the description given by de Coninck and Stekhoven for species from the coast of the North Sea.

Ditlevsen established a new genus in 1919, *Trigonolaimus*, which de Coninck and Stekhoven considered synonymous with genus *Odontophora* Bütschli, 1874. They considered *Odontophora armata*, described by them, identical to *Trigonolaimus armatus* Ditlevsen, 1919. After analyzing the works of these authors in detail, I came to the conclusion that these are two independent species. The species described by de Coninck and Stekhoven is distinguishable from that described by Ditlevsen with respect to indices of species given by de Man, a more truncated head, and longer cephalic setae. In the species described by Ditlevsen setae are absent throughout the body and amphids situated in the anterior part of the oral cavity; in the species described by de Coninck and Stekhoven the amphids are situated posteriorly. The later species (*Odontophora armata*) also has a finely annulate cuticle, which is smooth in the species described by Ditlevsen. Furthermore, these species differ from each other in shape of spicules and gubernaculum. All these features enable one to consider them separate species. For *O. armata* de Coninck and Stekhoven, 1933 I have proposed a new name, *O. deconincki*. *O. armata* is retained for the species described by Ditlevsen.

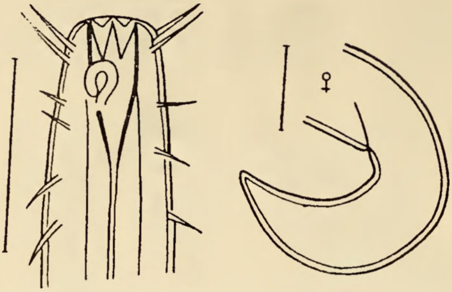


Figure 36. *Odontophora deconincki* nom. nov.

Geographic distribution: Found in the White, Baltic and North Seas, mainly in the lower and middle horizons of the littoral zone in slightly silted sand.

5. Order DESMODORIDA

15. Family MONOPOSTHIIDAE Filipjev, 1934

26. Genus *Monoposthia* de Man, 1889

32. *Monoposthia octalata* sp. n. (Figure 37)

Holotype ♂: Institute of Zoology, Academy of Sciences, USSR. Collection No. 62.

$$\frac{-}{22.0}\quad\frac{104.0}{33.0}\quad\frac{204.0}{38.0}\quad\frac{-}{50.0}\quad\frac{1{,}210.0}{34.0}\ 1{,}336.0\ \mu\mathrm{m};\ a=26.3;\ b=6.2;\ c=10.5.$$

Paratypes.

$$2\,♀\!:\ \frac{-}{22.0\text{–}23.0}\quad\frac{115.0\text{–}121.0}{38.0\text{–}43.0}\quad\frac{205.0\text{–}231.0}{44.0\text{–}55.0}\quad\frac{1{,}243\text{–}1{,}254}{44.0\text{–}56.0}\times\frac{1{,}342\text{–}1{,}406}{32.0\text{–}33.0}\ 1{,}463.0\text{–}1{,}507.0\ \mu\mathrm{m};\ a=22.8\text{–}24.2;\ b=6.4\text{–}7.3;\ c=12.1\text{–}12.4;\ V=83.2\text{–}85.0\%.$$

$$2\ \text{juv.}\!:\ \frac{-}{22.0\text{–}23.0}\quad\frac{77.0\text{–}110.0}{32.0\text{–}35.0}\quad\frac{181.0\text{–}203.0}{44.0\text{–}45.0}\quad\frac{-}{49.0\text{–}55.0}\times\frac{929.0\text{–}1{,}023.0}{24.0\text{–}27.0}\ 1{,}034.0\text{–}1{,}144.0\ \mu\mathrm{m};\ a=20.4\text{–}20.8;\ b=5.6\text{–}5.7;\ c=9.5\text{–}9.9.$$

Body not very long and tapers to 10/23 midbody diameter at anterior end and 5/7 at posterior end. Head flat and not demarcated from body. Tail conical. Cephalic setae 10.8 μm long. Small number of setae, 3.0 to 4.0 μm long, also present on tail. Cuticular annulations intersected by

eight longitudinal rays commencing at level of amphids. Amphids small, round, 4.0 μm in diameter (1/5 corresponding head diameter), and situated 3.1 μm from anterior end. Large vestibule, strengthened by wide sclerotized longitudinal rays, situated before oral opening. Oral cavity small and armed with single dorsal tooth 5.4 μm long. Esophagus with dilatations at anterior and posterior ends. Anterior dilatation 29.7 μm ×
222 18.9 μm and posterior bulb 54.0 μm × 29.1 μm.

Reproductive system of female consists of anterior unflexed tubes. Vulva considerably displaced toward anus. Spicules slightly arcuate and 35.1 μm long. Gubernaculum absent.

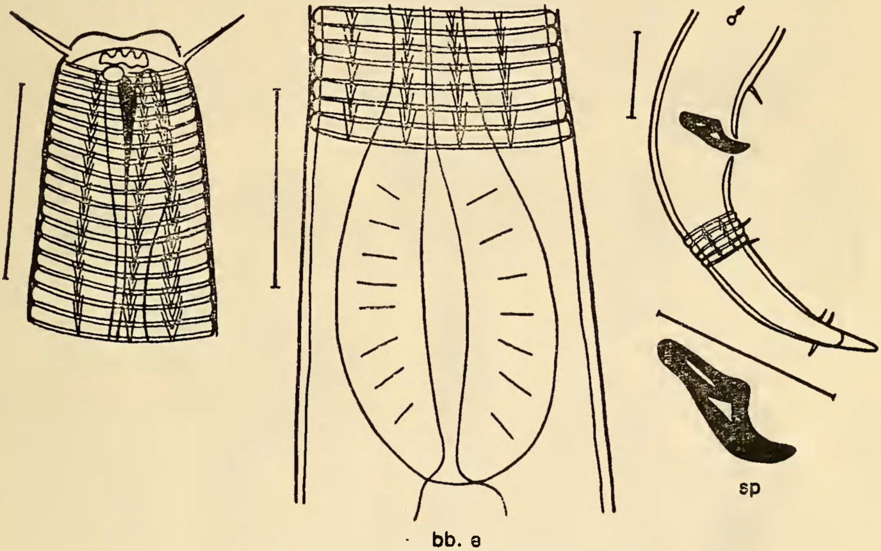


Figure 37. *Monoposthia octalata* sp. n.

With respect to characters and measurements, this species is closest to *M. loricata* Kreis, 1929, but distinguished by number of longitudinal rays (8 versus 12 in *M. loricata*) and presence of only one tooth (versus two in *M. loricata*). These two features suffice to separate *M. octalata* as an independent species.

Geographic distribution. Found in the White Sea in all horizons of the littoral zone in slightly silted sand.

16. Family SPIRINIIDAE Gerlach and Murphy, 1965

27. Genus *Chromodoropsis* Filipjev, 1918

Synonym: *Chromadora* de Man, 1907 nec Bastian, 1865.

33. *Chromodoropsis vivipara* (de Man, 1907) (Figure 38)
De Man 1907, pls. 3–4, fig. 13a–e (*Chromadora*); Filip'ev, 1918: 211.

2 ♂: L = 1,584.0–1,892.0 μm; a = 15.6–18.0; b = 6.1–7.2; c = 15.6–17.0.
1 ♀: L = 1,518.0 μm; a = 18.4; b = 6.0; c = 12.5; V = 58.7%.
2 juv.: L = 1,144.0–1,617.0 μm; a = 23.1–24.5; b = 4.9–6.1; c = 9.9–12.2.

The White Sea specimens conform well to the species described earlier by de Man with respect to all characters and measurements.

Geographic distribution. Found in the White, Barents, and North Seas in all horizons of the littoral zone in slightly silted sand.

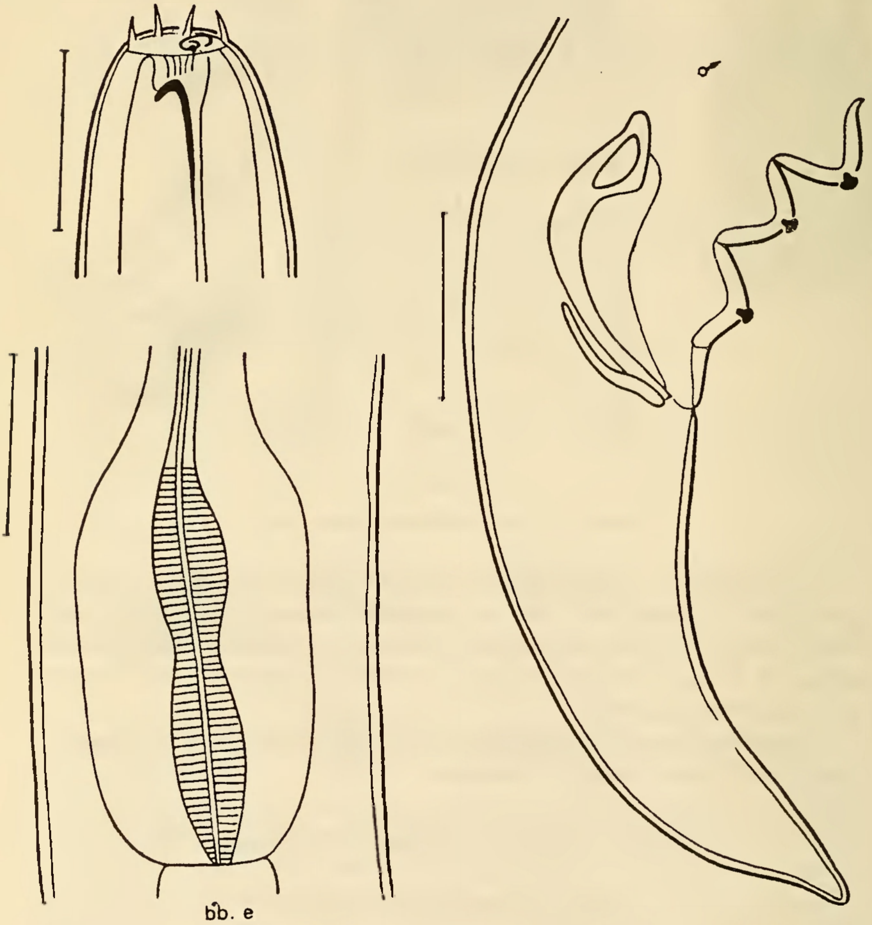


Figure 38. *Chromodoropsis vivipara.*

34. *Chromodoropsis nudicauda* sp. n. (Figure 39)

Holotype ♂: Institute of Zoology, Academy of Sciences, USSR. Collection No. 68.

$$\frac{-\quad 99.0\quad 225.0\quad -\quad 1{,}276.0}{35.0\quad 82.0\quad 89.0\quad 100.0\quad 55.0}\ 1{,}386.0\ \mu\text{m};\ a=13.9;\ b=6.1;\ c=12.6.$$

Paratypes.

$$1\ \text{♂}:\ \frac{-\quad 132.0\quad 242.0\quad -\quad 1{,}441.0}{44.0\quad 82.0\quad 96.0\quad 99.0\quad 77.0}\ 1{,}563.0\ \mu\text{m};\ a=15.8;\ b=6.5;\ c=12.9.$$

$$3\ \text{juv.}:\ \frac{-\quad 110.0\text{–}143.0\quad 247.0\text{–}264.0\quad -}{27.0\text{–}34.0\quad 82.0\text{–}93.0\quad 95.0\text{–}99.0\quad 104.0\text{–}111.0}$$

$$\times\frac{1{,}243.0\text{–}1{,}353.0}{55.0\text{–}77.0}\ 1{,}342\text{–}1{,}507\ \mu\text{m};\ a=12.1\text{–}13.9;\ b=5.4\text{–}5.8;\ c=12.0\text{–}13.6.$$

Body thick and tapers to 5/14 midbody diameter at anterior end and 10/13 to 5/7 at posterior end. Head rounded and not demarcated from body. Tail short and conical. Head with four very short setae (10.9 μm).

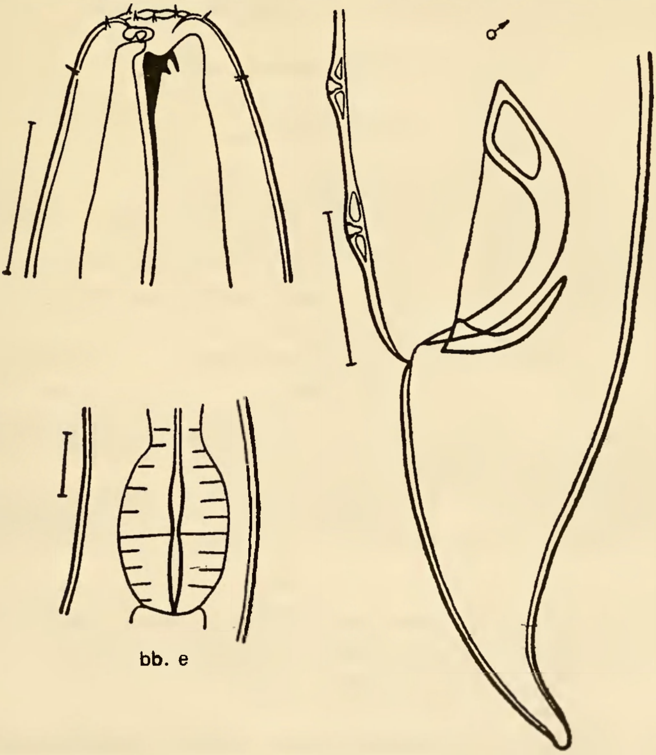


Figure 39. *Chromodoropsis nudicauda* sp. n.

Setae absent on tail. Cuticle finely annulate. Dark brownish strip occurs in sexually immature forms on ventral surface of body from anterior end to anus. It is probably pigmented. Such a pigmented strip is absent in sexually mature forms. Amphids, situated 1.4 μm from anterior end, resemble incomplete spiral 5.7 μm wide and 4.0 μm long (1/4 corresponding body diameter). Oral cavity small and armed with one dorsal tooth 7.5 μm long. Esophagus with large bulb 83.7 μm × 62.1 μm, equal to 1/3 esophageal length.

Sexual armature of male consists of 20 accessory organs, two spicules, and gubernaculum. Wall of accessory organs highly sclerotized and occupies approximately half distance from anus to esophagus. Spicules arcuate, broadened in proximal part, with velum, and 91.8 μm long. Gubernaculum simple and 43.2 μm long.

224 The White Sea specimens come closest to *C. vivipara* de Man, 1907, recorded from the coast of the North Sea. But *C. nudicauda* can be distinguished from *C. vivipara* with respect to indices *a* and *c*, length and shape of spicules and gubernaculum, accessory organs with densely sclerotized walls, and complete absence of setae on tail.

Geographic distribution. Found in the White Sea, predominantly in the lower horizon of the littoral zone in slightly silted sand.

28. Genus *Spirinia* Gerlach, 1963

Synonyms: *Spira* Bastian, 1865 and *Spirina* Filipjev, 1918.

35. *Spirinia parasitifera* (Bastian, 1865) (Figure 40)

Bastian, 1865: 159, pl. 13, figs. 201–203 (*Spira*); Filip'ev, 1918: 232 (*Spirina*); Allgen, 1933: 60, fig. 33 (? *Spirina nidrosiensis*)

3♂: L = 2,937.0–3,256.0 μm; a = 41.1–48.5; b = 17.8–24.2; c = 17.8–21.1.

2 juv.: L = 2,684.0–3,113.0 μm; a = 40.5–40.6; b = 18.8–20.2; c = 15.2–18.9.

The White Sea specimens conform well to the description given earlier with respect to main characters and measurements.

Geographic distribution. Found in the White, Barents, Norwegian, Baltic, and North Seas in all horizons of the littoral zone in slightly silted sand.

225 QUANTITATIVE DISTRIBUTION OF LEADING SPECIES OF NEMATODES IN THE LITTORAL ZONE OF KRUGLO'E BAY

To date no information has been given on the quantitative distribution of nematodes and the dynamics of their population in small areas of

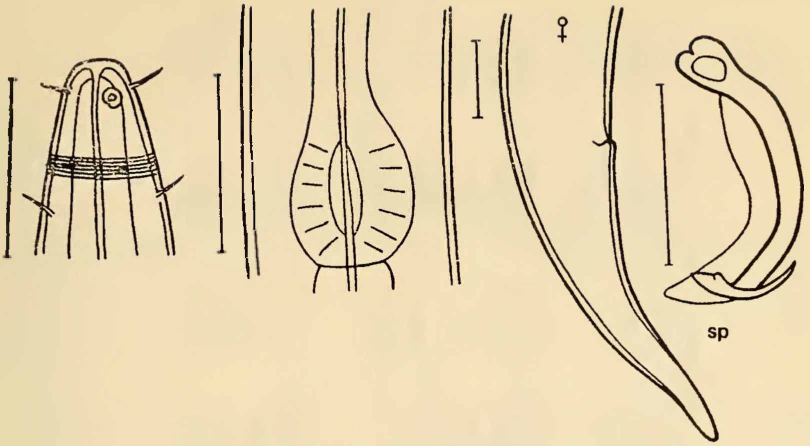


Figure 40. *Spirinia parasitifera.*

the littoral zone with respect to random collection at small intervals of time (for details see p. 233).

Of the 35 species recorded here, 7 occurred in large numbers in both seasons: *Timmia acuticauda, Anoplostoma rectospiculum, Axonolaimus paraspinosus, Enoplus demani, Paracanthonchus macrodon, Hypodontolaimus inaequalis,* and *Theristus setosus.* These species constituted 80 to 90% of the entire nematode population. An attempt has been made to characterize the population dynamics of the leading species in different seasons and to investigate their distribution throughout the section.

Timmia acuticauda (Figures 41 and 42, Table 5). The population of this species was low throughout the section during the summer of 1970. Some increase was observed on July 16, 1970 in the upper and middle horizons of the littoral zone (108,712 to 210,312 specimens/m^2). Toward the end of July the population in these horizons diminished to 71,120 to 116,840 specimens/m^2. Later, during the course of August and through-
226 out the beginning of September an extremely low population level was observed throughout the section, never exceeding 20,000 to 30,000 specimens/m^2. In early September this species was found to be entirely absent in the lower horizon of the littoral zone.

In autumn of 1971 the population of *T. acuticauda* was very high. In the beginning of September two population peaks were observed, one in the middle horizon (1,107,440) and the other in the upper horizon
227 (1,026,160 specimens/m^2). This species was almost absent in the lower horizon. During mid-September one population peak was distinctly evident in the upper horizon of the littoral zone (3,287,260 specimens/m^2), which persisted here until the end of the observation period.

225 Table 5. Population of *Timmia acuticauda* in the littoral zone of Kruglo'e Bay at stations of different heights above 0-depth

Date	1.95 m	1.78 m	1.55 m	1.44 m	1.41 m	1.37 m	1.25 m	1.15 m	0.99 m
1970									
July 7	—	2,032	—	—	—	9,652	25,400	3,556	152,400
July 16	9,652	62,992	210,312	185,420	108,712	106,680	52,324	33,528	8,636
July 27	9,652	6,604	71,120	116,840	94,448	58,928	6,604	14,224	5,080
Aug. 6	23,876	22,352	37,592	9,652	33,020	21,336	—	6,096	—
Aug. 17	3,556	56,896	12,192	32,004	—	10,668	70,104	3,048	—
Aug. 28	2,032	29,972	15,548	51,816	25,908	—	9,144	6,096	—
Sept. 3	3,566	45,720	5,588	6,096	16,764	—	—	5,588	—
1971									
Sept. 8	42,672	103,124	911,860	1,026,160	291,592	1,107,440	54,356	5,588	—
Sept. 17	7,112	104,648	3,287,268	830,072	184,404	181,356	23,876	2,032	27,432
Sept. 28	27,432	325,628	2,560,320	1,059,688	49,784	377,444	5,588	5,588	—
Oct. 9	11,684	46,736	3,286,760	1,241,044	260,096	203,708	34,544	42,164	6,604

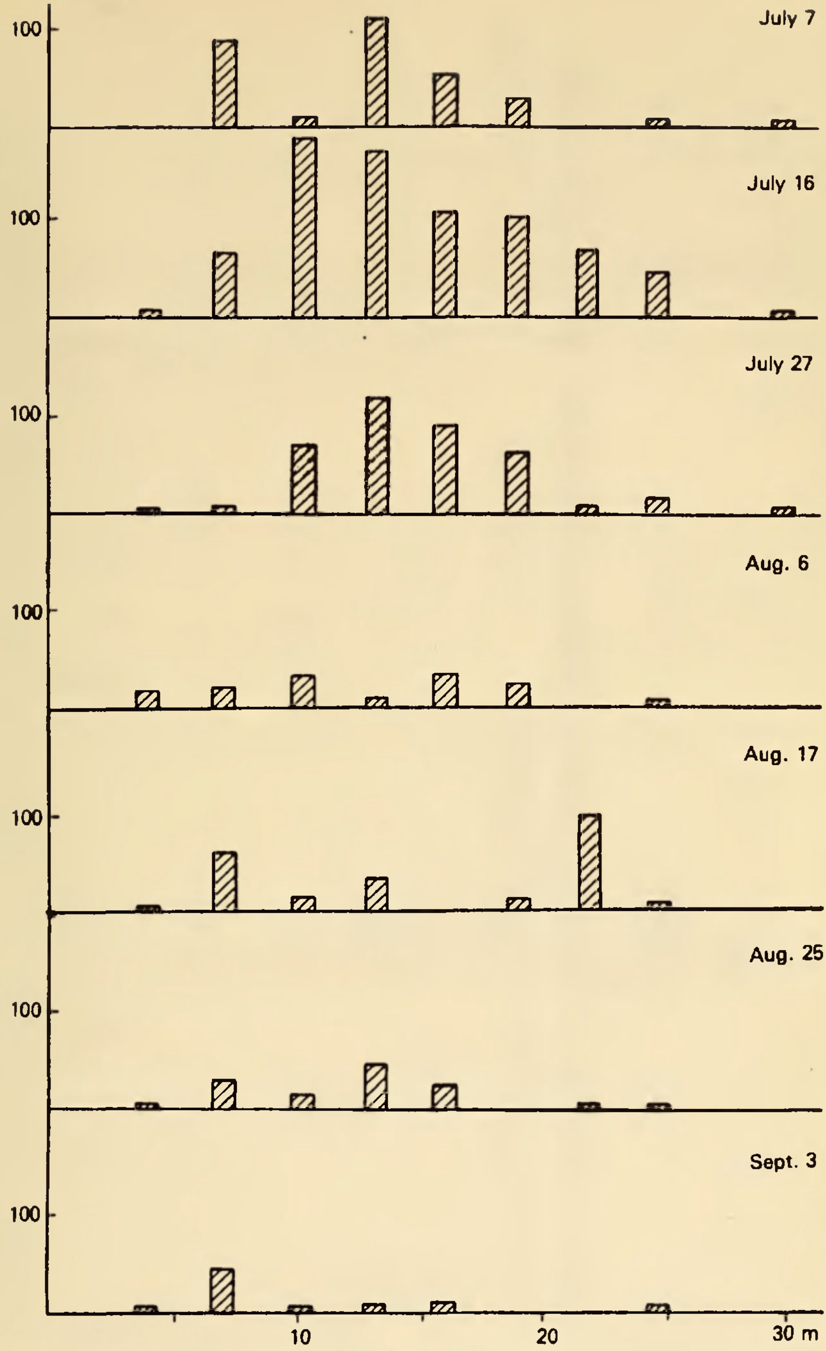


Figure 41. Population dynamics of *Timmia acuticauda* in the littoral zone of Kruglo'e Bay during summer of 1970.

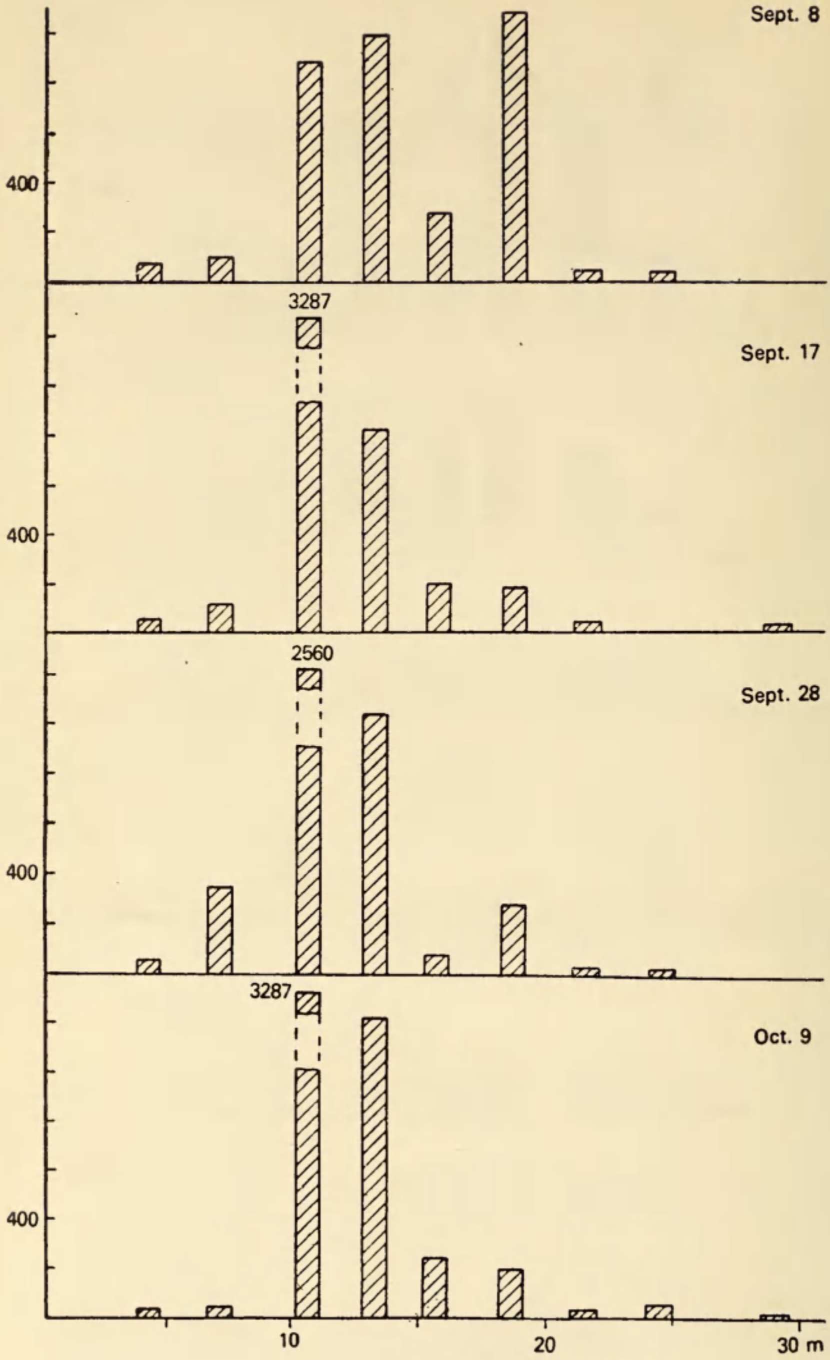
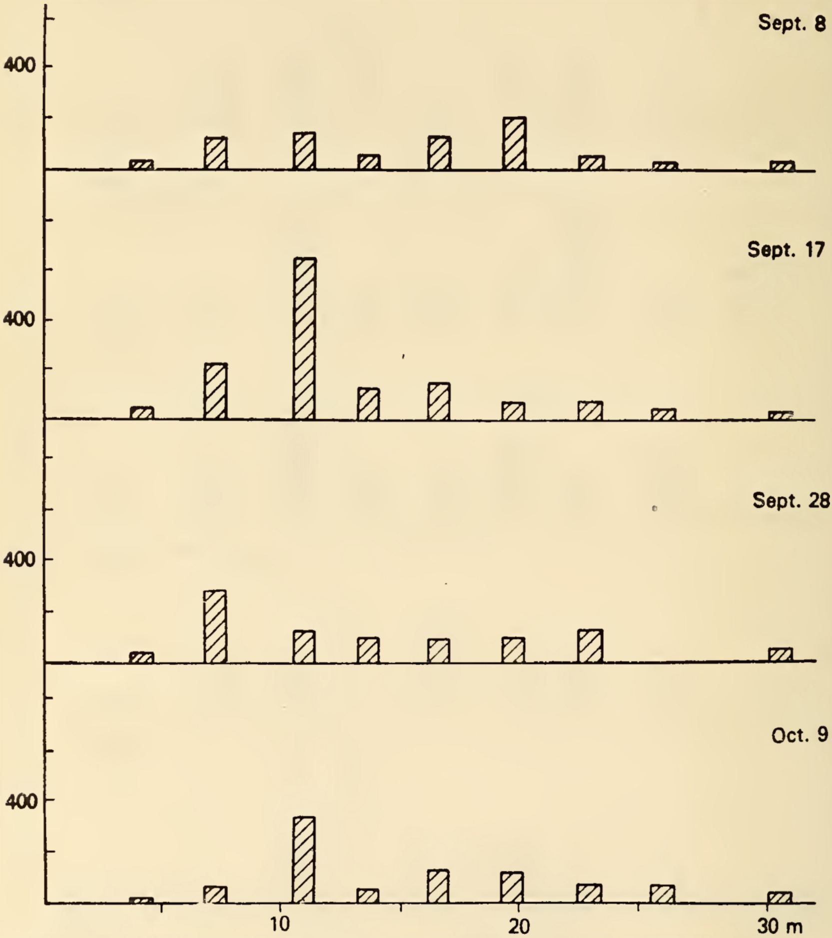


Figure 42. Population dynamics of *Timmia acuticauda* in the littoral zone of Kruglo'e Bay during autumn of 1971.

229 Figure 43. Population dynamics of *Anoplostoma rectospiculum* in the littoral zone of Kruglo'e Bay during summer of 1970.

The population dynamics of *T. acuticauda* could therefore be characterized as: low population during summer, great increase during autumn, localization of specimens in a small area of the littoral zone (lower stratum of upper horizon and part of midde horizon), and sharp reduction in population toward the lower horizon. 228 Probably this species finds more favorable conditions of existence at the junction of the upper and middle horizons of the littoral zone.

Anoplostoma rectospiculum (Figures 43 and 44, Table 6). In the beginning of July, 1970 the species population was rather low throughout the section (4,064 to 162,560 specimens/m^2) with a slightly higher density in the lower horizon. In the middle of June the population rose to



230 Figure 44. Population dynamics of *Anoplostoma rectospiculum* in the littoral zone of Kruglo'e Bay during autumn of 1971.

Table 6. **Population of *Anoplostoma rectospiculum* in the littoral zone of Kruglo'e Bay at stations at different heights above 0-depth**

Date	1.95 m	1.78 m	1.55.m	1.44 m	1.41 m	1.37 m	1.25 m	1.15 m	0.99 m
1970									
July 7	—	—	4,064	136,652	10,688	9,656	83,820	72,644	165,560
July 16	63,500	337,312	238,760	350,520	124,968	230,632	221,996	33,528	25,908
July 27	115,316	214,884	219,456	233,680	102,108	303,276	182,880	198,628	25,400
Aug. 6	193,040	81,280	519,684	204,216	132,080	164,592	179,832	71,628	15,748
Aug. 17	4,064	218,440	113,284	522,732	204,216	162,052	333,756	51,816	35,560
Aug. 25	6,604	102,616	201,168	282,956	368,300	54,864	213,860	164,592	34,036
Sept. 3	3,556	118,872	160,528	283,464	144,780	96,012	249,428	74,168	—
1971									
Sept. 8	3,048	120,396	148,844	44,704	132,588	214,376	66,040	5,588	6,096
Sept. 17	3,556	219,964	678,180	103,632	158,496	47,244	41,656	4,572	6,604
Sept. 28	8,636	271,780	107,696	83,820	71,120	96,520	22,352	—	4,572
Oct. 9	1,016	73,152	348,996	77,216	130,048	136,144	2,540	20,828	13,716

200,000 to 300,000 with a maximum density in the upper (337,312) and middle (350,520 specimens/m^2) horizons. At the end of July approximately the same pattern of distribution persisted throughout the section. In the beginning of August only one population peak occurred in the upper horizon (519,684 specimens/m^2). In the middle of the month the maximum population was found in the middle horizon (522,732 specimens/m^2). At the end of August and early in September the population gradually reduced throughout the section to 100,000 to 200,000 specimens/m^2.

During autumn, 1971 a low density throughout the section was observed with a maximum population in the upper and middle horizons. In the middle of September the population was maximum in the upper horizon (678,180) and varied in the middle and lower horizons (4,572 to 158,496 specimens/m^2). Toward the end of September and early in October a gradual reduction in population occurred throughout the section, remaining maximal in the upper horizon.

The population dynamics of *A. rectospiculum* could therefore be characterized as almost uniform during the summer and autumn seasons, (although somewhat higher during summer). This species is mainly localized in the middle horizon during summer and in the upper horizon during autumn.

Axonolaimus paraspinosus (Figures 45 and 46, Table 7). In the beginning of summer, 1970 this species was distributed along the section symmetrically with respect to the middle horizon where the maximum density occurred (93,436 specimens/m^2); in the upper and lower horizons the population density was low. In the middle of July the high density of population in the middle horizon was still evident (61,468 to 75,184 specimens/m^2); the population rose however in the upper horizon but remained as low as before in the lower horizon. Toward the end of July maximum populations were still evident in the upper (84,836) and middle (109,728) horizons. In the beginning of August only one peak (168,656) in the upper horizon was detected, which persisted to the end of summer. In the other two horizons the population remained low (10,000 to 40,000 specimens/m^2).

In the beginning of September, 1971 a higher population with a maximum in the middle horizon of the littoral zone was observed (249,428), but a small rise also evident in the upper horizon (103,124 specimens/m^2). In mid-September the population peak shifted to the upper horizon (197,100/m^2); approximately the same pattern of distri-
229 bution continued until the end of the month. In the first ten days of October the population peak reappeared in the middle horizon (335,280 specimens/m^2).

A. paraspinosus thus revealed a lower density of population during

Table 7. Population of *Axonolaimus paraspinosus* in the littoral zone of Kruglo'e Bay at stations of different heights above 0-depth

Date	1.95 m	1.78 m	1.55 m	1.44 m	1.41 m	1.37 m	1.25 m	1.15 m	0.99 m
1970									
July 7	3,048	2,032	5,240	59,436	93,436	49,784	8,636	14,732	40,640
July 16	5,080	62,992	7,112	61,468	75,184	—	13,208	6,096	4,572
July 27	72,136	84,836	—	65,024	23,368	109,728	6,604	—	30,480
Aug. 6	168,656	58,928	—	—	13,208	14,224	—	—	15,748
Aug. 17	134,112	66,548	24,384	10,668	48,768	10,668	—	—	45,212
Aug. 25	4,572	54,356	36,576	—	52,324	15,748	26,924	5,588	—
Sept. 3	27,432	132,080	17,780	—	42,672	22,860	9,652	—	508
1971									
Sept. 8	9,652	103,124	—	133,604	172,212	249,428	23,876	—	7,620
Sept. 17	13,208	197,104	104,140	68,580	132,080	6,604	41,148	4,572	54,356
Sept. 28	19,304	144,272	36,068	125,476	77,216	48,260	8,636	5,588	14,224
Oct. 9	6,096	92,964	49,784	355,280	102,616	50,292	11,684	8,636	—

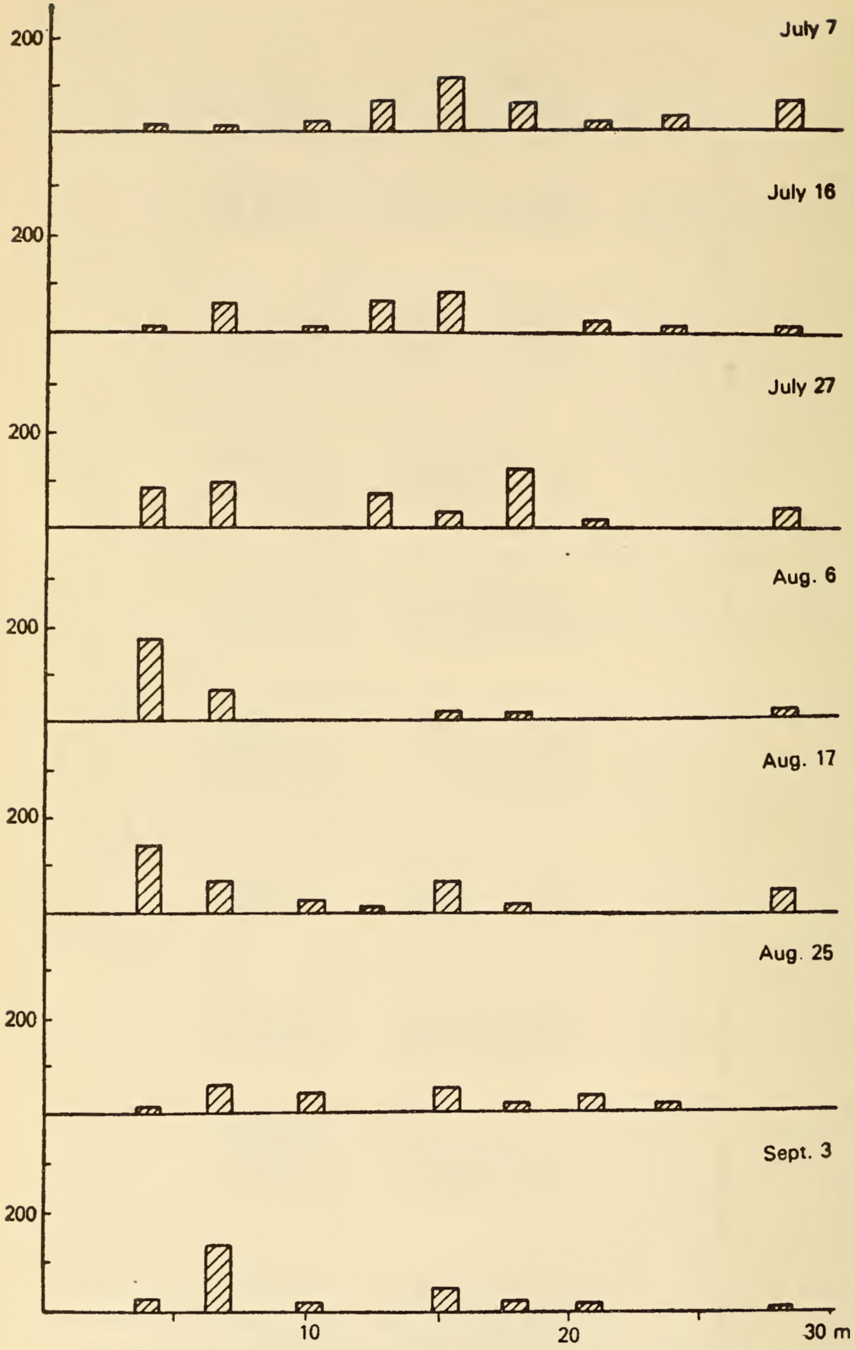
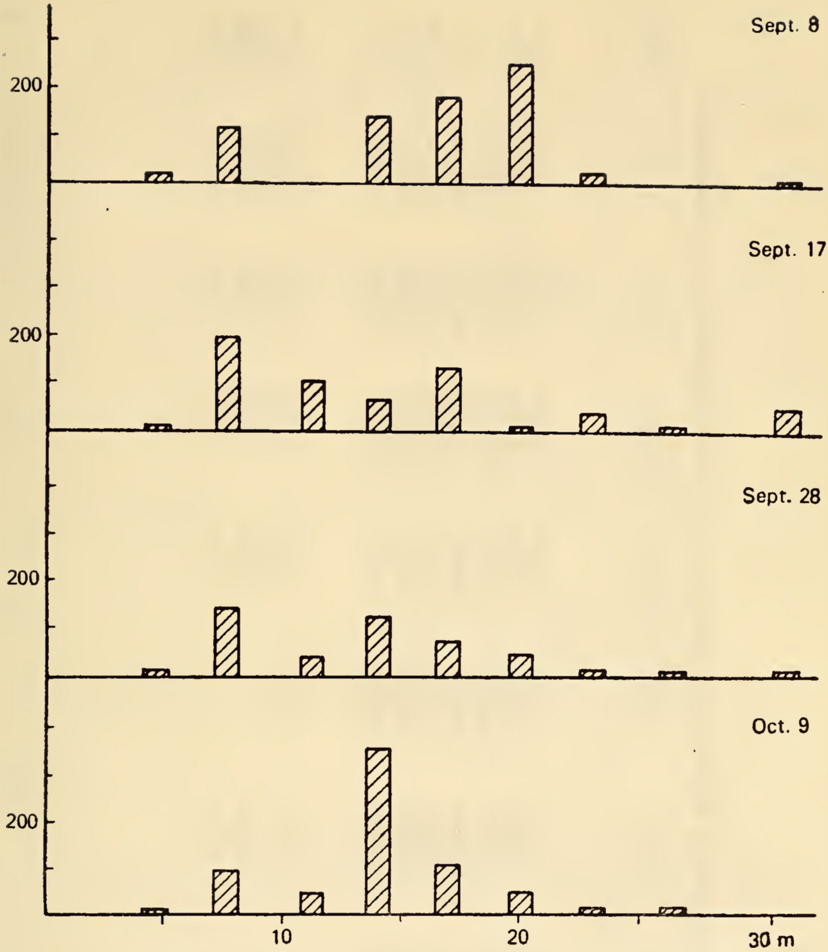


Figure 45. Population dynamics of *Axonolaimus paraspinosus* in the littoral zone of Kruglo'e Bay during summer of 1970.



233 Figure 46. Population dynamics of *Axonolaimus paraspinosus* in the littoral zone of Kruglo'e Bay during autumn of 1971.

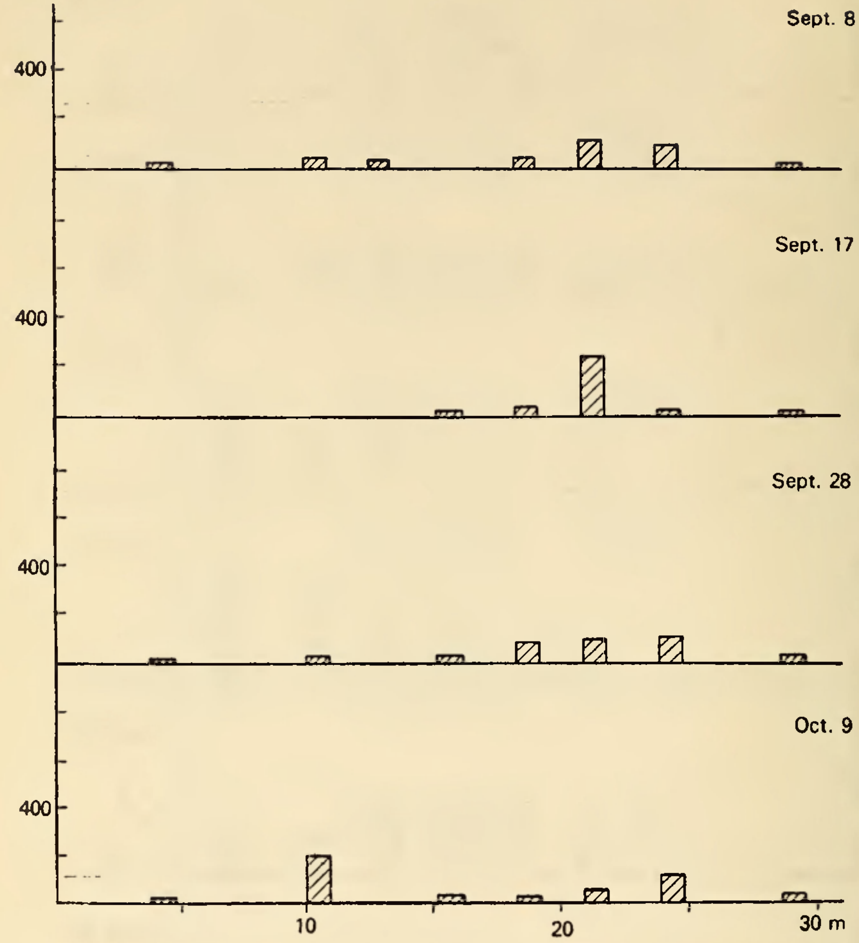
summer than in autumn. It remained mainly in the upper and middle 230 horizons of the littoral zone where peaks of population appeared by turns due to the appearance of a large number of young (p. 339). During both seasons the population remained low in the lower horizon.

Enoplus demani (Figures 47 and 48, Table 8). In the beginning of July the population was low throughout the section (30,000 to 60,000 specimens/m^2). In mid-July a gradual rise in population took place: in the middle horizon to 310,896, in the lower to 267,208 specimens/m^2. Approximately the same pattern persisted at the end of July. In early

Table 8. Population of *Enoplus demani* in the littoral zone of Kruglo'e Bay at stations of different heights above 0-depth

Date	1.95 m	1.78 m	1.55 m	1.44 m	1.41 m	1.37 m	1.25 m	1.15 m	0.99 m
1970									
July 7	1,524	17,780	3,556	71,120	56,896	69,088	33,528	28,956	40,640
July 16	68,580	105,664	42,164	205,740	124,968	310,896	182,880	16,764	267,208
July 27	23,876	32,512	131,572	129,540	117,856	227,584	196,596	305,308	
Aug. 6	23,876	51,308	163,068	204,216	250,952	343,408	401,828	495,300	62,992
Aug. 17	8,128	9,144	125,984	321,056	320,040	324,612	157,988	162,560	81,280
Aug. 25	15,748	29,972	191,008	25,872	184,912	290,576	124,460	96,520	132,080
Sept. 3	35,052	26,416	112,776	106,680	465,328	231,648	201,168	405,895	3,048
1971									
Sept. 8	9,652	—	37,084	22,352	13,716	35,560	113,792	90,932	2,032
Sept. 17	—	—	—	—	26,416	60,452	267,716	31,496	6,604
Sept. 28	2,540	—	36,576	—	33,020	87,376	93,980	109,728	9,652
Oct. 9	1,016	—	99,568	—	27,940	34,036	68,580	125,984	30,988

234 Figure 47. Population dynamics of *Enoplus demani* in the littoral zone of Kruglo'e Bay during summer of 1970.



235 Figure 48. Population dynamics of *Enoplus demani* in the littoral zone of Kruglo'e Bay during autumn of 1971.

August the population rose in the middle (204,216 to 343,408) and lower (410,828 to 495,300 specimens/m^2) horizons. By the middle and end of August it had gradually declined throughout the section to 100,000 to 200,000 specimens/m^2. In early September two increases in populations were observed, one in the middle horizon (465,328) and the other in the lower (405,895 specimens/m^2). In the upper horizon the population remained rather low throughout the summer season.

In autumn, 1971 the density of this species throughout the section was low (10,000 to 30,000), being somewhat higher in the lower horizon

231

Table 9. **Population of *Paracanthonchus macrodon* in the littoral zone of Kruglo'e Bay at stations of different heights above 0-depth**

Date	1.95 m	1.78 m	1.55 m	1.44 m	1.41 m	1.37 m	1.25 m	1.15 m	0.99 m
1970									
July 7	1,524	—	6,096	128,524	171,196	287,020	33,528	105,156	345,440
July 16	48,768	105,664	83,820	206,248	217,932	97,536	78,232	22,860	55,880
July 27	72,136	58,420	93,472	428,752	102,108	101,092	74,676	42,672	157,480
Aug. 6	168,148	88,392	163,068	242,316	138,684	78,740	77,216	17,780	487,680
Aug. 17	3,556	151,384	60,960	192,024	348,996	227,076	281,432	20,828	172,212
Aug. 28	—	82,804	31,496	292,608	316,484	141,224	124,460	28,448	17,272
Sept. 3	—	104,648	141,224	207,772	137,160	91,440	172,720	17,272	508
1971									
Sept. 8	6,604	189,484	371,856	289,560	172,212	570,992	132,080	8,636	37,592
Sept. 17	1,524	184,912	417,576	414,528	263,144	73,660	71,628	31,496	418,592
Sept. 28	5,588	434,340	288,544	166,116	72,724	251,460	47,244	127,508	193,040
Oct. 9	5,588	106,172	249,936	336,296	167,640	128,016	71,120	58,928	5,588

(90,000 to 100,000 specimens/m^2). In mid-September a population peak (267,716 specimens/m^2) was observed in the lower horizon. Until the end of autumn the population density remained low throughout the section.

The highest population of *E. demani* was observed during the summer season. Localization took place in the middle and lower horizons but 232 maximum density was usually observed in the middle horizon of the littoral zone. Population density was low in the upper horizon in both seasons.

Paracanthonchus macrodon (Figures 49 and 50, Table 9). In the beginning of summer, 1970 two population peaks were observed; in the middle horizon (287,020) and in the lower (345,440) specimens/m^2. Nematodes were encountered singly in the upper horizon. In the third and fourth weeks of July a population maximum occurred in the middle horizon (217,930 to 428,750 specimens/m^2). In early August a population increase occurred in the lower horizon (487,680 specimens/m^2). Population density remained high in the middle horizon throughout the season.

During autumn, 1971 two maxima were observed in the upper (371,856) and middle (570,992 specimens/m^2) horizons. In the middle of September the two peaks merged at the border of the upper and middle horizons (414,528 to 417,576 specimens/m^2). Another population peak was observed in the lower horizon (418,592 specimens/m^2). Toward the end of September the population declined throughout the section, but with the onset of October rose in the middle horizon (128,016 to 336,296 specimens/m^2).

The highest population of *P. macrodon* was observed during autumn. This species preferred the middle horizon of the littoral zone during both seasons. However it drifted toward the lower horizon during summer, while maximum density shifted toward the upper horizon during winter.

Hypodontolaimus inaequalis (Figures 51 and 52, Table 10). In the beginning of summer, 1970 two population peaks were observed in the middle horizon (101,092 and 158,496 specimens/m^2), while in the upper and lower horizons the population was low. A slight increase in population density occurred in the middle of July throughout the section, but the maximum density remained in the middle horizon (58,420 to 164,084 specimens/m^2); it was also high in the lower stratum of the upper horizon (98,044) and in the upper stratum of the lower horizon (104,140 specimens/m^2). Increase in population continued to the end of July with a maximum in the middle horizon (220,980 specimens/m^2); toward the beginning of August a small slump to 80,000 to 100,000 specimens/m^2 was seen. In the middle of the month the population peak shifted to the

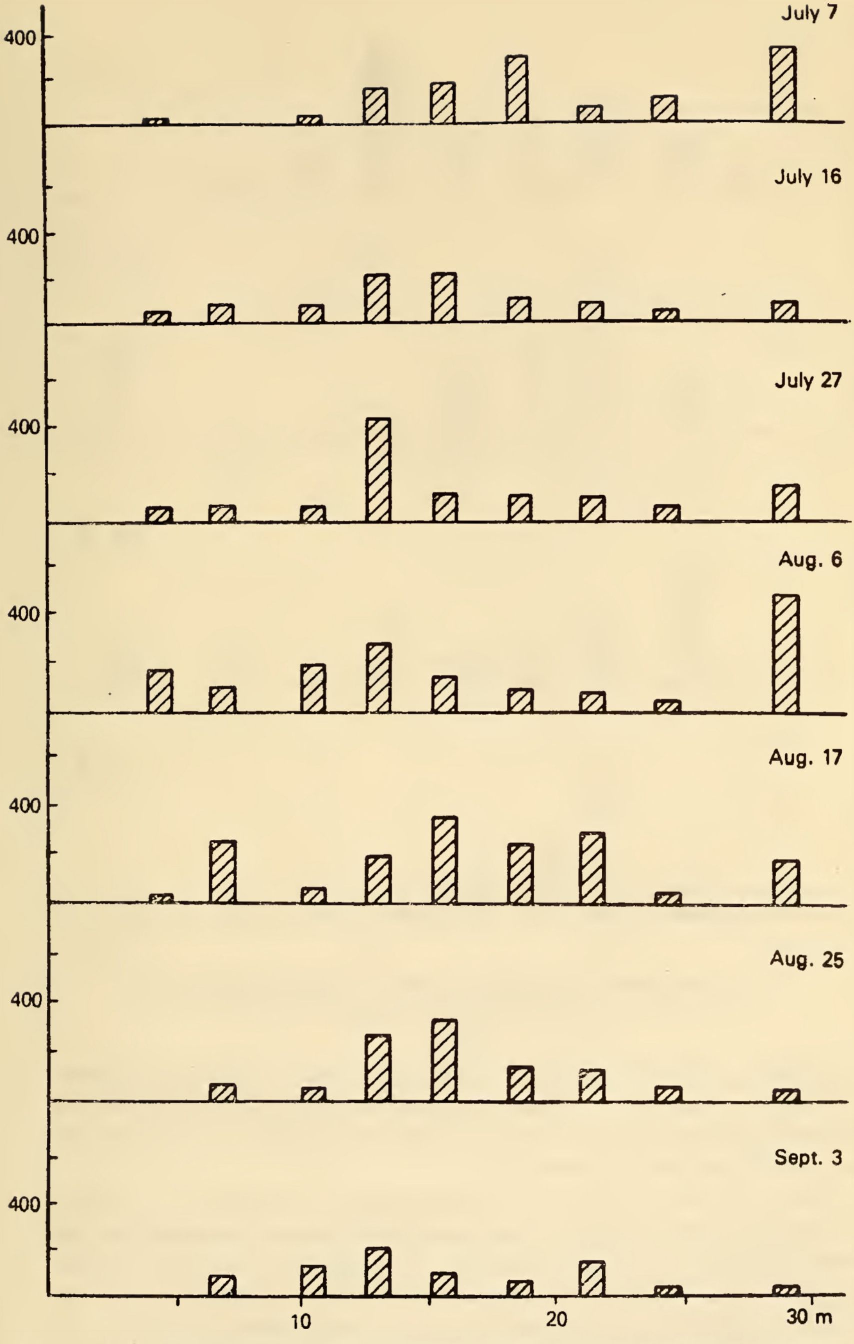
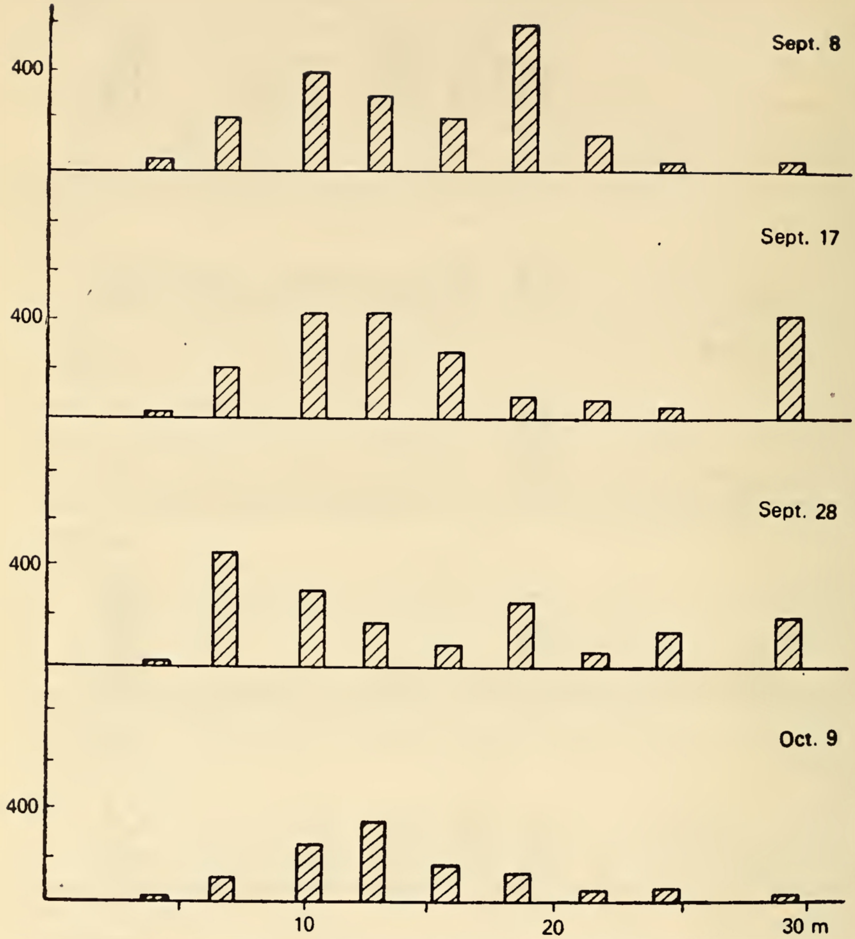


Figure 49. Population dynamics of *Paracanthonchus macrodon* in the littoral zone of Kruglo'e Bay during summer of 1970.



237 Figure 50. Population dynamics of *Paracanthonchus macrodon* in the littoral zone of Kruglo'e Bay during autumn of 1971.

upper part of the lower horizon of the littoral zone (281,432 specimens/m^2). Toward the end of August and early in September the population 235 gradually reduced throughout the section, but the peak continued to be localized in the middle horizon.

During autumn of 1971, at the beginning of September, the population was less than that in summer; the greatest number was seen from the lower stratum of the upper horizon of the littoral zone to the upper stratum of the lower horizon (44,704 to 132,588 specimens/m^2). In the middle of September two population peaks were observed: one in the upper horizon (208,788) and the other in the lower horizon (131,064

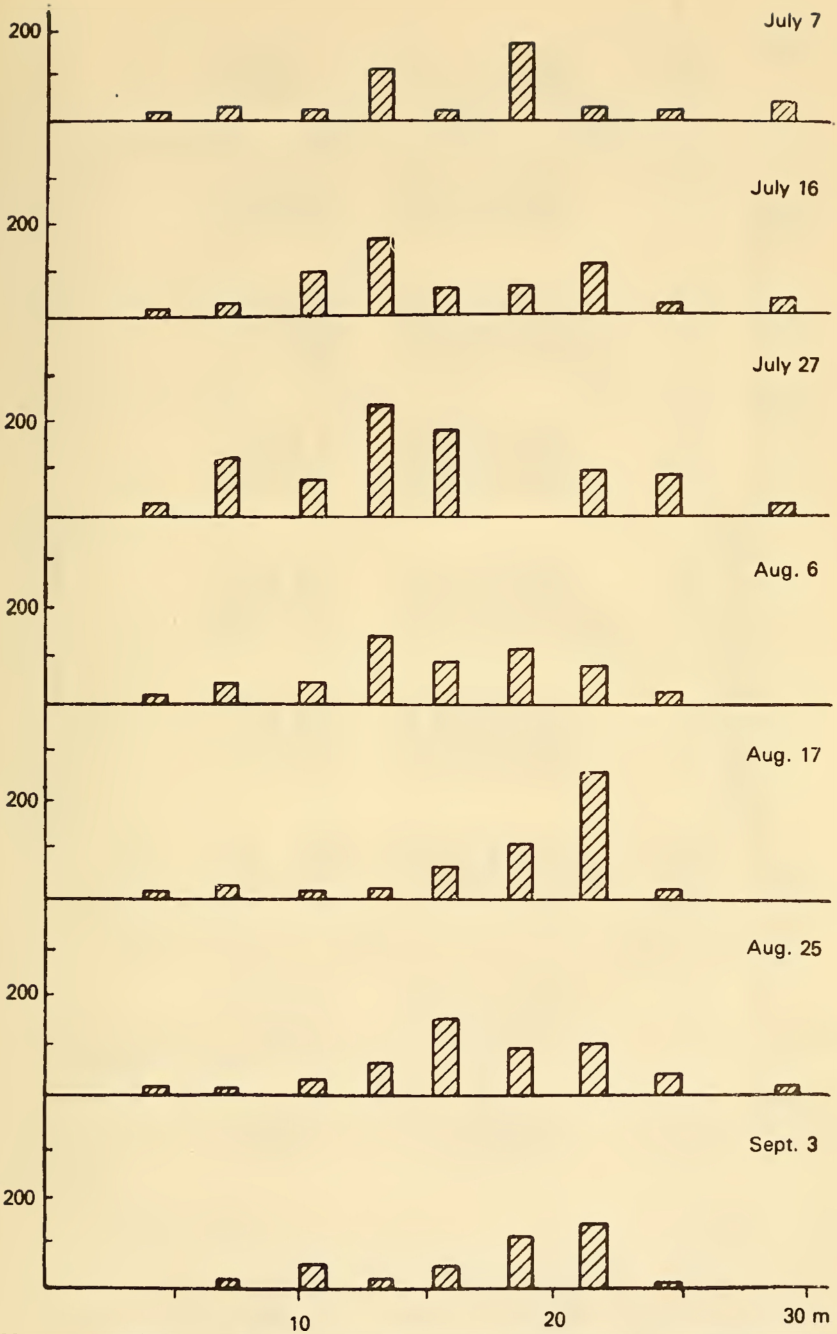
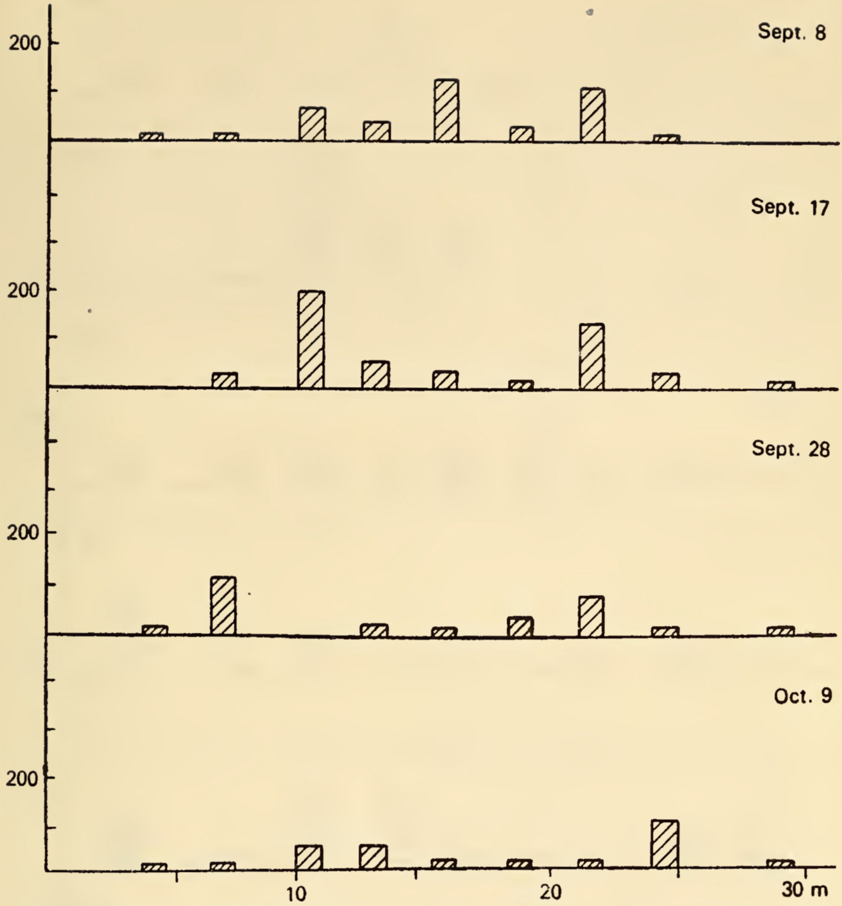


Figure 51. Population dynamics of *Hypodontolaimus inaequalis* in the littoral zone of Kruglo'e Bay during summer of 1970.

Table 10. Population of *Hypodontolaimus inaequalis* in the littoral zone of Kruglo'e Bay at stations of different heights above 0-depth

Date	1.95 m	1.78 m	1.55 m	1.44 m	1.41 m	1.37 m	1.25 m	1.15 m	0.99 m
1970									
July 7	1,524	7,620	1,016	101,092	15,748	158,496	16,764	14,732	40,640
July 16	14,224	28,448	98,044	164,084	58,420	61,976	104,140	12,192	34,544
July 27	19,812	110,744	71,120	220,980	172,720	109,728	80,264	71,120	10,160
Aug. 6	24,384	59,436	48,260	145,288	99,060	114,808	85,852	29,972	—
Aug. 17	116,684	28,448	16,256	42,672	77,724	118,364	281,432	17,272	—
Aug. 25	2,032	9,652	30,988	60,452	143,764	93,980	115,316	45,212	6,096
Sept. 3		26,416	47,244	25,400	51,300	108,204	134,620	17,272	—
1971									
Sept. 8	9,652	17,272	74,168	44,704	132,588	35,560	120,904	8,636	—
Sept. 17	—	34,544	208,788	68,580	39,624	13,208	131,064	35,560	6,604
Sept. 28	10,668	108,712	—	20,828	16,256	38,608	82,296	11,684	4,572
Oct. 9	3,048	13,208	50,292	51,816	9,144	8,128	5,588	105,156	8,636



239 Figure 52. Population dynamics of *Hypodontolaimus inaequalis* in the littoral zone of Kruglo'e Bay during autumn of 1971.

specimens/m^2). Toward the end of September and the onset of October a reduction in population occurred throughout the section.

Thus, during summer a greater population, compared to autumn, was seen. *H. inaequalis* was mainly found in the lower stratum of the upper horizon to the upper stratum of the lower horizon during both seasons.

Theristus setosus (Figures 53 and 54, Table 11). The population was low throughout the section (30,000 to 90,000) in the beginning of July, 1970 with one peak in the middle horizon (326,644 specimens/m^2). Toward the middle of July an increase occurred in population in the middle horizon (250,952 to 626,872 specimens/m^2) due to the appearance of a

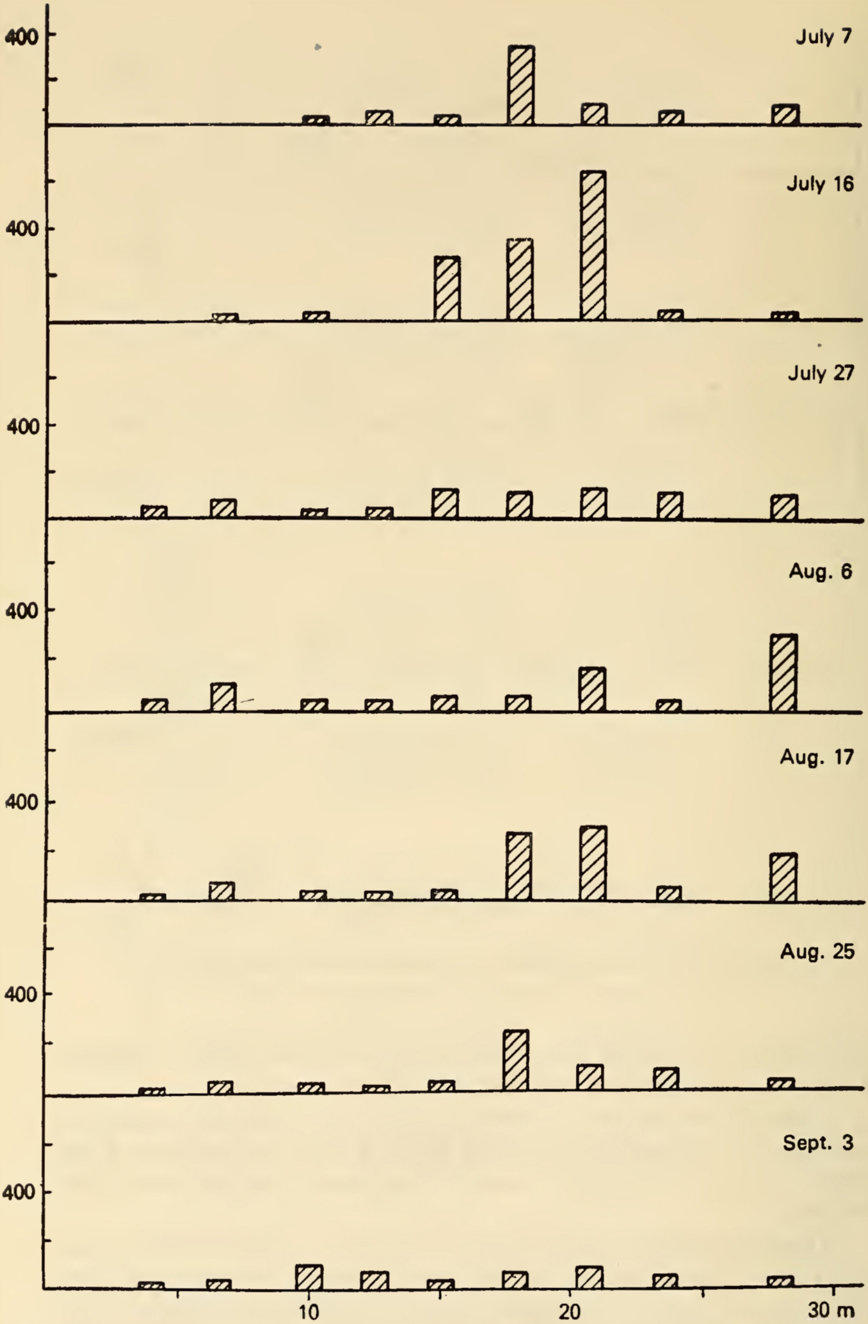
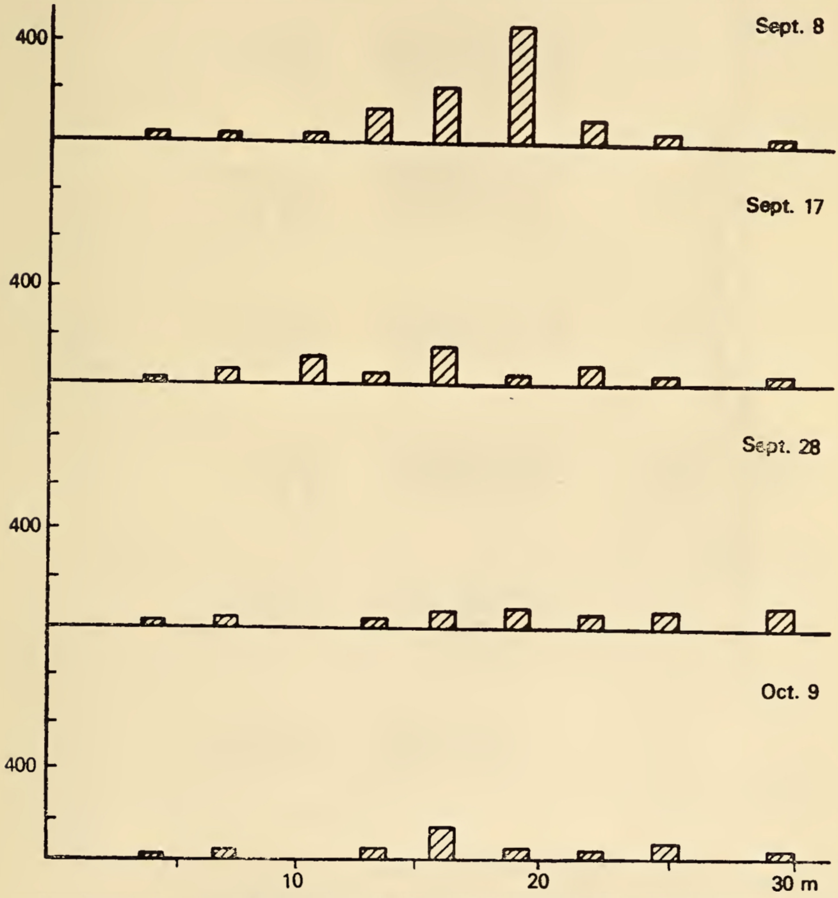


Figure 53. Population dynamics of *Theristus setosus* in the littoral zone of Kruglo'e Bay during summer of 1970.

large number of young (p. 342). At the end of July the population was again low throughout the section and did not exceed 90,000 to 110,000 specimens/m^2. In the beginning of August approximately the same pattern persisted, with a rise in population to 314,960 only in the lower horizon. Toward the middle of August the peak declined to 180,340, but 236 on the border of the middle and lower horizons an increase to 259,588 to 281,940 specimens/m^2 was seen. Toward the end of August the population maximum remained only in the middle horizon (226,568 specimens/m^2), and in early September a general decline in population occurred throughout the section.

In the beginning of September, 1971 approximately the same pattern was seen as recorded at the end of August, 1970 (peak of population in



241 Figure 54. Population dynamics of *Theristus setosus* in the littoral zone of Kruglo'e Bay during autumn of 1971.

Table 11. Population of *Theristus setosus* in the littoral zone of Kruglo'e Bay at stations of different heights above 0-depth

Date	1.95 m	1.78 m	1.55 m	1.44 m	1.41 m	1.37 m	1.25 m	1.15 m	0.99 m
1970									
July 7	—	—	508	53,848	32,004	326,644	96,520	33,020	50,800
July 16	—	21,336	27,940	—	250,952	337,312	626,872	29,464	12,700
July 27	72,136	97,536	11,176	25,908	109,728	109,728	114,808	106,680	81,280
Aug. 6	40,132	117,856	9,652	9,652	66,040	36,068	179,324	6,096	314,960
Aug. 17	4,064	85,344	28,448	32,004	19,812	259,588	281,940	51,816	180,340
Aug. 25	2,032	53,848	41,656	35,052	12,700	226,568	115,316	90,932	6,096
Sept. 3	3,556	26,416	82,804	62,992	16,764	62,992	85,852	51,308	508
1971									
Sept. 8	3,048	8,636	18,796	89,408	255,044	464,312	96,520	42,672	6,096
Sept. 17	1,524	46,288	104,140	34,544	144,780	34,036	77,216	24,384	6,604
Sept. 28	24,892	36,068	—	21,336	66,040	67,564	37,084	64,008	70,612
Oct. 9	6,604	26,416	—	51,816	157,988	68,072	8,626	62,992	8,636

the middle horizon 464,312 specimens/m^2). Later a decrease in population occurred throughout the section with the maximum being retained in the middle horizon.

237 Thus the population of *T. setosus* was maximum during the summer season. The middle and lower horizons of the littoral zone were preferred for habitation.

Reviewing the foregoing analysis, it can be said that almost all the leading species of nematodes preferred the middle horizon of the littoral zone for habitation in summer as well as in autumn. Only *Timmia acuticauda* revealed a tendency to concentrate in the upper horizon during the autumn season. *Anoplostoma rectospiculum* was found mainly in the middle horizon during summer and in the upper horizon during autumn. *Axonolaimus paraspinosus* alternated between the upper and middle horizons. *Enoplus demani* and *Theristus setosus* preferred the middle and lower horizons during summer but only the middle horizon during autumn. *Paracanthonchus macrodon* concentrated in the middle and lower horizons during summer and in the middle and upper horizons during autumn. *Hypodontolaimus inaequalis* concentrated between the lower stratum of the upper horizon and the upper stratum of the lower horizon of the littoral zone during both summer and autumn.

One could probably say that these species exhibit selective habitation in the littoral zone because, even within the limits of such a small area of study, an extremely varied picture of distribution of individual species was evident.

239 INFLUENCE OF IMPORTANT FACTORS ON LIVING CONDITIONS AND POPULATION DYNAMICS OF NEMATODES

To explain the distribution phenomenon of organisms of meiobenthos, hydrobiological studies have been undertaken to elucidate those factors which exert considerable influence on them. Data is presented in six elaborate works by authors abroad in a more generalized form (Delamare Deboutteville, 1960; Swedmark, 1964; Jansson, 1968, 1971; McIntyre, 1969; Pollock, 1971). As shown in these works, the distribution and population dynamics of meiofauna are influenced by the following factors: granulometric composition of sediments, size of capillary passages occupied by some species of nematodes, presence of sufficient quantity of interstitial water, effects of temperature, salinity, oxygen, and others.

Of the works published in the Soviet Union giving exhaustive characteristics of the living conditions of organisms in the littoral zone such as temperature, salinity, etc., one should mention those of Gur'yanova, Zaks and Ushakov for the littoral zone of Western Murmansk

(1930a) and the littoral zone of Kol'sk Gulf (1930b), and Gur'yanova and Ushakov (1927) for the littoral zone of Eastern Murmansk. Kuznetsov (1947) has detailed the effects of light and temperature on organisms of the littoral zone of the White Sea under permanent ice cover. Zatsepina, 240 Zenkevich and Filatova (1948) have presented data characterizing the temperature and hydrochemical conditions in the drier zone of the northern part of Kol'sk Bay. A very detailed work on the thermodynamics and hydrochemistry of the littoral zone of Eastern Murmansk and some regions of the White Sea has been published by Chernovskaya (1956, 1957, 1958). Of foreign works on the hydrobiology and hydroche- 241 mistry of littoral waters, articles by Wohlenberg (1937) and Linke (1939) on the littoral zone of the North Sea are noteworthy.

It was not the purpose of the foregoing authors to include every factor affecting the living conditions of organisms in the littoral zone. The parameters scrutinized were selected in such a way as to show the different degrees of their influence on such living conditions and the population dynamics of meiofauna (using examples of the predominant group of nematodes). The factors studied comprised only the granulometric composition of the sediments, temperature, presence of sufficient feeding base, and salinity.

Granulometric Composition of Sediments

Of the factors influencing the surrounding medium inhabited by sand-dwelling meiofauna, a granulometric analysis of sediments must be given first place. It may not be the size of the particles which limits the distribution of organisms, but aspects such as interstitial spaces and the amount of pore water with minerals and organic substances dissolved in them (Jansson, 1967c).

Works on the nature of the bed and its influence on meiofauna are comparatively few in number (Delamare Deboutteville, 1960; Swedmark, 242 1964; Jansson, 1966, 1967c; and others). An experimental approach to the study of the correlation between granulometric composition of sediments and meiofauna has seldom been employed (Wallace, 1958; Gray, 1966a, 1966b, 1966c; Jansson, 1966, 1967c).

The purpose of my study was to establish whether any correlation exists between size of particles of sediment and population density of nematodes and their individual species, and to compare size of capillary passages in which nematodes live with body size of organisms.

To show the correlation between nematode density and particle size of the sediment they inhabit, correlation coefficients were worked out (Table 12). For the total population of nematodes the correlation coefficient (r) was 0.39, its error (m_r) 0.28, and its reliability (t) 1.39.

When n = 9, the standard criterion value of Student's test (t_{st}) was 2.3. Thus I obtained an unreliable (negative) correlation between total population of nematodes and average size of sediment particles inhabited by them. In other words, I found no direct relation between total nematode population and granular composition of the sediment.

Table 12. Correlation between density of leading species of nematodes and average size of particles

Leading species	r	m_r	t	t_{st}	Reliability of correlation
Anoplostoma rectospiculum	−0.29	0.31	0.9	2.3	Not reliable
Paracanthonchus macrodon	−0.60	0.21	2.9	2.3	Reliable
Hypodontolaimus inaequalis	−0.47	0.26	1.8	2.3	Not reliable
Timmia acuticauda	−0.27	0.31	0.9	2.3	Not reliable
Axonolaimus paraspinosus	0.70	0.17	4.1	2.3	Reliable
Theristus setosus	0.44	0.27	1.6	2.3	Not reliable
All nematodes	−0.39	0.28	1.4	2.3	Not reliable

Of the six leading species of nematodes examined, four exhibited no direct correlation between the characters listed above. *Paracanthonchus macrodon* revealed a positively reliable correlation, i.e., one may speak
243 of some affinity of individuals of this species for sediment with a high content of fractions 300 to 500 μm. In *Axonolaimus Paraspinosus* a positively reliable correlation was also obtained and in this case one may speak of some sort of adaptation of individuals to a sediment with an average particle size of 300 to 400 μm. For these two species correlation with type of sediment is possibly related to the fact that maximum population can be achieved in sediments with a definite size of particles, but after a certain time the population shifts to other stations where the size of particles differs. For this reason the granular composition probably does not influence the distribution of one or the other nematode species in sections with sand of medium granular size.

There are a number of works on microbenthos in which the problems of distribution of some groups of organisms in relation to type of sediment have been discussed. In particular, Agamaliev (1967) and Burkovskii (1969) have shown a correlation between particle size of sediment and distribution of psammophytic infusoria.

As mentioned above, it is not the particle size itself which determines the population density of organisms but the interstitial spaces of the sediment in which they live. For this reason it is more appropriate to compare not the length of the organism with the particle size, but the diameter of the organism with the diameter of the capillary passages in which it lives. In this case the terms "micro-, meso-, and euryporal species," used by Agamaliev and Burkovskii, acquire a greater meaning. Renaud-Debyser (1963) examined the main types of capillary spaces occurring in different "packings" of sediment. Sand particles may be situated either on the tops of cubes or on the tops of rhomboids; in the first case pores with maximum space form and in the second with minimum space. In this connection she distinguishes two types of arrangement of sand particles—cubic and rhomboid. Pores formed in this way merge in slits of different sizes. She derived coefficients expressing the correlation between particle size of sediment and diameter of the corresponding type of capillary space and slits. Utilizing these coefficients, I drew a graph reflecting these relations (Figure 55). Four curves reflect the relation between particle size and type of space. The limiting factor influencing the habitation of organisms is probably the minimum size of the capillary passages which these organisms may inhabit. Such spaces are slits existing in a rhomboidal arrangement of particles and later I shall discuss just such types of spaces. Proceeding from the foregoing,

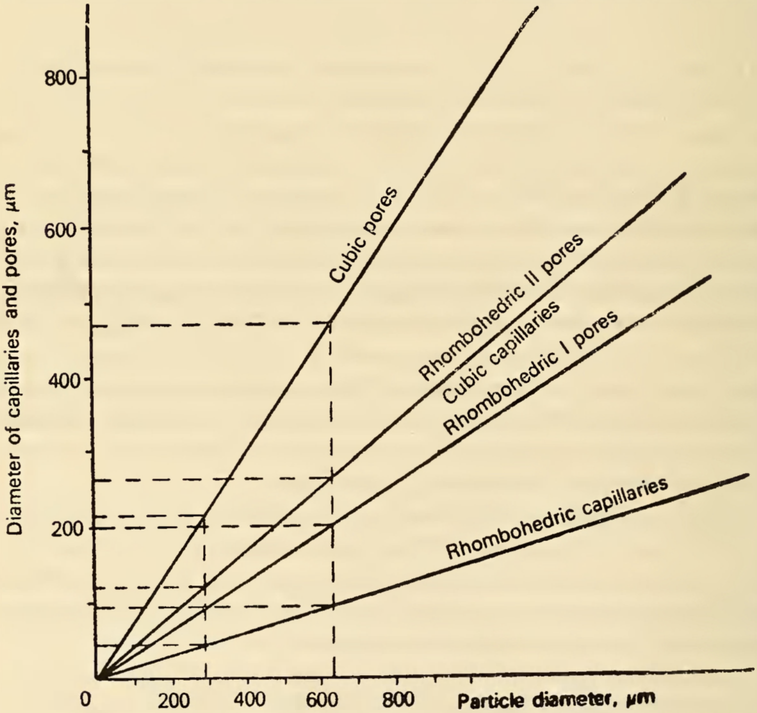


Figure 55. Correlation of slit and pore size with the granular composition of the sediment in different packings (textures).

the percent content of slits (capillaries) for each station was calculated. This corresponded with the percent fraction of particles of this or that size (Table 13, Figure 56). For each species of nematode inhabiting one station or the other the maximum diameter of the body was calculated and the content of each measured class with respect to diameter cal-
244 culated in percent (Table 13). The data is graphically presented in Figure 56.

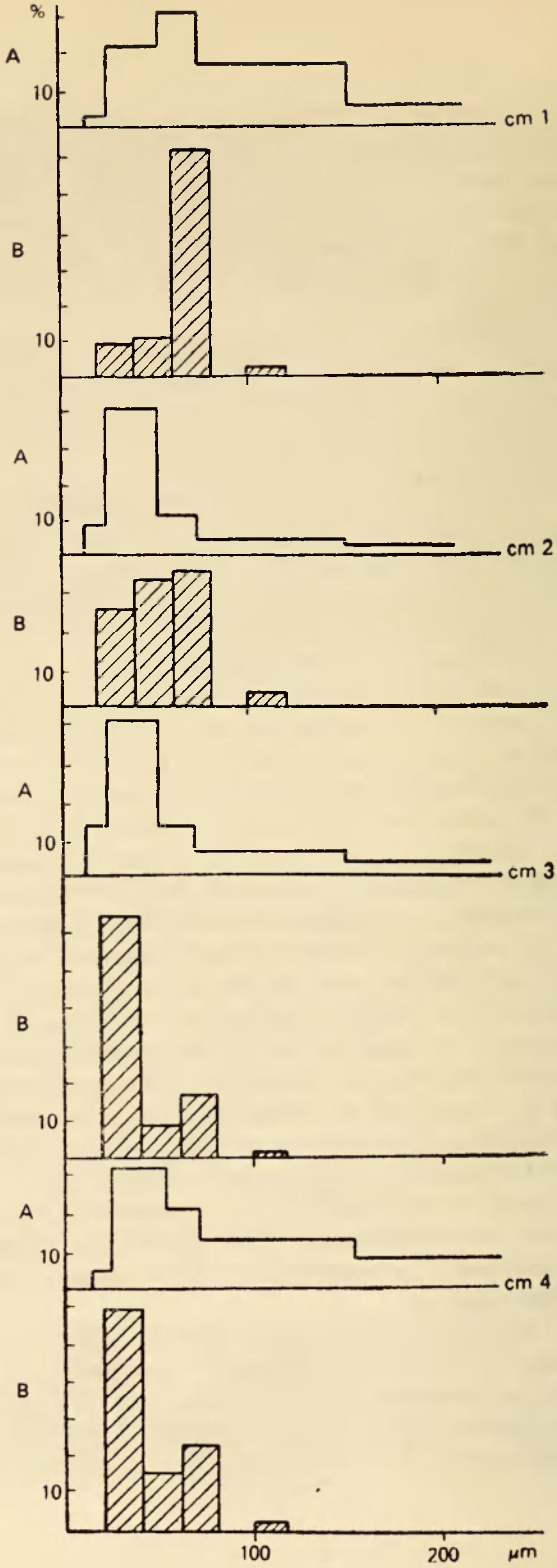
Rhomboidal slits of 20 to 80 μm diameter predominated at stations 1 to 4, 8, 9. At these stations nematodes with an average body diameter of 20 to 80 μm predominated. In the given case one can see the coincidence of maximum distribution of capillaries of different diameter and nematodes of almost that same diameter.

The predominating species in these stations were: *Metoncholaimoides filicauda*, *Anoplostoma rectospiculum*, *Timmia acuticauda*, *Paracanthonchus macrodon*, *Theristus flevensis*, and others. For the prevalence of these
245 species there must have been sufficient capillary passages, the diameter of which was either equal or greater.

At station No. 5 slits of larger size (300 μm and above) predominated. About 90% of the nematodes at this station had a body diameter of 20 to 110 μm, i.e., for habitation they had capillary passages in which the diameter was 1.5 to 2.0 times the body diameter. In other words, at this station minimum slit size was not a limiting factor for the organisms.

At station No. 7 most of the capillaries had a diameter of 40 to 60 μm. The diameters of the remaining capillary passages were represented more or less equally. Two maxima were distinguished in the distribution of nematodes. One comprised nematodes with an average diameter of 40 to 110 μm, and the other comprised nematodes with a body diameter of 165 μm. The first peak was formed by *P. macrodon*, *Hypodontolaimus inaequalis*, and *Theristus setosus*, and the second by *Enoplus demani*. In this case the average diameter of the organisms somewhat exceeded the minimal diameter of the capillaries. It may be assumed that *H. inaequalis* and *T. setosus*, with an average diameter of 60 to 100 μm, were capable of slightly dilating capillary passages in which the diameter was less than their body diameter. The presence of capillaries with small diameters had no impact on the distribution of *E. demani* in the section under study, because representatives of this species are rather large organisms (average length, 4.8 mm) and capable of boring a passage corresponding to their body size.

This situation allows one to assume another criterion for drawing dimensional limits for meiofauna. Those organisms that are capable of living in minimum capillary passages of a given sediment by virtue of their size and without harm to themselves belong to meiofauna. Organisms capable of actively making for themselves a "living space" in



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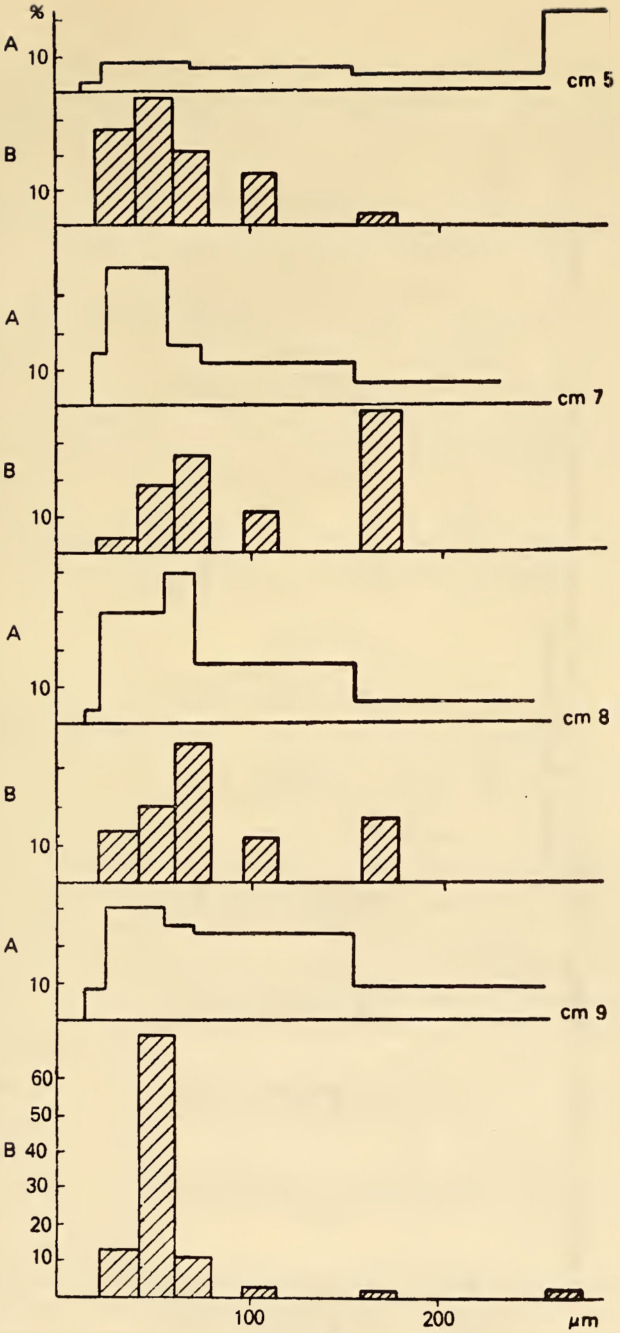


Figure 56. Number (in %) of rhomboid capillaries (A) and nematodes of definite diameter (B) in samples collected on September 17, 1971 in the littoral zone of Kruglo'e Bay.

Table 13. Correlation in percentage of minimum size of slits (A) and nematodes of definite diameter (B) in the littoral zone of Kruglo'e Bay (September 17, 1971)

Height of stations over 0-depth (in m)	20–40 μm		40–60 μm		60–80 μm		95–110 μm		165 μm		264 μm	
	A	B	A	B	A	B	A	B	A	B	A	B
1.95 (1)	2.6	27.5	22.0	8.4	31.0	60.4	16.3	3.7	4.7	—	4.7	—
1.78 (2)	6.9	25.3	39.0	33.6	9.7	35.5	3.6	4.7	3.3	—	3.3	0.9
1.55 (3)	13.5	67.8	42.2	10.2	14.1	19.5	7.0	2.5	4.3	—	4.3	—
1.44 (4)	7.6	61.1	33.7	15.1	21.2	23.1	12.5	0.7	7.2	—	7.2	—
1.41 (5)	3.9	27.0	15.6	35.9	17.3	20.3	12.1	13.4	7.2	3.4	7.2	—
1.37 (6)	2.3	45.7	12.4	18.4	14.6	17.1	11.6	7.4	5.4	11.4	5.4	—
1.25 (7)	14.1	4.5	36.4	17.1	15.6	26.1	11.0	11.8	5.4	40.5	5.4	—
1.15 (8)	3.1	14.0	27.6	17.6	37.8	40.1	14.3	12.9	4.0	15.4	4.0	—
0.99 (9)	8.4	11.2	29.8	70.0	24.2	12.0	22.4	2.0	7.2	0.9	7.2	1.9

which conditions of existence in no way depend on minimal capillaries in the sediment may be categorized as macrofauna.

To summarize, I could establish no direct relation between density of nematodes and granulometric composition of the sediment in the section under study. Probably in a section with median-granular sand the granular composition is not a factor influencing the distribution of one or the other species. The limiting factor is the minimal size of capillary in which other representatives of meiobenthos can also live. For the sediment investigated the minimal capillary size was 20 to 80 μm. Such capillaries suffice for the inhabitation of *M. filicauda*, *A. restospiculum*, *T. acuticauda*, *P. macrodon*, *T. flevensis*, and others. *H. inaequalis* and *T. setosus* are capable of widening the minimal capillary passage. The presence of minimal capillaries exerts almost no influence on the distribution of *E. demani*, which is capable of actively making for itself a "living space".

The criterion for the upper limit of meiobenthos, i.e., their capacity to live in minimal capillary passages, has been established.

Temperature

Temperature conditions on sandy coasts of seas have long attracted the attention of researchers. Summarizing the data obtained by a number of authors (Pennak, 1940; Angelier, 1953; Ruttner-Kolisko, 1954; McIntyre, 1964; Johnson, 1965; Jansson, 1966, 1967a, 1968, and 1971; Salvat, 1964; Smidt, 1951), some generalizations for a temperate Arctic region can be made. During winter (season of minimum temperatures) negative temperatures are observed at depths of 1.0 m and more. During spring (autumn) when gradual warming up (thawing) of coastal waters takes place day and night, the amplitude of air temperature achieves a
248 significant value and vertical stratification of ground temperature is seen. The greatest fall in temperature (more than 10°C) takes place in the upper 2.0 cm layer of sand. My study commenced at the end of spring—beginning of summer. In determining seasons for the White Sea the classification of Chernovskaya (1956) was followed: spring—May, June and beginning of July; summer—second half of July, August and September; autumn—end of September and October. As such the period of collecting material in 1970 comprised spring-summer and the period in 1971 summer-autumn.

In the conditions of the continental situation of the White Sea, waters in the littoral zone warm up significantly. For example, in 1970 the temperature of water washing the littoral zone rose from 14.8 to 16.0°C from the 1st to the 5th of July, declined to 11.5°C from the 6th to the 8th of July, and then throughout the rest of the month gradually rose to 15 to

16°C. August is the warmest month on the White Sea (Chernovskaya, 1956). During this month a considerable warming of surface waters to 17.5°C took place in the first ten days. Later a gradual cooling of waters in the littoral zone occurred toward the end of August to 14.1°C and on September 8th to 12.5°C.

In 1971 studies were conducted in the summer-autumn season. On September 7th the water temperature in the littoral zone was 8.5°C, i.e., 4° lower than the temperature in the similar period in the previous year. Toward the end of September and beginning of October the water temperature gradually dropped to 2.5°C, by which time initial freezing had covered the upper horizon with a thin crust of ice.

I attempted to correlate temperature changes during the two seasons with the population dynamics of the leading group of meiobenthos, namely, nematodes. Dynamics of the average population during the spring-summer period of 1970 have been given in Figure 57. The average population from nine stations throughout the section was calculated each day. The temperature of the day of collection was calculated as the average of 7 to 10 days preceding the day of sampling and including the day of collection.

By means of monofactorial dispersion analysis the extent of influence of time on the population dynamics of nematodes was derived. It was found that the index of intensity of influence (η_x^2) = 0.825, its error (m_η)$=$0.019, and its reliability (F)$=$43.4 when Fischer's standard criterion is F_{st} 2.3—3.1—4.3 (degree of freedom; $v_1=6$, $v_2=56$).

Finally the index of intensity of influence may be written: $\eta_x^2 \sim 0.825 \pm 0.044$. In other words, the influence of the time factor on nematode population is reliable with a probability of $\beta=0.999$ and may not constitute less than 78%, because the time factor is interconnected with changes in many parameters (such as temperature in the first place, salinity, chemistry of water, etc.). In the given case I shall first of all concentrate on changes in temperature because in my opinion changes

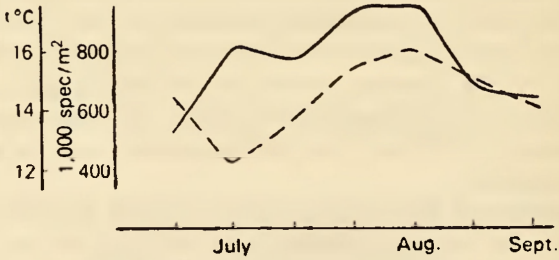


Figure 57. Graph depicting changes in average temperature and average population of nematodes during summer of 1970 (broken line—temperature; continuous line—population).

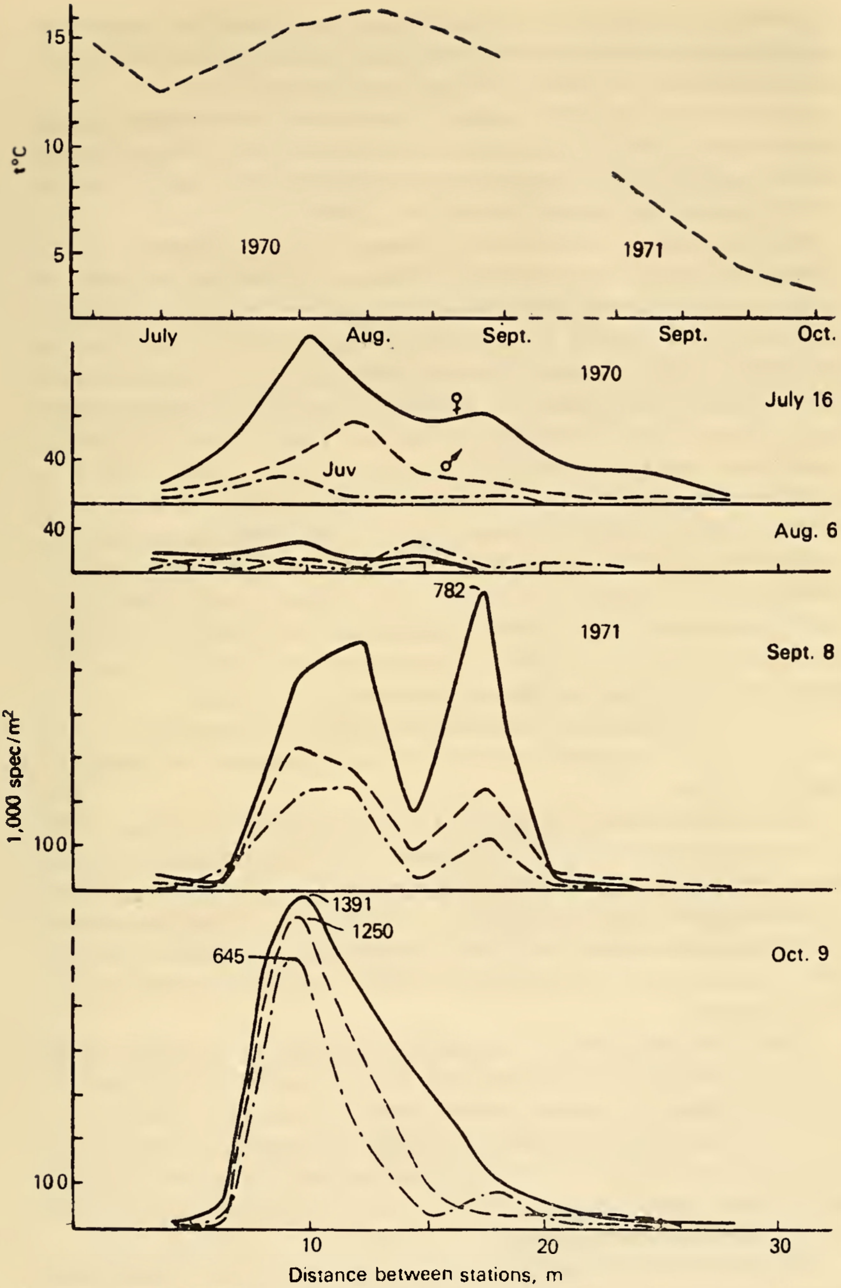


Figure 58. Dynamics of *Timmia acuticauda* population during summer of 1970 and autumn of 1971.

Graph of temperature variations.

in salinity, chemistry of interstitial water, etc., could not have substantially influenced the nematode population during the period of study (the reason for this is given in the section on salinity).

As seen in Figure 57, a direct correlation between temperature 249 variations and population dynamics is discernible. This to some extent justifies my hypothesis about the predominant position of the temperature parameter with relation to the time factor.

Air temperature has a direct influence on the temperature of the ground as well as water which the organisms inhabit (Kinne, 1963); it influences fauna, for example, through speed of multiplication of individual species (Orton, 1919; Gerlach and Schrage, 1971). As 90% of the nematode population comprised seven dominant species, it was interest- 250 ing to analyze subsequently in what way temperature influenced the speed of multiplication in different seasons. This in turn indicated to some extent the geographic affinities of the species under study. It is practically impossible to project a zoogeographic pattern on the basis of analysis of marine fauna of nematodes due to considerable inaccuracies in the identification of species within the limits of this group; species described by some authors may prove to be different species (Platonova, 1967). Some researchers (Steiner, 1916a; Kreis, 1934; Allgen, 1954, 1957) regard the majority of nematodes as cosmopolitan, but due to reasons given earlier, this question remains controversial even now.

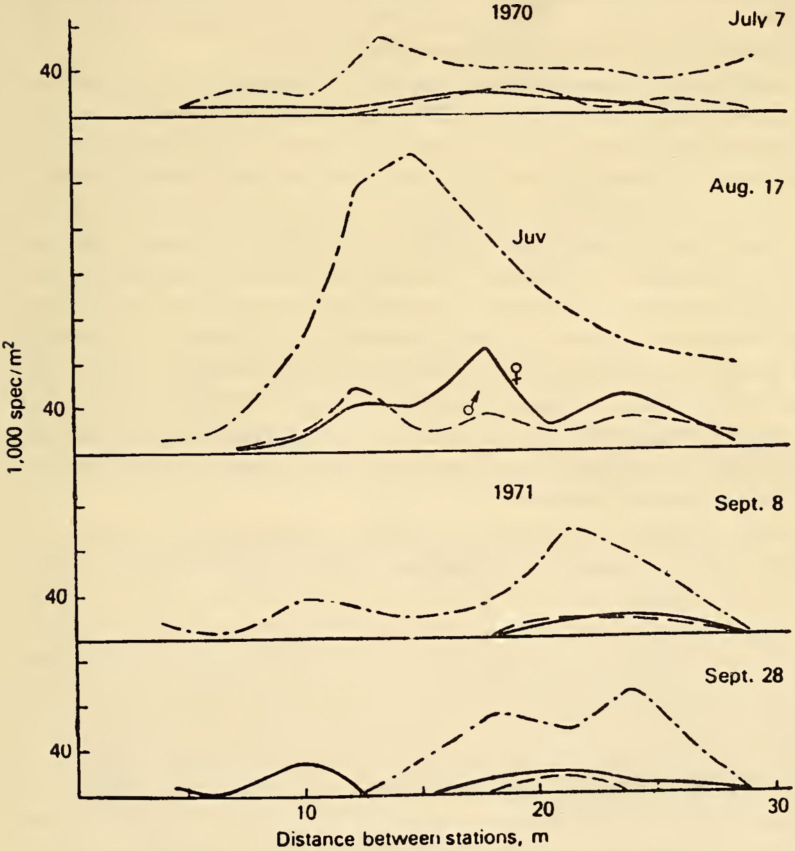
Let us now separately analyze the population composition of the leading species of nematodes during the spring-summer and summer-autumn seasons.

Timmia acuticauda (Figure 58). In the beginning of summer, 1970 females predominated in the population (for example, on July 16th their population was 30,000 to 100,000 specimens/m^2). Juveniles were fewer in number (4,000 to 8,000 specimens/m^2). The lowest average temperature during the season studied occurred at the beginning of summer (12.5°C). The low population of this species persisted throughout the section to the end of summer.

During autumn of 1971 an increase in population of this species up to 2,000,000 specimens/m^2 occurred, with the temperature falling from 8.5 to 2.5°C. Females, as before, predominated (for example, on September 17th their number was 400,000 to 1,400,000 specimens/m^2). Males were somewhat less (300,000 to 1,300,000) and juveniles almost half the number of males. Approximately the same ratio between the sexes persisted to the end of the autumn season.

Thus from the above account it follows that the speed of multiplication of this species at high temperatures was extremely low and maximum multiplication took place in autumn. This species could probably be regarded as Arctic since it multiplied at low positive temperatures. The species tolerates high summer temperatures without harm because almost all nematodes are eurythermal and euryhaline, adapting to sharp changes in temperature and salinity (Jansson, 1967a, 1968). However, it is known that some organisms which are eurythermal during the period of growth may be stenothermal during the period of multiplication (Ekman, 1953).

Enoplus demani (Figure 59). In the beginning of the spring-summer season the number of males, females, and juveniles was not large and their total population did not exceed 71,120 specimens/m². From the middle of July a gradual increase in number of juveniles was recorded and in the beginning of August their number reached 346,450 to 367,790 specimens/m² in the lower horizon, and throughout the course of August their population remained at 100,000 to 250,000 specimens/m². It should be noted that 90% of the population concentrated in the middle and



251 Figure 59. Population dynamics of *Enoplus demani* during summer of 1970 and autumn of 1971.

lower horizons of the littoral zone. Probably, the upper horizon of the littoral zone was least favorable for this species due to sharp changes in daily temperatures, high salinity of interstitial waters because of evaporation, and several other factors. The ratio of males to females was 1:1. Females numbered from 61,970 to 97,530 and males 39,110 to 83,310 specimens/m^2. Males and females were three to four times fewer than juveniles. During autumn a general decline in population from 9,650 to 113,790 (September 8, 1971) to 2,540 to 93,980 specimens/m^2 occurred toward the end of September with a lowering of temperature. Reduction in the total population was mainly due to the reduction of juveniles; their number in summer was 110,100 to 178,000 but in autumn 35,500 to 52,100 specimens/m^2. Correspondingly, the number of males and females also declined.

Probably the most favorable temperature condition for multiplication lies between 12 to 16°C. The least intensive process occurs during autumn. Hence this species may be considered arctico-boreal.

251 **Anoplostoma rectospiculum** (Figure 60). In the beginning of July the population was relatively low, 85,500 specimens/m^2 on the average, in the section and the proportion of males, females, and juveniles approximately 1:1:1. Toward the middle of July the number of males, females, and juveniles increased 2.0 to 2.5 times. Throughout the rest of summer the total population averaged 152,500 to 197,000 specimens/m^2 and the same proportion between males, females, and juveniles was maintained.

During autumn a rise in general population was recorded, mainly due to an increase in number of juveniles, which predominated in the population of this species throughout the summer-autumn season. Their maximum number was observed in mid-September (626,300 specimens/m^2 in the upper horizon of the littoral zone). Toward the end of September the total population declined a little and remained at about the same level in the first ten days of October.

Thus this species maintained a sufficiently high population during the course of the two seasons investigated. During summer the same ratio persisted between adults and juveniles, but during autumn, i.e., under low positive temperature conditions (2° to 8°C) juveniles predominated. Males and females were somewhat fewer in autumn compared to their number in the spring-summer season. During the summer of 1970 the female population was 35,900 to 88,900 but during autumn of 1971 only 27,200 to 37,500 specimens/m^2. Probably this species could be considered arctico-boreal but, as distinguished from *E. demani*, finds more favorable
252 temperatures for multiplication during autumn. However, even during summer at temperatures of 12 to 16°C multiplication was fairly intense.

Paracanthonchus macrodon (Figure 61). During the summer season the total population ranged from 97,300 to 183,900 specimens/m^2. Juve-

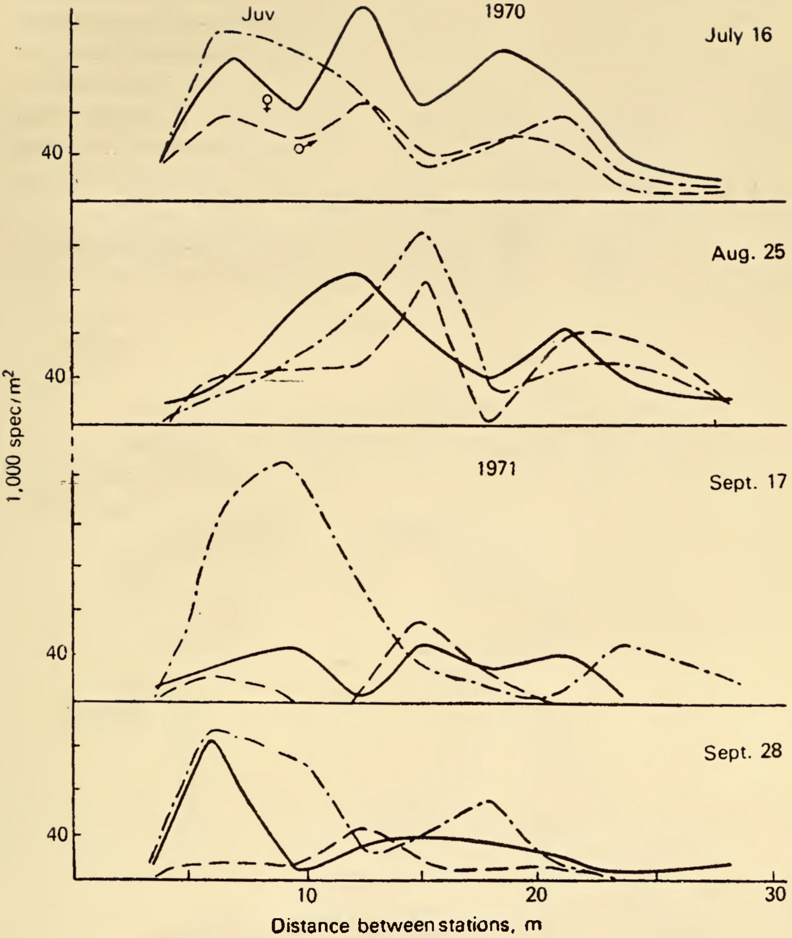


Figure 60. Population dynamics of *Anoplostoma rectospiculum* during summer of 1970 and autumn of 1971.

niles predominated insignificantly during summer but were maximal at the beginning of August. The maximum total population was recorded in the lower horizon of the littoral zone (251,960). The maximum number of males (122,930) and females (116,330 specimens/m^2) was recorded in the middle of August.

During autumn (as in the case of *A. rectospiculum*) a sharp rise occurred in total population (132,150 to 238,000 specimens/m^2). Juveniles occupied a leading position and reached their maximum in mid-September. Two population peaks were observed in the middle (414,520) and lower (363,220 specimens/m²) horizons of the littoral zone. Later a gradual decline in numbers was observed with a lowering of temperature from 6° to 3°C. In October however their population was higher or at least equal to their maximum during summer. Males (31,400 to 61,000) and females (18,050 to 52,400 specimens/m²) were higher in number than in summer. The maximum population in 1971 was recorded in the upper horizon of the littoral zone (females on September 17th—208,780; and males on October 9th—207,260 specimens/m²).

253 Thus, multiplication of the species took place in a wide range of temperatures (2 to 16°C) but multiplication was more intense from 2° to 8°C

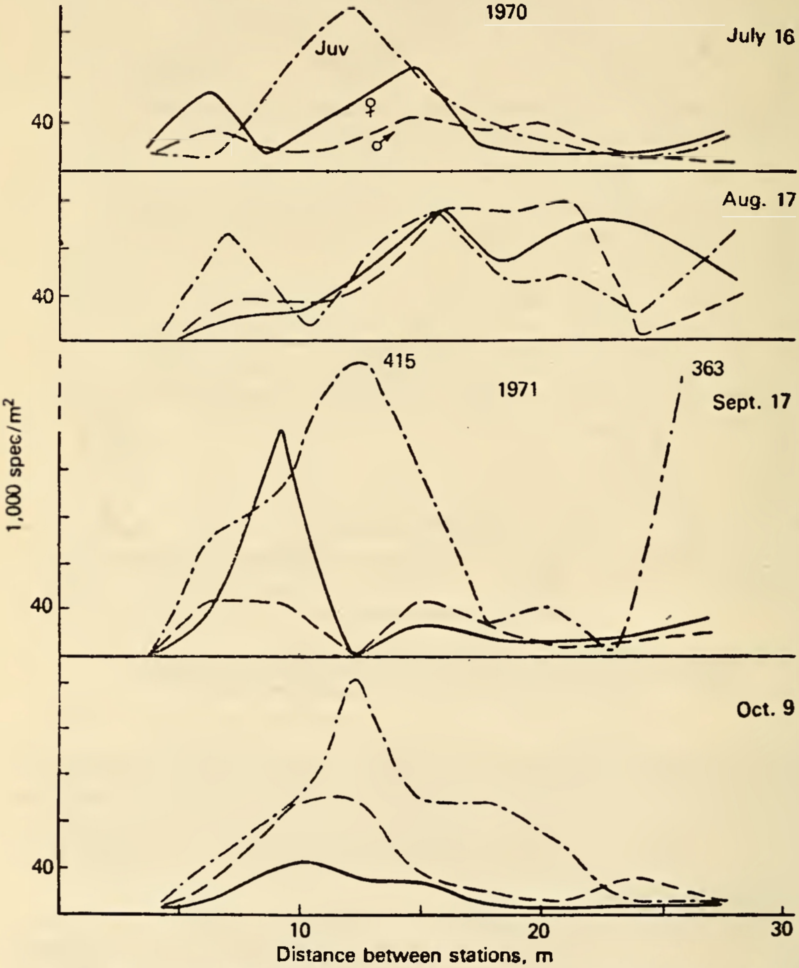
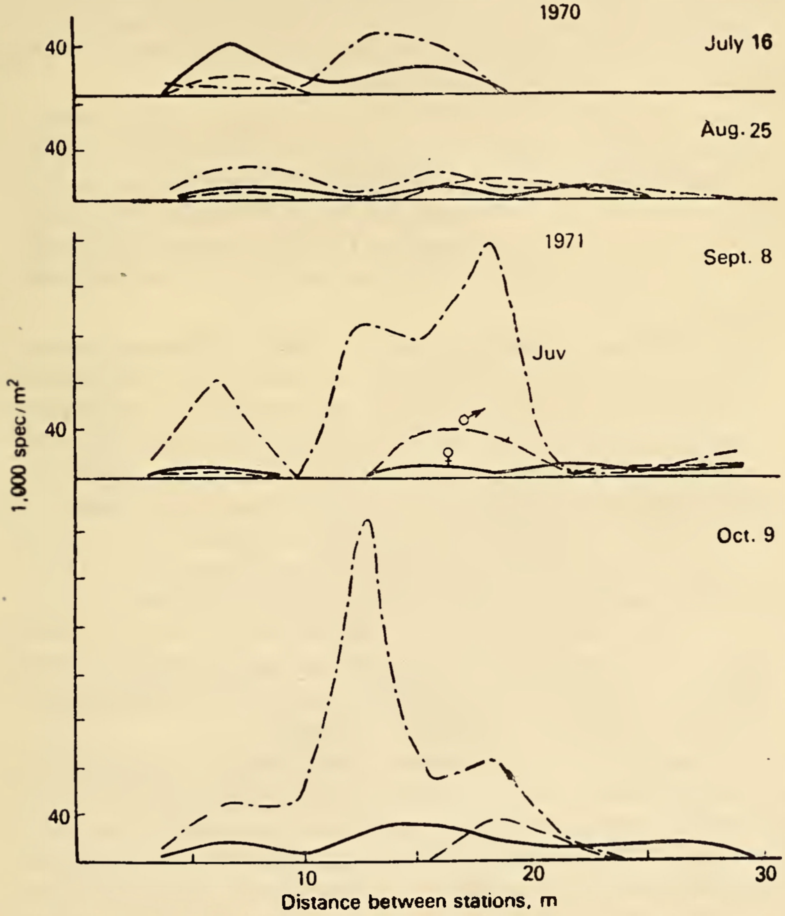


Figure 61. Population dynamics of *Paracanthonchus macrodon* during the summer of 1970 and autumn of 1971.

during autumn. This species may be considered arctico-boreal, preferring lower positive temperatures than *E. demani.*

Axonolaimus paraspinosus (Figure 62). The population was high toward the beginning of summer. On July 16, 1970 the maximum population (75,180 specimens/m^2) was recorded in the middle horizon. During August an extremely low population was observed throughout the section. Toward the end of August the average population ranged from 26,920 to 50,000 specimens/m^2. Juveniles slightly dominated in the population throughout the summer season (14,000 to 38,600), followed by females (9,040 to 33,600), and lastly males (8,270 to 38,600 specimens/m^2).

During autumn a much larger population was observed compared to



254 Figure 62. Population dynamics of *Axonolaimus paraspinosus* during summer of 1970 and autumn of 1971.

the summer season. In the beginning of September, for example, the average density of population constituted 121,550 specimens/m^2 with a maximum value in the middle horizon of the littoral zone—249,420 specimens/m^2. With a decline in temperature to 5° to 6° C in the middle and at the end of the month, the general population declined (average, 87,800). In the month of October a rise in population took place and in the middle horizon a peak occurred (335,280 specimens/m^2). Juveniles
254 predominated in the population with an average density during the season of 41,200 to 94,700 specimens/m^2. The number of females remained almost the same as recorded in 1970. Males were somewhat more numerous in autumn than in summer (14,400 to 30,100 specimens/m^2). Multiplication of *A. paraspinosus* took place in a wide temperature range (2 to 16°C) but more intensely during autumn in a temperature range of 2° to 8°C. This species may be placed with arctico-boreal forms, preferring multiplication at low positive temperatures.

Hence I isolated four arctico-boreal species, out of which *E. demani* prefers much higher positive temperatures for multiplication (12° to 16°C), and *P. macrodon* and *A. paraspinosus* tend toward lower positive temperatures (2° to 8°). *A. rectospiculum* is an intermediate form since during summer in a temperature range of 12 to 16°C the process of multiplication took place rather intensely but even more so at still lower temperatures.

Hypodontolaimus inaequalis (Figure 63). During the summer season of 1970 the maximum population was recorded in July and August (average ranged from 50,640 to 103,400), which declined toward the end of August and beginning of September to 63,600 to 69,600 specimens/m^2. During the course of July juveniles predominated in the population, mainly in the middle horizon of the littoral zone where, for example, on July 27, 1970 the maximum density was 220,980 specimens/m^2. In early
255 August the proportion of males, females, and juveniles was 1 : 1 : 1. From mid-August to the end of the season the juvenile average declined from 31,800 to 14,100 specimens/m^2. The number of males and females throughout the summer season remained about the same (females 16,200 to 30,700, and males 16,520 to 36,500 specimens/m^2). Generally, males were slightly more than females in the population.

During autumn of 1971 the general population of *H. inaequalis* remained approximately the same as during summer (from 51,920 to 86,724 specimens/m^2); maximum density occurred in the upper horizon of the littoral zone in mid-September (208,780 specimens/m^2). The population composition qualitatively differed from that in the preceding season; adults predominated in the population and until mid-September the number of males and females was approximately the same. For example, on September 17, 1971, the population density of females throughout the section was 26,410 to 104,140 and males 23,360 to 104,640 specimens/m^2. Toward the end of September females predominated in the population, but in October males predominated even though the absolute number of the latter declined compared to September. The juvenile population reduced from 26,600 to 5,920 specimens/m^2 toward the end of September: moreover juveniles were found mainly in the lower horizon of the littoral zone.

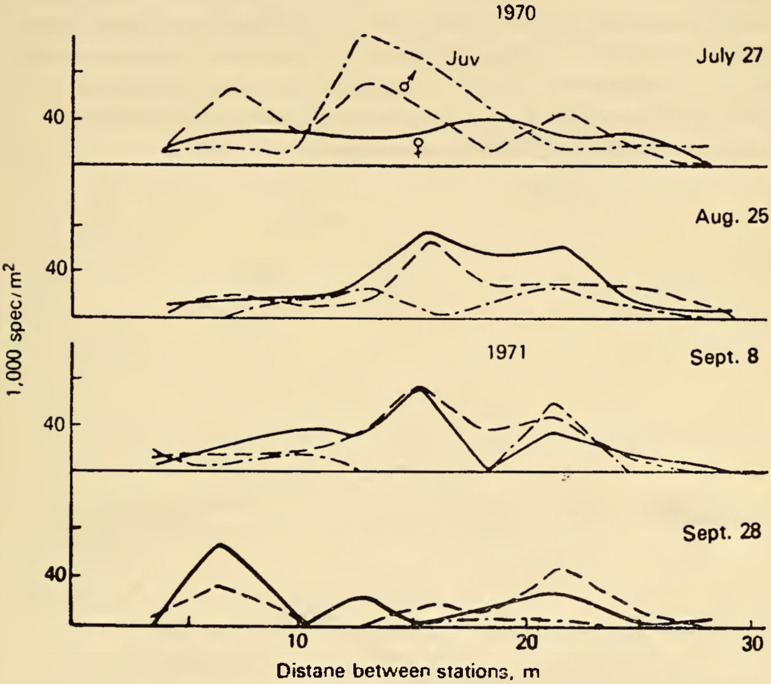


Figure 63. Population dynamics of *Hypodontolaimus inaequalis* during summer of 1970 and autumn of 1971.

From the pattern of distribution and an analysis of population composition of the species, the inference may be drawn that the process of multiplication takes place at high positive temperatures (8° to 16°C). This species prefers the middle horizon of the littoral zone for multiplication. In autumn reproduction was almost nil and only a few juveniles were found in the lower horizon because the process of cooling of water and initial freezing touches the lower horizon later than the upper and middle horizons. Hence this species may be classified as boreal.

Theristus setosus (Figure 64). The general population during the course of July, 1970 was rather high and maximum concentration occurred in the middle and upper strata of the lower horizon of the littoral

256 zone. For example, on July 16, 1970 the density of species in these areas was 250,900 to 626,870 specimens/m². During August and in early September the average declined from 141,450 to 56,560 specimens/m². Juveniles distinctly predominated in the population; their maximum density during the season was 574,540 (July 16, 1970) and occurred in the middle horizon of the littoral zone. In August their absolute number reduced from 88,600 to 23,400 specimens/m². The rate of reduction was approximately uniform in density of males and females. The number of males and females from the beginning of July to the beginning of August was approximately equal. The highest density of males and females was observed in the middle and end of August. For example, on August 17, 1970 the maximum number of females was 87,880 specimens/m² and of males August 25, 1970—20,100 specimens/m².

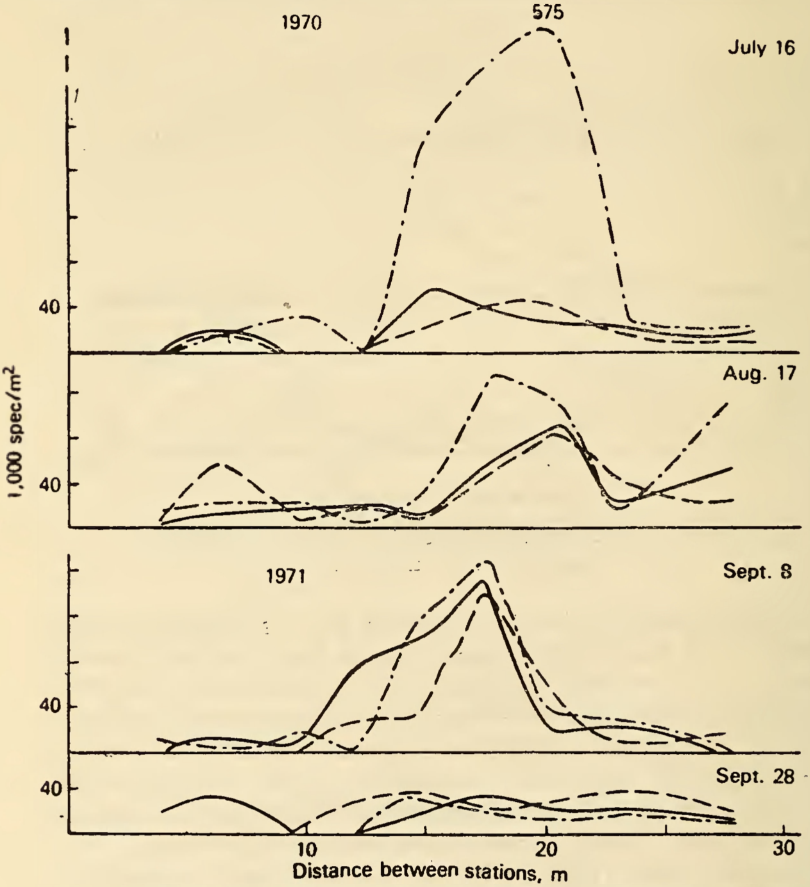


Figure 64. Population dynamics of *Theristus setosus* during summer of 1970 and autumn of 1971.

During autumn of 1971, at the beginning of September, the pattern of distribution of males, females, and juveniles was similar to that at the end of summer, 1970, i.e., juveniles predominated but by small numbers (average density, 51,800). The number of females was slightly lower and that of males still lower (42,100 specimens/m^2). Toward the end of September the number of juveniles declined as did the absolute number of males (to 18,800) and females (to 18,300 specimens/m^2).

In the two seasons a distinct tendency is discernible. Reproduction was intense at the beginning of summer (12° to 14°C) but during autumn considerably slowed down, and at low positive temperatures (2° to 4°C) almost ceased. *T. setosus* should probably be grouped with boreal species.

257 Thus, of the seven leading species two proved boreal. In these two species of nematodes the period of appearance of maximum number of juveniles occurred during the summer season at high positive temperatures (8° to 16°C). As is known, boreal species living in arctic regions with high temperatures for a short period of the year have a short period of multiplication. The farther south, the longer the period of reproduction because at lower latitudes the period of high positive temperatures is prolonged (Ekman, 1953).

The seven species discussed above can be divided into three groups on the basis of their zoogeographic situation.

1. Arctic species: *Timmia acuticauda*, with maximum reproduction during autumn in a temperature range of 2° to 8°C.

2. Arctico-boreal species: (a) *E. demani*, preferring higher positive temperatures (12° to 16°C) for reproduction.

(b) *P. macrodon* and *A. paraspinosus* multiplying with greatest intensity at low positive temperatures (2° to 8°C).

(c) *A. rectospiculum*—intermediate type multiplying well in a wide range of positive temperature (2° to 16°C).

3. Boreal species: *H. inaequalis* and *T. setosus*, with maximum reproduction during summer in a temperature range of 8° to 16°C.

Such a grouping of species confirms the boreal nature of the littoral zone of the White Sea (Gur'yanova, 1948, 1949). Here Kuznetsov (1947) may be mentioned who conducted winter observations in the upper waters of Kandalaksh Bay. According to his data coastal ice acts as a powerful insulation against severe winter conditions. At the time of ebbtide the ice, without damaging the integrity of the ice cover, sinks to the bottom and, lodging on projecting rocks, forms a sort of roof. Under this roof the temperature remains close to 0° even at the time of severe freezing. Consequently the littoral zone of the western region of the White Sea remains under more favorable temperature conditions than the littoral zone of the eastern part. During summer the littoral zone warms up very well due to the relatively southern situation of the sea and severe insolation. During winters it is not so severely cold due to the ice roof. In terms of temperature conditions this region is very close to boreal. This well confirms my analysis of the nematode fauna. Six of the seven leading species are boreal or arctico-boreal.

Feeding

Wieser (1953a, 1959) proposed the division of marine nematodes into four ecolo-morphological groups on the basis of mode of feeding or nutrition (see p. 56).

Works devoted to the feeding habits of meiofauna are rather scarce. Perkins' work (1958) remains the most important to date; he studied the feeding habits of Turbellaria, Copepoda, and Nematoda. Examining the intestinal contents of a large number of nematodes, Perkins came to the conclusion that nematodes of group 1B (nondiscriminating detritophages) feed on diatoms and bacteria in equal measure. Representatives of group 2A include in their ration bacteria and algae that inhabit the bottom. Nematodes of this group procure food by scraping the sandy surface. Nematodes of group 2B feed mainly on bacteria. Regarding this group Perkins differs from Wieser (1953a) who labels these nematodes predators. Perkins found a high percentage of bacteria and diatoms in their intestinal contents. In my opinion this contradiction is reconciled if one acknowledges that nematodes of group 2B have a wide nutritional 258 spectrum. As a matter of fact they could well be classed as detritophages but due to inadequacy of food often change over to predation, employing the powerful armature of their oral cavity (I would tentatively classify them as predators).

Organic detritus, various types of microphytobenthos, and bacteria constitute the food base of nematodes and some other groups of meiobenthos (Bruce, 1928; Remane, 1952; Wieser, 1953a; Dahl, 1953; Renaud-Debyser and Salvat, 1963; Chitwood and Murphy, 1964; Hopper and Meyers, 1966).

According to the classification given by Wieser the dominant species of the littoral zone of Kruglo'e Bay can be divided into the following groups: 1B—*Anoplostoma rectospiculum*, *Axonolaimus paraspinosus*, and *Theristus setosus*; 2A—*Hypodontolaimus inaequalis* and *Timmia acuticauda;* and 2B—*Enoplus demani* and *Paracanthonchus macrodon.* The correlation among these during the summer and autumn seasons is shown in Figure 65. Throughout the summer season nondiscriminating detritophages (1B) predominated, with an average population of 225,550 to 425,830 specimens/m^2. At the beginning of summer their population was low, then rose to dominancy, and gradually dwindled to 263,200 toward the end of summer. Predators (2B) were close to the dominating group, with an average density of 194,350 to 395,300 specimens/m². But a different pattern in population dynamics was evident: lowest at the beginning of summer the population became maximum in midsummer, but declined only slightly at the end of summer. Hence in early September group 2B predominated (319,060 specimens/m²). Representatives of group 2A, which feed on overgrowths, came third. Their average population was 91,940 to 172,450 specimens/m². In general, nematodes of group 2A showed a gradual reduction in population from the beginning of summer to its end.

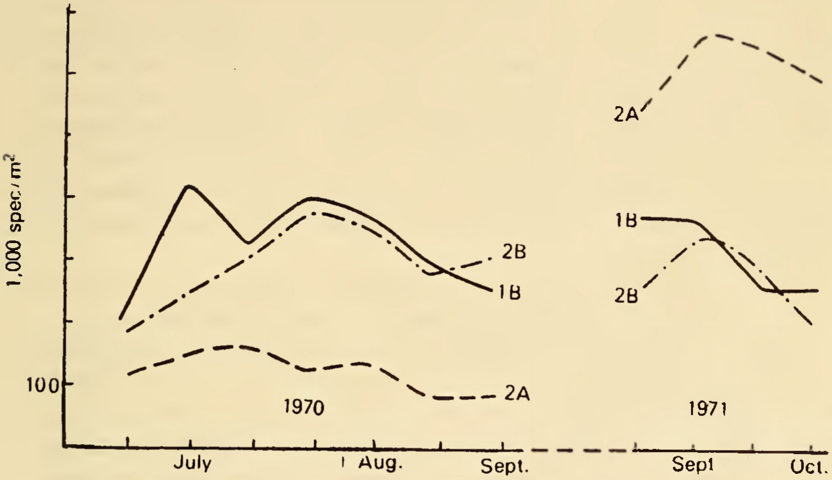


Figure 65. Population variations in groups of nematodes feeding during summer, 1970 and autumn, 1971.

1B—*Anoplostoma rectospiculum, Axonolaimus paraspinosus, Theristus setosus*; 2A—*Hypodontolaimus inaequalis, Timmia acuticauda*; 2B—*Enoplus demani, Paracanthonchus macrodon.*

In autumn the ratio of nematode groups in Wieser's classification changed. First place was held by group 2A with an average population of 560,300 to 684,324 specimens/m², i.e., five to six times higher compared to the average population in summer (for reasons see p. 346). The ratio between nondiscriminating detritophages and predators approximated the summer one. At the beginning of autumn detritophages (group 1B) predominated (380,250); by October their population had declined (to 273,060) and was almost the same as that of predators (group 2B), especially in midautumn (281,012 specimens/m²). The general tendency toward population reduction continued in predators, however, right to the end of autumn.

259 Wieser (1953a) correlated the species composition of nematodes from nine main biotopes with the four nutritional types described above. Perkins (1958), using Wieser's classification, observed that on the coast of Uitsteblya* a correlation of nutritional types characteristic of biotopes three and four could be established (third biotope—finely silted sand of the littoral zone with a predominance of group 1B and 2A; fourth biotope—weakly silted sand with predominance of groups 1B and 2B).

Looking at my material I found that for slightly silted sand (fourth type of biotope) the correlation mentioned by Wieser and Perkins was possible for summer, but in autumn group 2A predominated; the correlation between groups 1B and 2B showed almost no change during autumn except that at the end of the season their population declined somewhat. From these findings one may conclude that in one and the same biotope different correlations of nutritional groups are likely in different seasons of the year. This is probably due to changes in some factors of the surrounding medium (temperature, food base, etc.). In my study the autumnal development of microphytobenthos helped to increase the population of this group of nematodes, which predominantly feeds on diatomaceous algae.

The distribution of nutritional substances in the littoral zone is a primary factor in controlling the population density of meiofauna.

Organic detritus is an important source of nutrition for meiofauna (especially nematodes). Detritus is irregularly distributed on sandy beaches (Schmidt, 1969; Jansson, 1971). The irregular distribution of nematodes and other groups of meiobenthos might be partially explained by this fact. However, some authors (Ganapati and Rao, 1962; Renaud-Debyser, 1963) deny any direct relation between the quantity of detritus and density of meiofauna. This would indicate the utilization of other sources of nutritional substances by meiofauna (Jansson, 1968). A large accumulation of organic debris helps to increase the number of bacteria (Jansson, 1971). Some researchers (Zobell and Anderson, 1936; Zobell and Feltham, 1938; Zobell, 1942; Meadows and Anderson, 1966, 1968), having studied the distribution of bacteria on sandy beaches, arrived at the conclusion that the number of bacteria reaches maximum near the sandy surface in intermediate levels of high and low waters. Matveeva, Nikitina and Chernovskaya (1955) also observed a rise in the content of decay in the midhorizon of the littoral zone (up to 10,000 specimens bacteria/gram ground). All these facts confirm my data nicely, i.e., occurrence of high population of nematodes in the midhorizon of the littoral zone in both seasons—500,000 to 1,000,000 on the average during summer and 1,000,000 to 2,000,000 specimens/m^2 during autumn.

*Direct transliteration of Russian; actual geographic place not traceable as Perkins' work not available—Translator.

Temperature may have an indirect influence on the population dynamics of nematodes. For example, it may stimulate the development of growth of one or the other nutritional substance. Much higher temperatures may facilitate the development of large numbers of bacteria. The predominance of groups 1B and 2B during summer is obviously related to bacterial development. Autumnal development of microphytobenthos (1971) serves as another example of the indirect influence of temperature. A rapid blooming of phytoplankton and microphytobenthos commences with the onset of cooling during the autumn season (V.S. Shuvalov). The sharp rise in nematode population of group 2A, reaching 2,000,000 to 3,000,000 specimens/m^2 could be attributed to this, since their chief source of nutrition is diatomaceous algae.

As already mentioned, the chief sources of food of nematodes are organic detritus, bacteria, and microphytobenthos. Nematodes in turn serve as food for organisms of a higher trophic level. For some invertebrates nematodes are the primary food item. *Crangon crangon* feeds on
260 nematodes and harpacticoids (Plagmann, 1939) and *Nereis diversicolor* feeds on nematodes, copepods, ostracods, and turbellarians (Rees, 1940; Perkins, 1958). Among representatives of meiofauna there are predators which feed on smaller meiofauna. Among nematodes, representatives of genera *Halichoanolaimus*, *Enoplolaimus*, *Sphaerolaimus*, and others may be categorized as predators capable of feeding on each other and also on other organisms of meiofauna such as turbellarians (Remane, 1952; Wieser, 1953b; Chitwood and Timm, 1954). Data on nematodes constituting a dietary item of fish are available (Mironov, 1951; Milovidova, 1961; Bregnballe, 1961; Muus, 1967). According to Gerlach (1971) representatives of meiofauna constitute not less than 15% of the food utilized by different groups of organisms. In summarizing the little data available

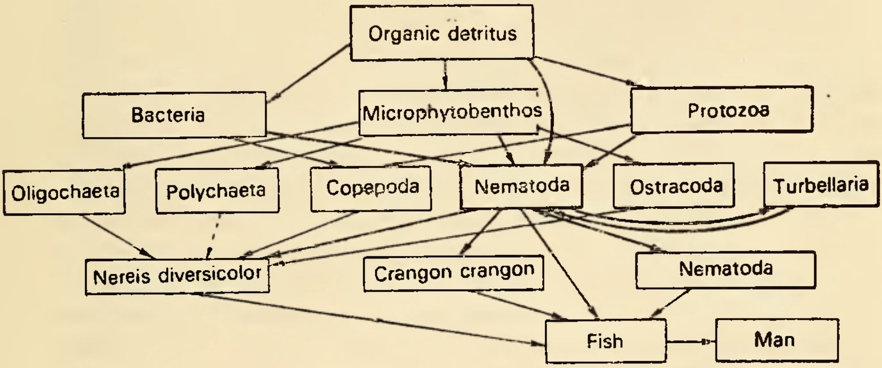


Figure 66. Scheme of food chain of major groups (from data of Plagmann, 1939; Rees, 1941; Perkins, 1958; and others).

on the feeding of nematodes and some other groups of meiofauna, a simplified scheme of trophic relation of nematodes with other groups of animals can be drawn (Figure 66). Obviously, meiobenthos (nematodes included) constitutes to some extent an intermediate link between micro- and macrobenthos, accumulating and processing minute food particles, which if directly utilized by macroforms would be disadvantageous from the point of view of energetics (Kiseleva, 1965). Gilyarov (1944) has also noted that extremely fine food does not justify the energy expended on its procurement.

Taking into account the large number of nematodes and the great speed of their multiplication, it may be construed that they play an important role in the energetic processes occurring in the sea.

Salinity

Because of the rivers emptying into the White Sea its salinity drops from 22 to 25‰ (Gur'yanova, 1948; Chernovskaya, 1956, 1958). As observed by Chernovskaya, the littoral zone of the White Sea is characterized by high salinity during high tide and rather low during ebbtide.

During the two seasons studied I assessed the salinity of waters of the littoral zone of Kruglo'e Bay every three to five days (Figure 67). During the spring-summer period of 1970 salinity was 9.5 to 24.8‰. In July the salinity was 20 to 21‰. Probably the surface drainage of fresh water influenced the saline value (Chernovskaya, 1956). From August 10 to 15 a considerable drop in salinity of water of the littoral zone occurred due to heavy rains. Later, during the second half of August and in early September, salinity rose to 24.0‰ and remained approximately at this level until the end of my observations (October 8th). In other words, in autumn the average value of salinity rose by 2.0 to 3.0‰. During autumn of 1971 the salinity ranged from 4.3 to 25.6‰. Such a wide range of fluctuation in salinity is apparently due to dilution effected by streams 261 draining into Kruglo'e Bay as a result of heavy autumnal rains. This was particularly notable at the end of September. In early October the streams froze and the salinity of coastal waters increased from 21.2 to 25.6‰. Chernovskaya (1956) has also reported a general rise in salinity of littoral waters of the White Sea at the end of September and in early October.

Thus the following generalizations can be drawn with regard to changes in salinity of littoral waters of the region under investigation. A drop in salinity characterizes the beginning of summer (July), an increase of 2.0 to 3.0‰ in the middle and end of summer, and a most unstable regime in the beginning of autumn.

Looking at Figure 68, it can be stated that fluctuations in salinity had practically no effect on the nematode population. For example, the

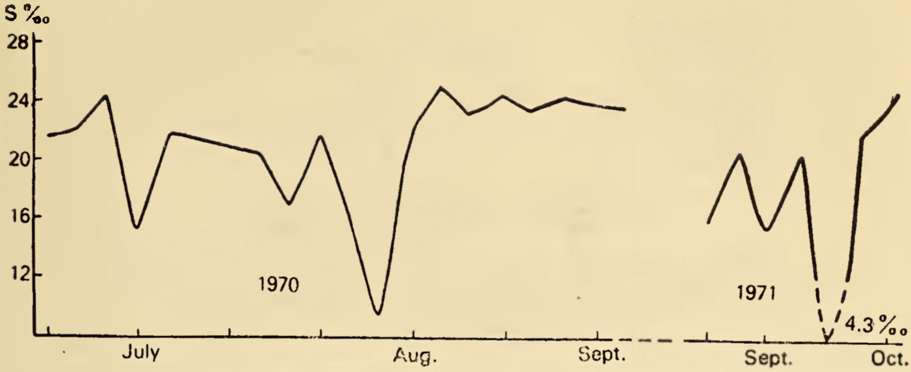


Figure 67. Changes in salinity of water of the littoral zone in Kruglo'e Bay during summer and autumn seasons.

highest average density (980,000 specimens/m^2) corresponded to the lowest average salinity (16.0‰) on August 17, 1970. Had there been some correlation between salinity and nematode population, reduction in salinity should have caused a corresponding reduction in the latter. This was never seen. Hence one may conclude that the nematode population in no way depends on variations in salinity of coastal waters. What could be the reason for this phenomenon?

The problem of effect of salinity on aquatic animals has been studied by the German researcher Kinne (1964a, 1964b, 1966). It is known that salinity of interstitial waters is governed to a significant degree by high and low tides. Hence, quite a large number of studies have been done on the salinity of water in regions covered by high and low tides (Gur'yanova and Ushakov, 1927; Bruce, 1928a; Gur'yanova, Zaks and Ushakov, 262 1930a, 1930b; Linke, 1939; Chernovskaya, 1948, 1956, 1957, 1958; Münch and Perzold, 1956; Ganapati and Rao, 1962; Renaud-Debyser, 1963; Salvat, 1964; Ax, 1966; Govindankutti and Nair, 1966; Jansson, 1967; Johnson, 1967; Fenchel, Jansson and Thun, 1967). It would seem that overlying waters of the littoral zone should be subject to extensive changes in salinity. However, even during spring in the period of ice melt or during autumn in the season of heavy rains, salinity remains fairly high. This is explained by the capacity of the bed to retain denser water. This capacity to retain water increases from a coarser to a silty bottom (Bruevich, 1946). In conditions of a minutely granular ground the salinity of interstitial water is on the average higher than the salinity of overlying water of the littoral zone (Gerlach, 1954; Chernovskaya, 1958; Ganapati and Rao, 1962; Jansson, 1967, Johnson, 1967; McIntyre, 1968; Barnett, 1968). Jansson (1967b, 1968) established the existence of a permanent gradient of salinity in the ground for a prolonged period of time. The

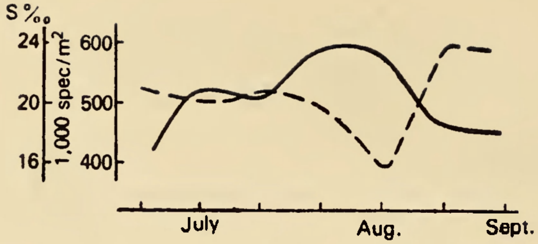


Figure 68. Change in average salinity and average number of nematodes in summer of 1970 (broken line—salinity, and thick line—number of nematodes).

capacity of the ground to preserve a relatively high salinity at ebbtide is the most important factor in the life of littoral organisms living in grounds subject to considerable dilutions (Chernovskaya, 1958). Meiofauna thus exists in more favorable conditions of salinity than epifauna or pelagic forms of shallow waters.

On silted grounds where salinity of interstitial waters of the upper 2.0 cm depends mainly on the salinity of overlying waters, variations may be significant (Smith, 1956; Barnett, 1968). For this reason littoral organisms inhabiting these beaches are capable of tolerating considerable changes in salinity. In this context the problem arises about the capacity of meiofauna living in the littoral zone to tolerate great fluctuations in salinity. Capstick (1959) has recorded a great toleration in nematodes with respect to a wide range of salinity. Such a capacity to tolerate notable fluctuations in salinity has been demonstrated experimentally for a number of other groups of meiofauna—Turbellaria (Jansson, 1968) and Harpacticoida (Jansson, 1967b, 1968) for example.

With reference to my material, the small degree of influence of salinity on the population of nematodes could be explained in two ways:

a) Capacity of interstitial waters to retain a much higher salinity than coastal waters;

b) Capacity of marine nematodes to tolerate great variations in salinity.

Conclusions

262 One to two samples from one square meter can yield with 75% accuracy the real population pattern of meiofauna in a given area in the littoral zone.

Chislenko's divider, which expedites counting of organisms of meiobenthos, can be recommended for compartmental processing of the sample. The error in estimating number of organisms in the entire sample, using the divider, does not exceed 1.4 to 1.5. The lower limit of the absolute number of organisms for which such an error is not significant, is 100 individuals. Distribution of organisms in the sectors of the divider may be considered equally reliable, ignoring the slight differences in size of compartments. The order of selection of organisms from compartments does not affect the end results. To obtain more accurate data an auxiliary divider for stirring the samples may be utilized.

In the summer season of 1970 and the autumn season of 1971 the following groups of meiobenthos were found in the littoral zone of
263 Kruglo'e Bay: eumeiobenthos—Foraminifera, Nematoda, Harpacticoida, and Turbellaria; pseudomeiobenthos—Oligochaeta, Polychaeta, and juveniles of mollusks Bivalvia and Gastropoda. The population of the entire meiobenthos during the summer season ranged from 70,600 to 2,524,760 specimens/m^2 and the biomass from 0.7 to 576.2 g/m^2; during autumn the population ranged from 141,730 to 6,283,960 specimens/m^2 and the biomass from 3.1 to 115.7 g/m^2.

During the two seasons selected for investigations an irregularity of distribution of meiofauna in the littoral zone was observed. Meiofauna of the middle horizon was the richest and that of the lower horizon the poorest. One possible reason for this phenomenon could be the irregular distribution of food material. Eumeiobenthos constituted 80 to 95% of the total meiofauna population.

The leading group of meiobenthos consisted of free-living marine nematodes. Their population during the summer of 1970 ranged from 4,570 to 1,778,000 specimens/m^2 and the biomass from 0.6 to 264.6 g/m^2; during autumn of 1971 the population ranged from 77,720 to 6,156,900 specimens/m^2 and the biomass from 10.0 to 861.0 g/m^2.

During the summer season shifts in population maxima were seen. In July to early August the population peak shifted from the middle horizon of the littoral zone to the lower stratum of the upper horizon; from mid-August the population peak reversed, i.e. toward the lower horizon of the littoral zone. During autumn the population peak shifted from the lower and middle horizons of the littoral zone to the upper horizon, and a sharp rise in population was observed in the latter from 200,000 to 6,000,000 specimens/m^2.

An examination of the White Sea material revealed 76 species of nematodes; 35 were found in the littoral zone. Brief descriptions of 22 fairly common species have been given and more detailed descriptions of 13 species new to science.

Of the 35 species recorded during both seasons, 7 predominated: *Timmia acuticauda*, *Anoplostoma rectospiculum*, *Axonolaimus paraspinosus*, *Enoplus demani*, *Paracanthonchus macrodon*, *Hypodontolaimus inaequalis*, and *Theristus setosus*. The highest population observed during summer comprised *E. demani*, *H. inaequalis*, and *T. setosus*. A rapid increase in population density was observed for *T. acuticauda*, *A. paraspinosus*, and *P. macrodon* during the autumn season. Population density was approximately the same for *A. rectospiculum* during the summer of 1970 and the autumn of 1971.

Except for *T. acuticauda*, almost all the leading species of nematodes preferred the middle horizon of the littoral zone for habitations in both summer and autumn. *E. demani*, *P. macrodon*, and *T. setosus* also revealed rapid increases in population in the lower horizon of the littoral zone. *T. acuticauda*, *A. rectospiculum*, and *A. paraspinosus* revealed a high density of population during autumn in the upper horizon of the littoral zone. One may speak of "selectivity of habitats" among species in the littoral zone during different seasons.

A direct relation between density of all nematodes or individual species and size of particles of the sediment in which they live could not be established.

The limiting factor influencing the distribution of most nematode species is the minimal diameter of the capillaries in which they exist (in my study, from 20 to 80 μm). Such a diameter of capillaries suffices for the habitation of *M. filicauda*, *A. rectospiculum*, *T. acuticauda*, *P. macrodon*, *T. flevensis*, and others. *H. inaequalis* and *T. setosus* are capable of widening the minimal capillary passages. The presence of minimal capillary diameters exerts little influence on the distribution of *E. demani*, which actively constructs the minimal space essential for its life. On the basis of this a criterion for the upper limit of meiobenthos has been suggested, namely, the capacity of organisms to inhabit minimal capillary passages.

Of the seven species examined on the basis of temperature optimum for reproduction, three groups can probably be identified on the basis of zoogeographic affinities:

1. Arctic species: *T. acuticauda* with maximum reproduction in the temperature range of 2 to 8°C.
2. Arctico-boreal species: *E. demani*, preferring high positive temperatures for multiplication; *P. macrodon* and *A. paraspinosus*, multiplying intensely during autumn at low positive temperatures (3 to 8°C); and *A.* 264 *rectospiculum*, an intermediate type in which the process of reproduction takes place at both high and low positive temperatures.
3. Boreal species: *H. inaequalis* and *T. setosus*, with maximum reproduction during summer in a temperature range of 8° to 16°C.

An analysis of the leading species of nematodes confirmed the boreal character of the littoral zone of the White Sea.

During summer, 1970 nondiscriminating (omnivorous) detritophages predominated in the littoral zone of Kruglo'e Bay (1B). Predators (group 2B) came next, while the density of "eaters" of overgrowths (2A) was low. During autumn, 1971 the predominant position was held by the latter group. The ratio between detritophages and predators remained approximately the same as during summer. Thus in one and the same biotope different ratios of nutritional types (groups) of nematodes were observed. This is probably related to changes in some factors of the surrounding medium (temperature, quantity and distribution of food substances, and others).

The high population of nematodes in the middle horizon of the littoral zone during both seasons can be explained by the presence of a rich food base here, namely, bacteria. The autumnal population increase of "eaters" of overgrowths (*T. acuticauda*) is associated with the vigorous development of microphytobenthos.

Interstitial waters are capable of retaining a higher salinity over a prolonged period than coastal waters. Free-living nematodes are euryhaline and tolerate wide variations in salinity. Considering these two factors it can be stated that the influence of salinity on the population dynamics of nematodes is negligible.

Considering the vast population of meiofauna, the paucity of taxonomic and ecological studies of its many groups, and the great role played by representatives of meiobenthos in the energetic processes of the sea, one hopes that hydrobiologists will soon be motivated to raise the level of study of meiobenthos to that achieved for macrobenthos.

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