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INVESTIGATIONS ON COLONIZATION OF NEW SUBSTRATES BY
NEMATODES (*NEMATODA*) AND SOME OTHER PERIPHYTON
ORGANISMS*

Description of a process of colonization of new substrates by periphyton organisms in the lake littoral was the aim of the study. Free-living nematodes (*Nematoda*) were the main objective of the study. A degree of attachment of nematodes to a substrate, length of their life cycles, and changes in numbers were determined as based on observations which pertain to the biology and ecology of nematodes. Regularities in the process of colonization of new substrates were described. Taking an advantage of the field and laboratory experiments an analysis was made of the process of colonization, its mechanisms and controlling factors.

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I. INTRODUCTION

Characteristic of regularities in the process of colonization of new substrates by periphyton organisms, with an attempt made to define factors which controlled the process, was the theme of the study.

Colonization of both natural substrates present in the littoral zone of a lake and those artificially introduced into a reservoir was investigated.

The study is based on field observations as well as on field and laboratory experiments.

Free-living nematodes being the constant and numerous component of periphyton, were the main objective of the study.

A number of observations pertaining to biology of nematodes were made in order to explain some regularities which occur in the process of colonization of new substrates. Other organisms (*Algae*, *Tendipedidae*, *Oligochaeta*), which were more abundant in periphyton, were also studied.

A process of colonization of new substrates by periphyton organisms is a natural phenomenon, which takes place constantly in water reservoirs. In spring, for example, periphyton appears on the higher aquatic plants that start growing in a reservoir. It may also appear on various non-living materials introduced into water merely by chance, or purposefully by a man, at any season of a year, as well as on any kind of substrates flooded with water, when its level changes. In natural conditions periphyton constitutes a biocenose which forms and organizes itself constantly, and therefore, the most important problems concern its formation during the process of colonization.

In literature, one can find a variety of views concerning definitions of periphyton, its terminology, as well as the position and role of periphyton in water biocenoses.

Historical review of several definitions and terms used in this field was given by Naumann (1931), Duplakov (1933), Roll (1939), Šramek-Hušek (1947), and Cooke (1956).

The term "periphyton" was introduced by Behning in 1924. The author understood it as an assemblage of animals and plants settled down on various materials introduced into a reservoir. Later on, the term has been extended to comprehend the animal and plant organisms which settle down on all solid substrates present in a reservoir. Two terms, which were introduced earlier in the literature: "Aufwuchs" – by Seligo in 1905 and "Bewuchs" – by Hentschel in 1916, were of the similar meaning (acc. to Cooke 1956).

In more recent American literature, besides the term "periphyton", the descriptive terms: "attached material" and "seeding on" are used to denote the organisms that appear on various substrates in water reservoirs (Cooke 1956).

In Russian literature, besides the term "periphyton", other terms are also encountered, namely: the term "narosty" – usually used for the organisms that grow on living substrates and "obrosty" – for those that grow on non-living materials (Ziernov 1945, Lipin 1950). Also the term "obrastaniya" is often used (Gorbunov 1955, Sokolova 1959, and others).

Besides the terms mentioned above, which are the most often used, other terms can be also found in the literature. For example, Šrámek-Hušek (1946) has introduced the term "epiholon" to denote the grouping of organisms which are attached to various materials submerged in water reservoirs. Furthermore, he divided it into: "epilithon", "epiphyton", "epizoon", etc., according to the kind of substrate.

Various authors, irrespective of the fact which term they accept, put in it different ecological meanings. A great deal of them do not consider "periphyton" as an independent ecological unit¹. In 1933, after many years of study on periphyton, Duplakov has defined it as an independent biocenotic unit. Of the same opinion are: Karsinkin (1934), Šrámek-Hušek (1946), Wysocka (1952), and others. All these authors emphasize the fact that periphyton can be considered as an independent biocenotic unit, because it consists of the organisms that represent 3 fundamental trophic levels, namely, producers, consumers and reducers.

The approach to periphyton organisms differs in hydrobiological literature concerning classification of water organisms. Some authors do not recognize these organisms as an independent community. For example, Naumov (1961) classes them among benthos, Žadin (1950) – among microbenthos, and Lityński defines them as the attached and anchored benthos (however, he considers the groupings of the organisms that grow on the materials introduced into a reservoir as the independent microbiocenoses). Another group of authors regard periphyton as an ecological group within benthos (Ziernov 1949, Bogoslovskij 1960, Welch 1952). Others define periphyton as an independent grouping of water organisms, of equal rank as benthos or plankton (Lipin 1950, Odum 1953, Ruttner 1953).

In the majority of cases, only the organisms that attach to a substrate are considered as periphyton. However, a great deal of authors emphasize the fact that lots of nonattached organisms – planctonic or free-swimming forms – occur in periphyton abundantly (Young 1945, Newcombe 1950, Welch 1952, Ruttner 1953). Ruttner (1953) regards these organisms as a permanent component of periphyton, defining the latter as a grouping of plant and animal organisms; both, these that attach to a solid substrate and those that swim freely among the attached forms. In practice, many of authors recognize the nonattached forms as components of periphyton, in spite of the usually accepted definition. Other authors distinguish true-periphyton organisms and pseudo-periphyton organisms with various degree of attachment to a substrate (Willer 1923, Gorbunov 1955, Sladeczkova 1960, and others).

In the present work the meaning of the term "periphyton" is similar to that of Ruttner's definition (1953). Periphyton is considered here as an independent ecological unit. It consists of not only permanently sessile forms,

¹In further discussion of the literature, various terms of the similar meaning used by the authors cited will be substituted by the term "periphyton".

but also of temporarily sessile forms and free-swimming ones, which occur in periphyton abundantly, and which find there the suitable place to live in.

A great deal of papers, dealing directly or indirectly, with the problem of colonization of new substrates by periphyton organisms, can be found in the literature. Investigations of this kind depend usually on observations of the process of settling down various groups of organisms on substrates introduced to water reservoirs experimentally. The method depending on observations of the growth of periphyton on the artificial substrates, and not on the natural ones, is commonly used. It allows to collect the quantitative material quite easily, whereas the quantitative sampling from natural substrates is rather difficult.

Since glass was the most often used material as the substrate, the method is known in the literature as the glass slides method. The standard microscope slides were usually applied, but also glass plates of different shape and dimension, as well as sheets of plastic, of different alloys, and lumps of cement were used for experimentation. The list of the materials that served as the substrates has been presented by Cooke (1956). The glass slides were placed in water differently, either laid down on the bottom, or suspended in wooden frames on floats (Duplakov 1933, Abdin 1949, Wysocka 1952, 1957, Wysocka-Bujalska 1958b, and others), or placed in boxes with compartments (Karsinkin 1934), Various apparatuses were also invented (Bissonnette 1930, Brien 1954, Patrick and others 1954).

Papers pertaining closely to the process of colonization of new environments, with an emphasis laid on the process of organization of a new biocenose, deal with several problems.

A number of authors were concerned with succession of the periphyton biocenose (sequence of domination of species or groups of species, changes in numbers, etc.). Among them: Duplakov (1933), Smaragdova (1937), Ivlev (1934, 1954), Scheer (1945), Odum (1957), Wysocka (1952), Wysocka-Bujalska (1958a, 1961), Sladeczkova (1960), and others.

Some of the authors distinguished developmental stages of periphyton biocenose during the course of its formation in the result of settling of organisms. Duplakov (1933), for example, has distinguished 3 stages in the periphyton appearing on experimental substrates introduced into water reservoirs, namely, the period of cumulation (when species accumulated on the substrate), the period of reconstruction (when the settled species changed in numbers), and the period of stabilization (when the species composition stabilized). Ivlev (1933), Gorbunov (1955), and Wysocka-Bujalska (1958a, 1961) have also described various stages of periphyton biocenose.

The problem of "protective" or "antagonistic" relationships, existing among components (species) of periphyton biocenose during its formation, is another subject of investigation in papers dealing with colonization of new substrates by periphyton organisms. These investigations are based on the field observation mainly and contain an analysis of co-occurrence, or lack of co-occurrence of dominant species or groups of species, but some experiments, involving elimination of various species or suppression of their reproduction, were also made. Such observations were carried out by

Duplakov (1933), Smaragdova (1937), Ivlev (1933, 1954), and Wysocka (1952), Wysocka-Bujalska (1958a). All these authors have found the "protective" and "antagonistic" relationships existing among different species of periphyton biocenose, with different interrelations among the species investigated in various ecological conditions.

In some investigations on colonization of new substrates by periphyton organisms, the authors emphasize the role of factors differentiating and controlling the development of periphyton. Differentiating effect of the type of substrate on settling of periphyton organisms is a subject of the paper by Pieczyńska and Spodniewska (1963).

Besides the papers discussed above, that deal with the problem of settling of organisms directly, there is a number of papers that pertain to this problem only indirectly. In these papers an advantage was taken of the fact that periphyton organisms appeared rapidly on the newly introduced substrates. It made possible to analyze certain problems concerning the occurrence of periphyton organisms. An analysis of periphyton was usually made after a certain period of time, when the periphyton was already formed, with no, or little, attention given to the process of its formation.

Such papers deal with the comparison of periphyton of various reservoirs, with the time and space differences of its occurrence, with vertical stratification, etc.

Some recent papers deal with production of periphyton on substrates introduced experimentally into reservoirs (Newcombe 1950, Castenholz 1960, 1961, Waters 1961).

The "glass slides method" has been also used for practical purpose. In Poland Wysocka (1957, Wysocka-Bujalska 1958b) has used this method to study biological composition of polluted waters. The method was also taken into account in elaborations published by Kolkwitz (1950) and Liebmann (1951).

Since periphyton organisms settle down in masses on boats, ships and on various harbor equipment, the investigations aiming at destruction of these organisms are of great practical importance. Such investigations were carried out by Parker (1924), Hopkins (1935), Jonson and Miller (1935), Coe and Allen (1937), and others.

As it was shown, the investigations discussed above, concerning colonization of new substrates by periphyton organisms, cover various problems. Nevertheless, such aspects as description of regularities involved in colonization of new substrates in natural conditions and analysis of factors controlling the course of the colonization process, which are the theme of the present paper, were disregarded in the literature. It should be emphasized that the majority of the discussed papers concerned periphyton algae, only few papers dealt with animal components of periphyton.

II. METHODS

Investigations on colonization of new substrates by periphyton organisms were carried out in different parts of the littoral zone of the lake Mikołajskie

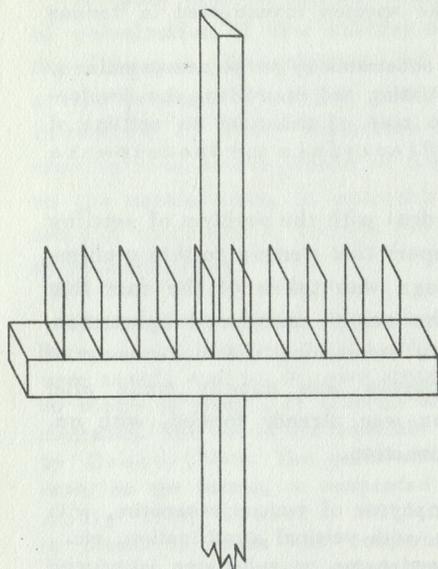
and, to a smaller extent, of the lakes: Śniardwy and Tałtowisko (Mazurian lake district). The work was done during the years 1960–1962.

Observations have been made on the occurrence and the settling process of periphyton organisms on natural substrates present in the reservoirs (mainly macrophytes) as well as on artificial substrates introduced into the lakes experimentally.

Microscope glass slides were most often used (2.5×7.5) as the experimental substrates. The glass slides were mounted in small boards with grooves (Fig. 1). Besides the glass slides, glass plates and tubes of different dimension were also used. They were either driven into the bottom, or suspended on special stands.

The quantitative samples of periphyton were collected from the experimental substrates by scraping off the periphyton from the defined area of the substrate. From plants, the quantitative samples were taken by cutting off some parts of their stalks. The surface of these parts was determined in the laboratory after the removal of periphyton.

Fig. 1 – Stand with glass slides for sticking into bottom (based on Wysocka-Bujalska's model – unpublished data)



Of the collected material the following taxonomic groups were elaborated: *Nematoda* – all individuals were taken out of the samples and counted, the sex and age structures of dominants and the species composition were determined.

Oligochaeta and *Tendipedidae* – only numbers were counted.

Algae – numbers and the species composition were defined by I. Spodniewska. She made the quantitative and qualitative analyses of this group, according to the method described in one of her papers (Spodniewska 1955).

The total quantity of periphyton was also determined by placing the scraped off periphyton into calibrated containers filled with water. The records of sediments were taken after 24 hours.

The numbers of individuals of the investigated species were related to the area of 100 cm^2 of the substrate surface and to the volume of 10 cm^3 of periphyton.

III. PERIPHYTON NEMATODES (*NEMATODA*)

1. Composition of species and chosen elements of their biology

In the former studies (Pieczyńska 1959, 1961, and unpublished data; Pieczyńska and Spodniewska 1963), carried out on several tens of the Mazurian lakes, it was found that the species *Prochromadorella bioculata* and *Punctodora ratzeburgensis* showed the clear predominance among the periphyton nematodes (about 90% of the total number of nematodes). These two species occurred in various proportions. Only in several lakes and in certain types of periphyton other species of nematodes predominated. These were: *Dorylaimus filiformis* Bastian 1865, *Prochromadorella viridis* (v. Linstow 1876) and *Rhabdolaimus terrestris* de Man 1880.

In the lakes under the present investigation the numbers of *Prochromadorella bioculata* and *Punctodora ratzeburgensis* also amounted to over 90% of total number of nematodes. However, the proportion of these two species varied on different substrates.

The total number of species found in the material was as high as 28 species of nematodes. The list of the species is as follows (taxonomic order acc. to Meyl 1960):

Diplogasteridae

1. *Diplogaster rivalis* (Leydig 1854)

Aphelenchidae

2. *Aphelenchoides* sp.

Plectidae

3. *Plectus cirratus* Bastian 1865
4. *Plectus granulatus* Bastian 1865
5. *Plectus parietinus* Bastian 1865
6. *Rhabdolaimus terrestris* de Man 1880

Monhysteridae

7. *Monhystera dispar* Bastian 1865
8. *Monhystera paludicola* de Man 1881
9. *Monhystera similis* Bütschli 1873
10. *Monhystera vulgaris* de Man 1880
11. *Prismatolaimus intermedius* (Bütschli 1873)

Chromadoridae

12. *Chromadorita leuckarti* (de Man 1876)
13. *Prochromadorella bioculata* (M. Schultze 1858)²
14. *Prochromadorella viridis* (v. Linstow 1876)²
15. *Punctodora ratzeburgensis* (v. Linstow 1876)

*Cyatholaimidae*16. *Achromadora terricola* (de Man 1880)17. *Ethmolaimus pratensis* de Man 1880*Ironidae*18. *Ironus ignavus* Bastian 1865*Tripylidae*19. *Tobrilus gracilis* (Bastian 1865)20. *Tobrilus longus* (Leidy 1852)21. *Tobrilus zakopanensis* (Stefański 1924)22. *Tobrilus* sp.*Mononchidae*23. *Mononchus macrostoma* Bastian 1865*Dorylaimidae*24. *Dorylaimus filiformis* Bastian 186525. *Dorylaimus flavomaculatus* v. Linstow 187626. *Dorylaimus helveticus* Steiner 191927. *Dorylaimus* sp.*Actinolaimidae*28. *Actinolaimus macrolaimus* (de Man 1884)

In the literature only fragmentary information can be found on the biology of the listed species that belong to the family of *Chromadoridae*, and which live in masses in periphyton.

Micoletzky (1925), Overgaard-Nielsen (1949), Goodey (1951), and Hyman (1951) wrote that these species feed on algae mainly.

Micoletzky (1925) and Hyman (1951) have emphasized the fact of high oxygen requirements of these species.

Meschkat (1934), during his laboratory and field studies, has found that the individuals of *Prochromadorella bioculata* and *Punctodora ratzeburgensis* secrete from their caudal glands the long threads of gluing substance, which enables them to fasten temporarily to a substrate. He stressed the fact that the threads of glue secreted by nematodes form the "skeleton" of the whole periphyton. The Meschkat's observation was also cited by Bronns (1939).

Because of the fragmentary literature data, which has been mentioned already, some observations on biology of periphyton nematodes were made in the present study. Only the indispensable problems, necessary for further interpretation of the colonization process of new substrates by periphyton organisms, were investigated.

Within this part of study some field and laboratory observations were made

² According to Meyl (1960) the genus to which these species belong is: *Chromadorina*. In the present paper, the genus *Prochromadorella*, often used in the literature and also in previous papers of the present author, was retained for these species.

on the degree of attachment (degree of connection with a substrate) of the dominant species *Prochromadorella bioculata* and *Punctodora ratzeburgensis*. The procedure of these investigations was as follows:

1. Individuals of the species investigated were taken out of the samples of periphyton growing on reeds, and placed into the Petri dishes containing the lake water with single cells of algae and small amount of detritus. The distribution of the nematodes was determined with the use of the stereoscopic microscope. It has been observed that after 10 to 20 minutes the nematodes attached themselves with the secreted substance to the particles of detritus and to the cells of algae. During several days of observation it was found that about 90% of the individuals were attached to the substrates. The secretion coming from the caudal glands in shape of threads about 100 μ long can be seen under the stereoscopic microscope at the proper lighting.

2. The glass slides, with stripes of glass glued on their margins (Fig. 2) in order to retain a thin layer of water over the periphyton during later observations under the microscope, were submerged in water of the littoral zone. After several days of submersion the appearing nematodes were examined every day. The slides were covered with glass plates while under the water surface, then taken out of water and immediately searched under the microscope. During each observation the majority of individuals were found attached to the substrate. The numbers of individuals found in the preserved material, after the experiment ended, were 6 time as high as during the observations made on the living material. It can be supposed that a great deal of individuals were hidden among threads of algae. It should be added that the observations were made on the "young" periphyton, 10 days of submergence period, at most, and that such periphyton does not form long "beard" yet, which would have made the observations more difficult.

3. Water in the littoral zone was agitated with an oar before sampling in order to strike off the periphyton organisms attached to reeds growing abundantly in this place. Having it done, the samples of water were taken and immediately searched. It was found that only 40% of the total number of nematodes were swimming in the water non attached to any particles of substrate, the rest of them were attached with the threads of glue to various particles of detritus or to alga cells.

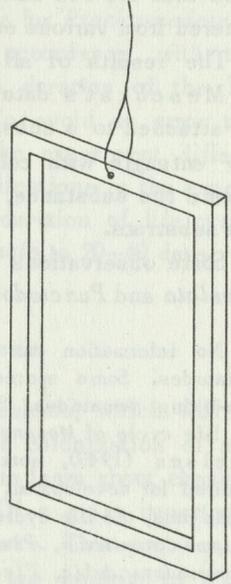


Fig. 2 - Plate used for study on the degree of attachment of nematodes

In all series of the experiment, the species *Prochromadorella bioculata* and *Punctodora ratzeburgensis* showed very similar degree of attachment to the substrate. However, some sex differences were noted. Females of these species showed somewhat higher degree of attachment than males. It was found that the sex ratio of females to males was on average 2:1 in materials gathered from various environments during several years of study.

The results of all the experiments discussed above, as compared with the Meschkat's data (1934), give a good evidence that periphyton nematodes are attached to a substrate strongly in mechanical way. In natural conditions they entangle with colonies of algae, and besides this, their caudal glands secrete the substance, with which they attach themselves quickly and firmly to a substrate.

Some observations were also made on the life cycles of *Prochromadorella bioculata* and *Punctodora ratzeburgensis*.

No information can be found in the literature on the life cycles of periphyton nematodes. Some sporadic observations that were made pertain, in general, to free-living nematodes. Steiner and Heinly (1922) have defined the duration of the life cycle of *Mononochus papillatus* (from egg to egg) as 50 days. Overgaard-Nielsen (1949), working on biology of soil nematodes, has determined the time required for development from egg to egg for several species of nematodes. According to his data, the life cycles of the species that occur also in fresh waters is as follows: *Alaimus primitivus*, *Plectus cirratus*, *Prismatolaimus dolichurus* — 20 to 30 days; *Achromadora dubia*, *Plectus parvus*, *Wilsonema auriculatum* — 20 days; *Anaplectus granulatus* — 25 days; *Tripyla setifera* — 30 to 40 days. For the other species, living exclusively in soil, the duration of life cycles ranges from 15 to 25 days.

The cultures of *Prochromadorella bioculata* and *Punctodora ratzeburgensis* were set in the laboratory in order to determine the life cycle of these species. The nematodes were kept in small containers, 2 cm³ of volume, filled with the lake water containing single cells of algae. The containers were covered with no. 25 bolting cloth and placed into an aquarium with water of high oxygen content. Observations were made in 2-day intervals. Each time, the containers had been removed from the aquarium and their contents transferred onto the Petri dishes and searched under the stereoscopic microscope. Then the nematodes were reintroduced into the containers. In 60% of cases the nematodes died after several days of observations. In the rest of cultures, in which the nematodes have survived, the following results were attained. Of 136 investigated individuals only 3 *Punctodora ratzeburgensis* and 2 *Prochromadorella bioculata* went through complete development, i. e., they laid their eggs, which developed into the adult individuals filled with eggs. The time required for this was 26, 30 and 33 days for the specimens of *Punctodora ratzeburgensis*, and 29 and 34 for these of *Prochromadorella bioculata*. During 16 to 22 days, 20 days on average, 40 individuals of *Punctodora ratzeburgensis*, and 34

individuals of *Prochromadorella bioculata* went partially through their development from the stage of young larva to the stage of an adult ready for reproduction. No difference was found in the rates of development of both species in the experiment. It was also observed that females of these species laid 3 to 10 eggs, on average 5 eggs, during 10 day period.

The results of these experiments: 26 to 34 day cycle for *Prochromadorella bioculata* and *Punctodora ratzeburgensis*, are in accordance with the Overgaard-Nielsen's data cited above (1949) on duration of the life cycles of other species of fresh water nematodes. To avoid an error that might result from the fact that living conditions in the experiment differed from those in nature, and that there was not enough replications in the experiment, it is safer to extend the obtained results on duration of life cycles of *Prochromadorella bioculata* and *Punctodora ratzeburgensis* to 20-40 days.

2. Seasonal changes in numbers

In order to achieve the proper interpretation of problems, which will be discussed later on in the paper, on the process of colonization of new substrates by periphyton organisms, it is also necessary to learn about changes in numbers of the investigated groups of organisms. Of a great importance is especially the rate of reproduction of these organisms. This problem, in its general scope at least, has been investigated for the majority of water organisms, whereas no reliable quantitative data on occurrence of periphyton nematodes and even other fresh water nematodes can be found in the literature.

A number of investigations concern the occurrence of fresh water nematodes during various seasons of the year (Borner 1922, Schneider 1922, Meuche 1939, Paetzold 1955) but unfortunately these data do not allow for generalization.

Meschkat (1934) investigated in details the annual changes in numbers of periphyton nematodes. The author found the maximum of numbers of nematodes in spring and their minimum - in winter.

Although quantitative investigations on occurrence of soil nematodes (the forms closely related to fresh water nematodes) are more extensive and numerous, they do not supply the consistent data. Micoletzky (1921) has found the maximum of numbers of soil nematodes occurring in autumn and their minimum - in winter. Seidenschwartz (1923) has described considerable changes in numbers of nematodes during the annual cycle with the highest numbers observed in summer, the smallest - in winter. He has also stated that various species of nematodes achieved their maximum numbers in different seasons of the year. Dziuba and Witkowski (1959) have observed conspicuous annual changes in numbers of nematodes, different in soil of various plant cultures. On the other hand, Overgaard-Nielsen (1949) has questioned the presence of seasonal changes in numbers of nematodes on the basis of his own data and those of Franz (1942) and Stockli (1943).

In the present paper thorough investigations on seasonal changes in numbers of nematodes were carried out on 2 stations in different places of the littoral zone of the lake Mikołajskie. On each station the material was collected from the shallow part of the littoral zone close to the shore, with depth of about 20 cm, and from its deeper part, about 1.5 m deep. The sites, where the stations were located, as well as the majority of the littoral, were overgrown with uniform belt of reeds (*Phragmites communis* Trin.).

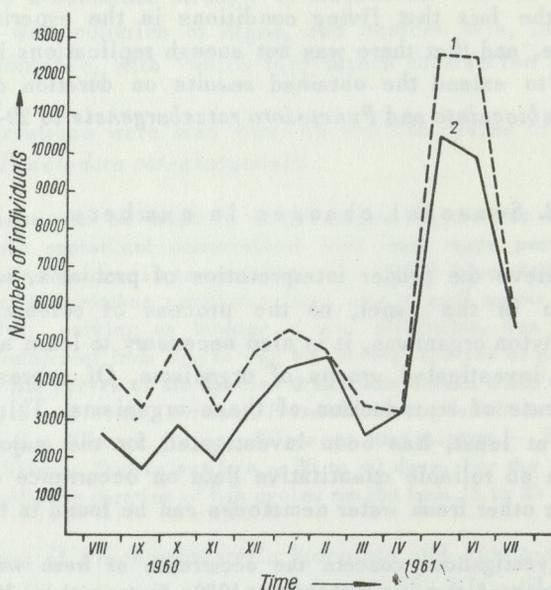


Fig. 3 — Seasonal changes in numbers of periphyton nematodes

1 — Number of individuals per 10 cm³ of periphyton; 2 — Number of individuals per 100 cm² of the substrate surface

Samples were taken once or several times a month from August 1960 to July 1961. In 1962 the additional material was collected mainly in order to check up the results (in February, May, June, and August). Each time, 6 or more samples were taken from young reeds (growing plants) and old ones (dead plants of the last year). The quantitative sampling technique has been described in Chapter II.

Similar numbers of nematodes were found on all the stations investigated. The courses of seasonal changes in numbers of nematodes were also alike in all the points of observation. Somewhat larger changes in numbers of periphyton nematodes were observed in shallow parts of the littoral zone

than those in deeper parts. The course of changes in numbers of periphyton nematodes is shown in Fig. 3. It has been plotted as a single curve³.

One clearly marked peak of numbers during the spring is characteristic for the trend of numbers of nematodes. There are no regular conspicuous differences in numbers during the rest of the year. Differences in numbers of nematodes between subsequent months of investigation are rather of casual origin. They are often of the same rank as differences among the samples of one series. Nevertheless, an increase in numbers of nematodes during the winter period (in periphyton covered with ice) is of a regular character. It occurs in all the samples (that year, the lake was covered with ice from January, 20 up to March, 5).

It is worthy to emphasize the fact, which is important from the methodological point of view, that the similar trends of numbers were obtained both, when numbers of nematodes were related to a unit of surface of the substrate, and in this case when they were related to a quantity of periphyton (Fig. 3). It may be a good evidence that both the methods of quantitative sampling of periphyton organisms are reliable and supply true information (in previous investigations — Pieczyńska 1959, 1961 — numbers of nematodes were related to a quantity of periphyton).

In 1961 the vernal increase in numbers of nematodes occurred at the beginning of May (Fig. 3). In 1962 a clear peak of numbers was also observed, but it was delayed until the second half of June. In 1962, at the beginning of May the density of nematodes was as high as 4,091 individuals per 100 cm² of the substrate surface, and in the second half of June it amounted to 9,785 individuals. During the summer season, the decrease in numbers of nematodes, similar to that in 1961, was observed. The numbers decreased down to the level preceding the peak period.

It was found that the vernal increase in numbers was closely related with duration of icing on the lake and with temperature of water. The delayed maximum of nematodes in 1962, as compared with that of 1961, coincided with later melting of ice on the lake, and lower than in 1961 the corresponding temperatures of water (Tab. I).

During the whole period of investigation the age structure of the dominant species *Prochromadorella bioculata* and *Punctodora ratzeburgensis*⁴ was analyzed. The obtained data showed clearly that the investigated species reproduced all the year round, since during the whole year all the develop-

³The diagram covers all the materials exclusive of the samples taken from those sections of reeds which were icebound, or just after the ice had melted, as well as the samples from young plants growing in the spring. These materials will be discussed in detail later on.

⁴It is impossible to discriminate the real age stages, i. e., the developmental phases between two subsequent moltings in the abundant material of nematodes. For the practical purpose individuals of the investigated species were classified

Mean temperatures of water ($^{\circ}\text{C}$) of the lake Mikołajskie
(The data obtained from the observatory
of the State Hydrometeorological Institute at Mikołajki)

Tab. I

Year	March	April	May	June	July
1961	3,3	6,3	11,8	19,5	19,0
1962	0,3	3,8	9,6	14,9	17,4

The striped areas indicate the periods of icing on the lake.

mental stages were encountered in the material. This is very important for interpretation of the colonization process of new substrates.

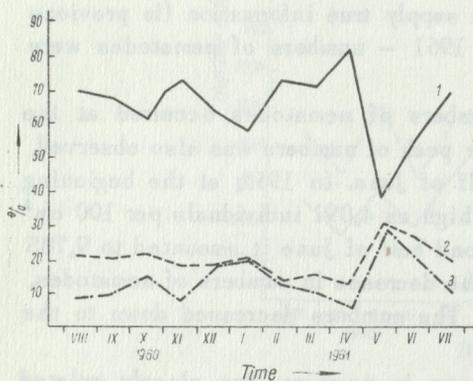
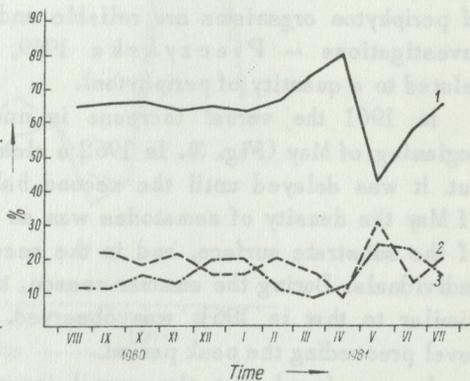
Punctodora ratzeburgensis*Prochromadorella bioculata*

Fig. 4 - Seasonal changes in the age structure of *Prochromadorella bioculata* and *Punctodora ratzeburgensis*

1 - adults, 2 - old larvae, 3 - young larvae

In the spring 1961 mass reproduction of nematodes took place, coinciding with the maximum in numbers. Incidence of young forms was much higher than that in other months of that year (Fig. 4). In 1962 larger percentage of the young forms was observed in the second half of June. It coincided with the delayed maximum of numbers.

into 3 age groups namely, young larvae, old larvae, and adults. The classification was made according to the differences in the anatomical features of the individuals (stage of development of gonads and the length ratio of the throat to the remaining part of the body). Although such a division is not very precise, it is sufficient to draw general conclusions about occurrence and incidence of the young and adult forms of nematodes.

Since the described increase in numbers of periphyton nematodes was observed in all the investigated places of the littoral zone during 2 subsequent years of study, it seems reasonable to consider this fact as a general rule of their occurrence.

IV. COLONIZATION OF NATURAL SUBSTRATES BY PERIPHYTON ORGANISMS IN THE LAKE LITTORAL

In the conditions of the investigated lakes mass colonization of natural substrates took place two times a year:

- 1) directly after melting of ice – colonization of the substrates on which periphyton had been destroyed by ice,
- 2) in the spring – colonization of shoots of higher water plants.

The material which has been discussed in the previous chapter, concerning the occurrence of periphyton nematodes in winter, consisted of periphyton collected from substrates submerged in water under the ice.

On the same stations of the lake Mikołajskie the material was also collected from substrates which were icebound. Thus, during the icing period samples of periphyton were taken both from the sections of reeds submerged in water under the ice and from those icebound.

In the winter 1960/1961 the lake has been covered with icing for 45 days. The maximal thickness of ice amounted to 16 cm. In the winter 1961/1962 the icing period has lasted for 122 days with the maximal thickness 49 cm (the data from the observatory of State Hydro-meteorological Institute at Mikołajki). Thus a considerable proportion of the substrates with periphyton was affected by ice.

The devastating effect of ice on periphyton organisms has been observed during the study.

Very few numbers of nematodes were observed in periphyton attached to the icebound sections of reeds, as compared with numbers of nematodes present in periphyton attached to lower parts of the same reeds (beneath the ice) (Tab. II). Small numbers of nematodes were also found in periphyton appearing on reeds near shore in the littoral part frozen down to the bottom.

On the basis of the investigations that were made, it can be suggested that one of the factors that account for a decrease in numbers of periphyton organisms attached to the substrates covered with ice, is their higher mortality in those conditions. Higher mortality rates of nematodes in such conditions were observed during two years of study. To define the mortality rate of nematodes the following observations were made. The icebound sections of reeds were brought to the laboratory and slowly defrosted at the temperature of about 1° C. Further observations of the periphyton were made under the microscope

The effect of ice cover on numbers of nematodes in periphyton of the lake Mikołajskie
(Numbers of individuals per 100 cm² of reed surface)

Tab. II

Substrates	1961					1962
	December	icing period		March	April	icing period
		January	February			February
Upper sections of reeds	3308	253	120	454	2601	102
Lower sections of reeds	3120	4306	4600	2576	3166	3653

Upper sections of reeds — the sections icebound during the icing period.

Lower sections of reeds — the sections of reeds below the ice cover.

after 6, 12, 24, and 48 hours from the defrostation time. Only about 30% of nematodes were alive. They moved (the movements were often induced by touching the nematodes with a needle). The remaining individuals were dead and shrunk, their tissues destroyed, which indicated that they had died much earlier, before the defrostation process began.

It can be also assumed that migration of nematodes towards the lower sections of the same plants was another factor that would account for the decrease in numbers of nematodes in periphyton covered with ice. This assumption can be supported by the fact described earlier in the paper, that the small but regular increase in numbers of periphyton organisms on these sections of reeds occurred in winter. Witkowski (1962), in his studies on the soil nematodes, has also observed translocation of nematodes into deeper layers of soil in winter.

However, it should be mentioned that migrations of nematodes towards lower sections of reeds could not account for the reduction of nematodes in the vast parts of littoral zone near shore, frozen down to the bottom.

Influence of icing on the plant components of periphyton was also analyzed in the study. Characteristic was made of the occurrence of dominant species of periphyton algae in deeper parts of the littoral at the investigated stations of the lake Mikołajskie. At both the stations similar changes in the dominance pattern of algae were observed, therefore the data were combined as presented in Tab. III. Icing had a considerable effect, similar to that described for periphyton nematodes, on the occurrence of periphyton algae. On the icebound sections of reeds, smaller numbers of species of algae, smaller total numbers of individuals, and somewhat altered dominance pattern, were observed. The devastating effect of icing on algae was expressed by the fact that a great deal of diatoms, which in normal conditions are attached to a substrate, occurred as the separate cells, detached from their pedicels.

After ice had melted, vast parts of the littoral zone were void of periphyton. In the lake Tałtowisko in 1960, and in the lake Mikołajskie in 1960 and 1961, two weeks after ice had melted, periphyton was hardly found on reeds growing near shore (these parts of the littoral had been frozen down to the bottom). In 1962 minimal amounts of periphyton were found in these parts of the littoral, 3 weeks after ice had melted. In deeper parts of the littoral only upper sections of reeds were void of periphyton directly following the ice melting. These parts of reeds were icebound during the winter. In 1961, for instance, in the lake Mikołajskie, 2 weeks after ice had melted, the amount of periphyton was $1.1 \text{ cm}^3/100 \text{ cm}^2$ of the surface on the upper sections of reeds, whereas on the lower sections of the same plants it amounted to $9.6 \text{ cm}^3/100 \text{ cm}^2$. Periphyton nematodes were a little more numerous there, than during the period of icing (Tab. II).

Of the algal material, the numbers of species and numbers of individuals were also smaller, the situation similar to that during the icing period (Tab. III).

The process of colonization of the upper sections of reeds located in the deeper parts of the littoral occurred more rapidly than the colonization of the analogous substrates near shore. It was due to the fact that well developed periphyton occurred in close proximity on the lower sections of the same plants.

Four to six weeks after the thaw the fully developed periphyton was found on all the sections of reeds on which it had been destroyed during the icing period. At that time the amounts of periphyton were similar on both the upper and lower sections of the plants the total amounts of periphyton on the upper sections of reeds were as high as $8.7 \text{ cm}^3/100 \text{ cm}^2$, whereas those on the lower sections amounted to $8.1 \text{ cm}^3/100 \text{ cm}^2$.

No quantitative differences were demonstrated in the character of colonization by periphyton nematodes of the upper and lower sections of plants (Tab. II). The composition of species of algae and of periphyton nematodes was also alike on these sections. It indicates that periphyton organisms settle down on the new substrates in the amounts and species composition similar to those in the nearest vicinity.

The discussed above facts, concerning the devastating effect of icing on periphyton organisms, argue, to a certain extent, with the literature data, according to which many of groups of water organisms hibernate in the ice. Ziernov (1949) has discussed the problem of survival of a number of species in ice, defining this group of species as "pagon".

The devastating effect of icing on periphyton organisms involves not only higher mortality rate of organisms, but also mechanical separation of the attached forms from the substrate during the freezing and melting processes.

In parts of the littoral zone near shore that freeze down to the bottom, the complete re-establishment of periphyton occurred in the spring. On the other

Occurrence of the dominant species
Periphyton at-

1960

August	September	October	November	December	January
<u>Epithemia argus</u>	<u>Epithemia argus</u>	<u>Epithemia argus</u>	<u>Epithemia argus</u>	<u>Epithemia argus</u>	icebound <u>Epithemia argus</u>
<i>Cymbella ventricosa</i>	<i>Tolypothrix</i> sp.	<i>Navicula</i> sp.		<i>Synedra ulna</i>	<i>Navicula</i> sp.
<i>Cymbella aspera</i>	<i>Melosira varians</i>	<i>Synedra ulna</i>		<i>Cymbella aspera</i>	
<i>Gomphonema</i> sp.	<i>Synedra ulna</i>	<i>Synedra acus</i>		<i>Navicula</i> sp.	
<i>Cymbella</i> sp.					
<i>Navicula</i> sp.					
++	++	+++	+++	++++	+
					reeds below
					<u>Navicula</u> sp.
					<i>Epithemia argus</i>
					<i>Cymbella aspera</i>
					<i>Cymbella ventricosa</i>
					+++

-

very low numbers

+

low numbers

++

average numbers

+++

high numbers

++++

very high numbers

and numbers of algae throughout the year
tached to reeds

Tab. III

1961					
February	March	April	May	June	July
reeds	upper sections of reeds*		old reeds		
<i>Epithemia argus</i>	<u>Gomphonema</u> sp.	<u>Fragilaria</u> sp.	<i>Cymbella ventricosa</i>	<i>Cymbella ventricosa</i>	<i>Epithemia argus</i>
<i>Navicula</i> sp.	<i>Navicula</i> sp.		<i>Rhopalodia gibba</i>	<i>Epithemia argus</i>	<i>Cymbella ventricosa</i>
<i>Gomphonema</i> sp.	<i>Synedra ulna</i>		<i>Navicula</i> sp.	<i>Navicula</i> sp.	<i>Gomphonema</i> sp.
	<i>Fragilaria</i> sp.		<i>Epithemia argus</i>		<i>Cymbella aspera</i>
+	-	++++	+++	++++	+++
ice cover	lower sections of reeds		young reeds		
<i>Cymbella aspera</i>	<u><i>Navicula</i> sp.</u>	<u><i>Navicula</i> sp.</u>	<i>Cymbella ventricosa</i>	<i>Cymbella ventricosa</i>	<i>Epithemia argus</i>
<i>Synedra acus</i>	<i>Cymbella aspera</i>	<i>Gomphonema</i> sp.	<i>Fragilaria</i> sp.	<i>Epithemia argus</i>	<i>Cymbella ventricosa</i>
<i>Cymbella ventricosa</i>	<i>Cymbella ventricosa</i>	<i>Epithemia argus</i>	<i>Epithemia argus</i>	<i>Cymbella aspera</i>	<i>Cymbella aspera</i>
<i>Gomphonema</i> sp.	<i>Gomphonema</i> sp.	<i>Cymbella ventricosa</i>			
<i>Navicula</i> sp.	<i>Epithemia argus</i>				
	<i>Fragilaria</i> sp.				
+++	+++	++	++	+	+++

* Upper sections of reeds: March — the sections of reeds that were icebound, April — the blooming area. The species of mass occurrence have been underlined.

hand, in deeper parts of the littoral only compensatory settling of periphyton took place on the upper sections of reeds. Thus, continuity of periphyton existed during the whole year round. This can account for higher differentiation in the occurrence of periphyton organisms in shallow parts of the littoral zone than in the deeper ones. Somewhat higher variation in numbers of nematodes in shallow parts of the littoral has been already mentioned. Similar regularity, or even more clearly expressed one, was characteristic for the dominance structure of groupings of nematodes.

Seasonal changes in the dominance structure of groupings of nematodes were also investigated on the described above stations of the lake Mikołajskie.

In the earlier paper (Pieczyńska 1961) it has been demonstrated that groupings of periphyton nematodes are characterized by great stability in time and the extensive scope of their occurrence. The similar groupings of nematodes (as to their species composition, dominance structure, and numbers) were encountered on the individual plants within an area of the littoral, about 50–100 m long. No directional changes were observed during the vegetation season. On the other hand, different groupings of nematodes were observed in different places of the littoral zone of a lake.

Two species *Prochromadorella bioculata* and *Punctodora ratzeburgensis* were clearly predominant on the stations of the lake Mikołajskie. The conspicuous seasonal differences were observed in the dominance structure of groupings of periphyton nematodes between the shallow and deeper parts of the littoral (Fig. 5). The dominance patterns were rather constant in the deeper parts of the littoral during the whole year. In the shallow parts of the littoral, on the contrary, the patterns varied considerably, they changed rapidly, especially in the winter and spring. During the vegetation season some degree of stabilization of dominance was observed in this environment. At that time the patterns resembled those of deeper parts in a given section of the littoral zone.

It seems probable that the considerable changes in occurrence of nematodes in the shallow parts of the littoral, as compared with those in the deeper ones, correspond with greater astatic character of these parts involving rapid changes in physical conditions as well as greater differentiation of the environment. Astatic character of the shallow parts is also connected with fluctuation of the water level. Considerable fluctuations of the water level were observed in the environments investigated (exemplifying data are given in Tab. IV). These fluctuations brought about temporary shifting of the shore line, which involved either drying off the vast area of the littoral and destruction of the periphyton in it, or flooding with water new areas, and periphyton development.

A significant differentiation in occurrence of periphyton in the shallow parts of the littoral in connection with the astatic conditions of this environment has been also mentioned by Ruttner (1953).

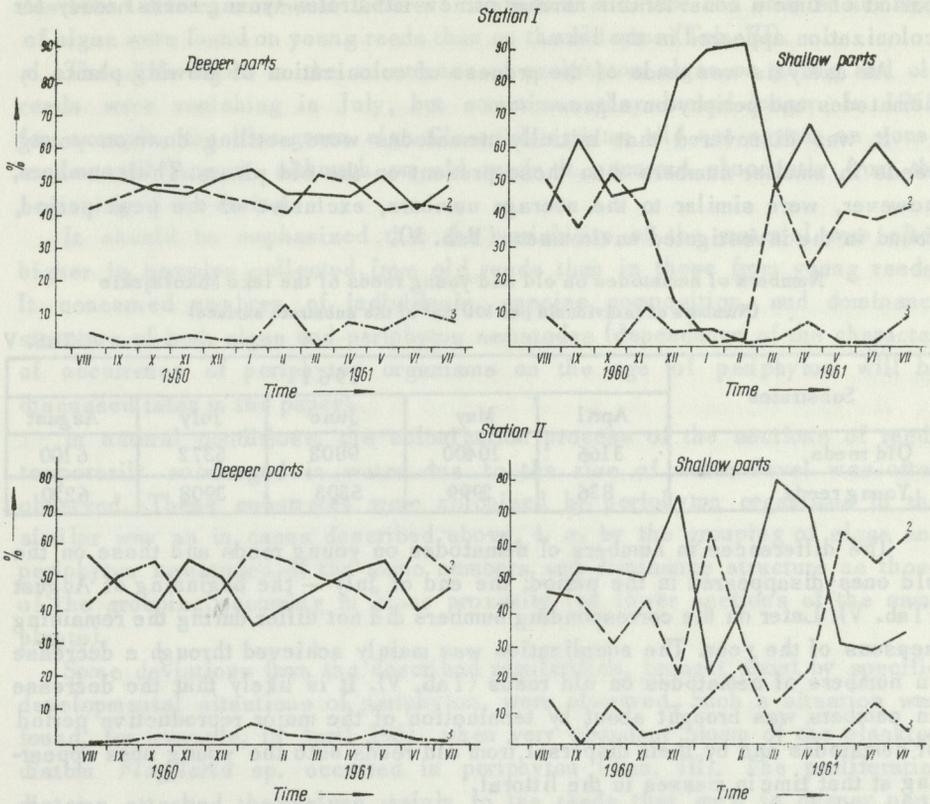


Fig. 5 - Seasonal changes in the dominance structure of groupings of periphyton nematodes

1 - *Prochromadorella bioculata*, 2 - *Punctodora ratzerburgensis*, 3 - other *Nematoda*

Oscillations in water level (cm) of the Lake Mikołajskie - in 1961
(The data obtained from the observatory of SHMI at Mikołajki)

Tab. IV

	Months									
	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Month average	58	66	62	58	50	48	44	35	27	34
Extreme limits	56-60	61-68	61-63	55-61	47-55	46-50	40-47	29-40	25-30	30-36

As it was stated at the beginning of this chapter, the period of growth of young plants in the spring is another period of mass colonization of natural substrates by periphyton organisms. In the lake examined, the littoral was

overgrown with a uniform belt of reeds, already mentioned, thus in a short period of time a considerable number of new substrates (young reeds) ready for colonization appeared in the lake.

An analysis was made of the process of colonization of growing plants by nematodes and periphyton algae.

It was discovered that initially nematodes were settling down on young reeds in smaller numbers than those present on the old plants. Their numbers, however, were similar to the average numbers, exclusive of the peak period, found in the investigated environment (Tab. V).

Numbers of nematodes on old and young reeds of the lake Mikołajskie
(Numbers of individuals per 100 cm² of the substrate surface)

Tab. V

Substrates	1961				
	April	May	June	July	August
Old reeds	3166	10400	9803	5372	6100
Young reeds	836	2999	5303	3908	6220

The differences in numbers of nematodes on young reeds and those on the old ones disappeared in the period: the end of July – the beginning of August (Tab. V). Later on the corresponding numbers did not differ during the remaining seasons of the year. The equalization was mainly achieved through a decrease in numbers of nematodes on old reeds (Tab. V). It is likely that the decrease in numbers was brought about by termination of the major reproductive period of nematodes and by their dispersal from old reeds onto the young ones appearing at that time in masses in the littoral.

In the spring of 1962, similarly to that in 1961, a considerable disproportion between numbers of nematodes was observed on old reeds and on the young ones (old reeds – 9,785 individuals/100 cm², young reeds – 3,900/100 cm²).

The grouping of nematodes appearing on young reeds showed almost an identical species composition and dominance structure as the grouping on old reeds. Nevertheless, in many of instances, the species of *Prochromadorella bioculata* was found in larger percentage on young reeds than on the old ones during the initial period of colonization. The dominance relations were equalized after the period of 10 days.

It was also observed that in the initial period of colonization somewhat larger percentage of the adult forms appeared on young reeds than on the old ones. On this basis, one can suggest that in the colonization process the adult forms are of a greater importance than the young forms.

In the spring of 1962, observations were also made on the process of colonization of newly-growing plants by periphyton algae.

The situation observed was similar to that of nematodes. Young reeds appearing in the spring were colonized by the species of algae that were present on old reeds in vicinity.

During the initial period of colonization, analogically to the situation described above, somewhat different dominance structure and smaller numbers of algae were found on young reeds than on the old ones (Tab. III).

The differences in the occurrence of periphyton algae on young and old reeds were vanishing in July, but sometimes they lasted longer. In 1962, for example, the blue-green alga *Gleotrichia pisum* did not appear on young reeds until August, although on old reeds it occurred abundantly from the beginning of the spring.

It should be emphasized that the variability of the material was often higher in samples collected from old reeds than in those from young reeds. It concerned numbers of individuals, species composition, and dominance structure of both algae and periphyton nematodes (dependance of the character of occurrence of periphyton organisms on the age of periphyton will be discussed later in the paper).

In natural conditions, the colonization process of the sections of reeds temporarily submerged in water due to the rise of water level was often observed. These substrates were colonized by periphyton organisms in the similar way as in cases described above, i. e. by the grouping of algae and periphyton nematodes of the same numbers and dominance structure as those of the grouping occurring in close proximity (on lower sections of the same plants).

Some deviations from the described regularities, brought about by specific developmental situations of periphyton, were observed. Such a situation was found, for example, in April 1961, when very abundant bloom of the plankton diatom *Flagilaria* sp. occurred in periphyton (Tab. III). The proliferating diatoms attached themselves mainly to the reeds that grew in deeper parts of the littoral in the strictly defined belt, 3–20 cm deep. The bloom had an extensive scope. It has been observed in a number of places in the littoral of the lakes Mikołajskie and Śniardwy. The blooming brought about a conspicuous reduction in numbers of both the nematodes and the remaining species of periphyton algae (e. g., the numbers of nematodes on the reeds with bloom amounted, on average, to 616 individuals per 100 cm², and on the same reeds, on sections where was no bloom, it amounted to 3,166 individuals per 100 cm²). The described differences disappeared during one month following the occurrence of the bloom.

V. EXPERIMENTAL STUDIES ON COLONIZATION OF NEW SUBSTRATES BY PERIPHYTON ORGANISMS

1. The course of the colonization process (the role of the compensatory settling and of reproduction of initially settled forms)

Theoretically, two ways of increment of numbers of periphyton organisms on a substrate undergoing the colonization process are conceivable.

These are: 1) reproduction of the initially settled forms, and 2) further compensatory settling.

A question arises what is the role of these ways in the colonization process of new substrates by various groups of periphyton organisms.

The knowledge of the biology of periphyton organisms itself allows to predict some differences in the course of the process for various species. It is conceivable that the fast reproducing forms, for instance, those from among algae, protozoans, or rotifers, get hold of a substrate through the intense reproduction of the individuals initially (even accidentally) attached to this substrate. On the other hand, there are some groups of organisms (nematodes also among them), rates of reproduction of which do not account for their increase in such situations when a considerable increase is observed.

The data concerning the rate of increase in numbers of nematodes (Tab. VI) show clearly that the numbers of nematodes increase very rapidly, starting from the first days following the submerging of the substrate.

Numbers of nematodes on glass slides after various periods of submergence
(Numbers of individuals per 100 cm² of substrate surface)

Tab. VI

Submergence period (days)	Numbers of nematodes		Numbers of replications
	average	extreme limits	
5	90	25-401	8
10	730	161-1112	8
15	1300	201-2101	10
20	2401	309-3655	10
30	3100	333-4968	28

The table comprises the materials from the lake Mikołajskie gathered during vegetation seasons 1960, 1961, 1962.

Analyzing the changes in the age structure of nematodes settling down on new substrates, it can be suggested that an increase in numbers of nematodes on these substrates does not result from reproduction of the initially settled forms. No increase in numbers of larvae was observed following the initial period of colonization (Fig. 6). The occurrence of such an increase would have been indispensable, if reproduction had been a major factor responsible for the increase in numbers of periphyton nematodes.

The data discussed above on biology of the dominants: *Prochromadorella bioculata* and *Punctodora ratzeburgensis*, even with the highest rate of reproduction assumed, indicate that reproduction of the initially settled forms cannot account for such a rapid increase in their numbers. From this,

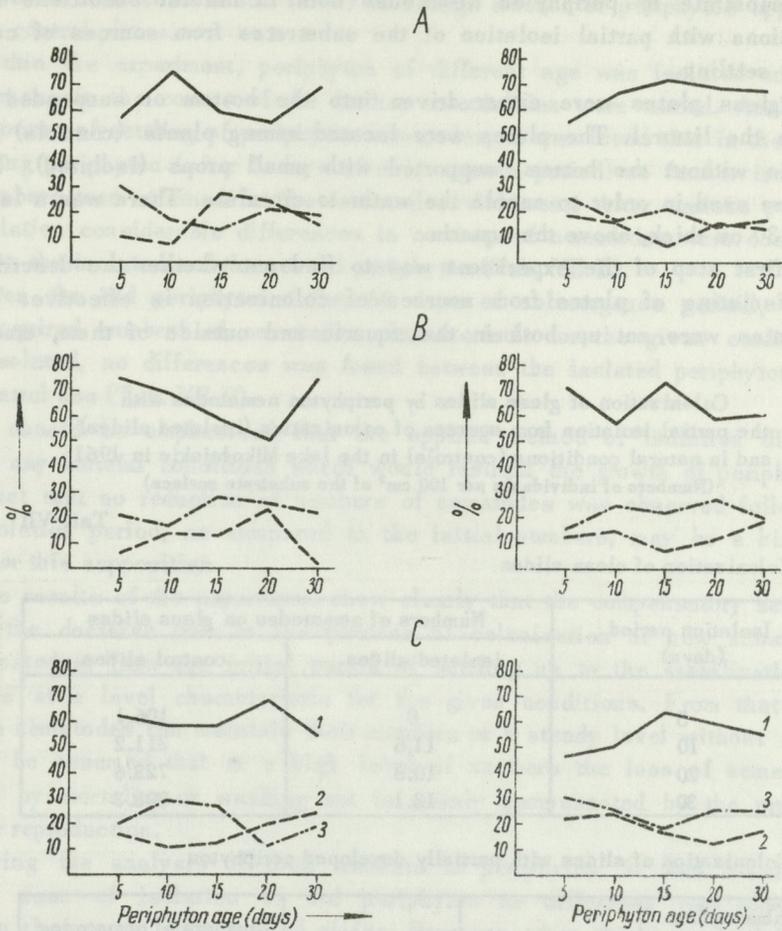


Fig. 6 -- Age structure of *Prochromadorella bioculata* and *Punctodora ratzeburgensis* at various stages of colonization process

1 -- adults, 2 -- old larvae, 3 -- young larvae. A -- Tałtowisko Lake -- June, July 1960; B-- Mikołajskie Lake -- August, September 1960; C -- Mikołajskie Lake -- August, September 1961

one can infer that for nematodes compensatory settling should play a decisive role in the increase of their numbers on new substrates, from the initial stages of colonization up to the moment when the numbers characteristic for given conditions are achieved.

A field experiment has been carried out in order to verify the put forward

hypothesis on the decisive role of compensatory settling in an increment of numbers of nematodes. The experiment involved observations on colonization of new substrate by periphyton nematodes both in natural conditions and in conditions with partial isolation of the substrates from sources of compensatory settling.

The glass plates were either driven into the bottom or suspended on stands in the littoral. The plates were located among plants (controls) and in aquaria without the bottom, supported with small props (isolated). The props were used in order to enable the water to circulate. There was a layer of water, 30 cm thick, above the aquaria.

The first step of the experiment was to find out whether the described way of isolating of plates from sources of colonization is effective. The clean plates were set up both in the aquaria and outside of them, among

Colonization of glass slides by periphyton nematodes with
the partial isolation from sources of colonization (isolated slides)
and in natural conditions (controls) in the lake Mikołajskie in 1961
(Numbers of individuals per 100 cm² of the substrate surface)

Tab. VII

A. Colonization of clean slides

Isolation period (days)	Numbers of nematodes on glass slides	
	isolated slides	control slides
5	0	106.1
10	11.6	311.2
20	10.8	723.6
30	13.1	803.3

B. Colonization of slides with partially developed periphyton

Submergence period prior to the beginning of the experiment (days)	Initial numbers of nematodes	Isolation period (days)	Numbers of nematodes following the isolation period	
			isolated slides	control slides
5	106	10	112	739
	106	20	138	889
60	635	10	697	620
	790	20	820	950

plants, as controls. Several observations were made from which it can be inferred that the applied method exactly supplied such isolation. The plates

set in aquaria were hardly inhabited. Only few individuals of nematodes and single cells of algae were found on them. At the same time considerable numbers of nematodes (Tab. VII A) and large amount of periphyton appeared on the control plates.

Within the experiment, periphyton of different age was isolated and the differences in the course of the further colonization were traced. Analyzing the process of settling of periphyton nematodes, it was found that in the case of young periphyton (after 5 days of submergence period) no further increase in numbers was attained in the isolated environment. After various periods of isolation considerable differences in numbers of nematodes were observed between the isolated and the control periphyton (Tab. VII B).

When the old periphyton (after 60 days of submergence period), which had acquired numbers of nematodes characteristic for the given conditions, was isolated, no differences was found between the isolated periphyton and the control one (Tab. VII B).

It should be emphasized that the applied method of isolation did not create any harmful conditions which would restrain the growth of periphyton. The fact that no reduction of numbers of nematodes was observed following the isolation period, as compared to the initial numbers, may be a kind of proof for this supposition.

The results of the experiment show clearly that the compensatory settling plays the decisive role in the process of colonization of new substrates by nematodes, from the initial period of settling up to the stabilization of numbers at a level characteristic for the given conditions. From that time on, the nematodes can maintain their numbers at a steady level without thus, it can be assumed that at a high level of numbers the loss of nematodes caused by mortality or washing out is mainly compensated by the process of their reproduction.

During the analysis of total amounts of periphyton, it was found that in the case of isolation of old periphyton no difference was observed between the control and isolated slides. However, when the young periphyton was isolated, the smaller amounts of periphyton were usually found on the isolated substrates, which resembles the situation described for nematodes. But in some cases (during other times of the vegetation period) the amounts of periphyton on the isolated and the control slides were similar, or even higher on the isolated slides. One can suppose that at this time the gross of periphyton consisted of species with high vegetative reproduction, which developed from the initially settled forms.

The facts reported in the present paper on decisive role of compensatory settling in the colonization process of new substrates by some periphyton organisms find their confirmation in the literature data. These data indicate that although periphyton nematodes have been observed in masses on experimental

substrates submerged in the littoral very few individuals were found on experimental substrates submerged in the pelagial zone, a long way off from the sources of colonization (Duplakov 1933, Sladeczkova 1960). It should be stressed that the nematodes that had been transferred with periphyton to the pelagial zone survived there for a long period of time (Pieczyńska, unpublished data).

Duplakov (1933) has reported that in the pelagial zone the species with vegetative reproduction are the most often found, that is, the species which can easily occupy a substrate starting with the small initial number of settled individuals.

2. Factors controlling the process of colonization of new substrates

A. The role of periphyton as the source of colonization

Analysing the colonization process of new substrates by periphyton organisms, it was found that numbers, species composition and dominance structure of the organisms which settled down on the new substrates were very similar to, or even identical with those in the surrounding environment.

Using a method of field experimentation, further analysis was made of the dependence between the course of colonization process and conditions in surrounding environment, the latter being the source of colonization.

Observations were made of the process of colonization by chosen groups of organisms of the experimental substrates introduced into the reservoir. The data obtained were compared with changes in numbers of these groups occurring in periphyton attached to the natural substrates in the littoral environment examined. The study was carried out on the lake Mikołajskie in the littoral overgrown with the uniform belt of reeds. The glass slides, mounted in stands, were used as the experimental substrates. The slides were submerged to the depth of about 30 cm. Around the stands, some reeds were cut off in order to achieve equal distances between the stands and the adjacent plants (about 40 cm). The slides were set once a month, from May to October, 1961.

Each month, samples of periphyton were collected from the slides that had been set up in earlier months. Simultaneously, the samples were also collected from the reeds that grew in vicinity of the slides. Each time, a series of 6 samples was taken both from the reeds and the slides. It should be added that in the area of experimentation there was no periphyton on the bottom; thus, the only source of colonization possible was the periphyton attached to reeds.

Analysis was made of total amount of periphyton, of numbers of *Oligochaeta* and *Tendipedidae* as well as of numbers and dominance structure of *Nematoda*. General characteristic of species composition of algae was also determined.

It was found that the numbers of periphyton organisms of the groups investigated setting down on the experimental substrates varied with time, with their maxima and minima attained at different periods of the vegetation season (Fig. 7).

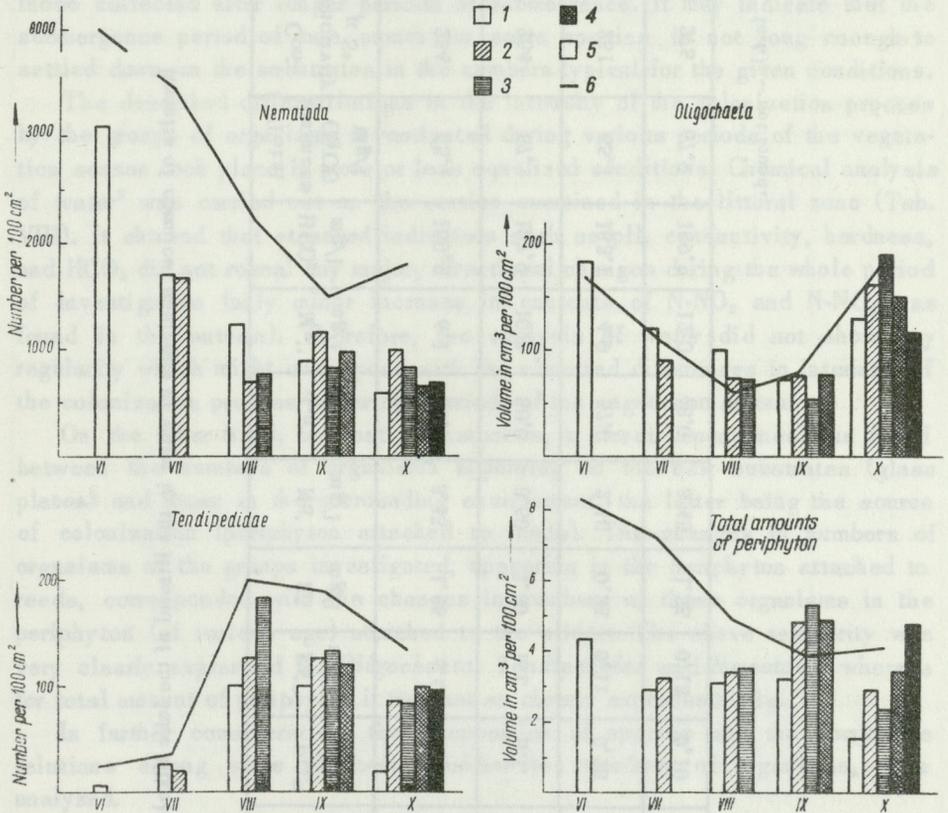


Fig. 7 — Dependence of numbers of periphyton organisms attached to glass slides from duration of submergence period of vegetation season and numbers of periphyton organisms in surrounding environments
 1 — periphyton after 1 month of submergence period, 2 — periphyton after 2 months of submergence period, 3 — periphyton after 3 months of submergence period, 4 — periphyton after 4 months of submergence period, 5 — periphyton after 5 months of submergence period, 6 — periphyton on reeds

Observations were made on the occurrence of periphyton organisms in the periphyton of various age (various submergence period — the time during which the slides were submerged in water).

No regular dependence was found between the numbers of organisms in periphyton and the age of periphyton (the initial period of colonization was not taken into consideration, the analysis concerned periphyton of the submergence

Results of chemical analyses of water in the littoral of the lake Mikołajskie

Tab. VIII

Date of sampling (1961)	pH	Dry weight mg/l	Conductivity μS^*	Total hardness CaCO ₃ mg/l	HCO ₃ mg/l	Mg ⁺⁺ mg/l	Ca ⁺⁺ mg/l	Na ⁺ mg/l	K ⁺ mg/l	Fe ⁺⁺⁺ mg/l	PO ₄ ^{'''} mg/l	Cl ['] mg/l	N-NH ₃ mg/l	N-NO ₂ mg/l	N-NO ₃ mg/l	N organic mg/l
13. VI	8.65	182	254	65.1	189.2	6.1	55.0	3.45	1.35	n.f.	0.11	9.8	0.02	0.001	0.04	1.32
17. VII	8.20	90	254	67.1	187.9	10.5	50.0	3.60	1.30	n.f.	n.f.	9.9	0.10	n.f.	0.01	1.16
11. IX	7.85	130	251	65.1	183.1	4.9	57.0	2.10	0.35	0.11	0.28	10.2	0.04	n.f.	0.03	2.00
23. X	8.00	118	275	67.9	189.2	12.0	48.0	3.45	1.35	0.13	0.10	9.9	0.04	0.004	0.06	2.06

* At the temperature 20°C (n.f.). — not found.

period of 1–5 months). The highest and the lowest numbers of the organisms examined were noted during various periods of the vegetation season, both in periphyton of one month of submergence period and in that of several months of submergence period. However, the total amounts of periphyton differed with the periphyton age. The quantities of periphyton collected at the time following 1 month of the submergence period, as a rule, were smaller than those collected after longer periods of submergence. It may indicate that the submergence period of one month for some species is not long enough to settled down on the substrates in the numbers typical for the given conditions.

The described differentiations in the intensity of the colonization process by the groups of organisms investigated during various periods of the vegetation season took place in more or less equalized conditions. Chemical analysis of water⁵ was carried out on the station examined in the littoral zone (Tab. VIII). It showed that standard indicators such as pH, conductivity, hardness, and HCO₃ did not reveal any major, directional changes during the whole period of investigation (only minor increase in contents of N-NO₂ and N-NO₃ was found in the autumn). Therefore, the analysis of water did not show any regularity which might correspond with the observed differences in intensity of the colonization process in various periods of the vegetation season.

On the other hand, in most of instances, a direct dependence was found between the numbers of organisms appearing on the new substrates (glass plates) and those in the surrounding environment, the latter being the source of colonization (periphyton attached to reeds). The changes in numbers of organisms of the groups investigated, appearing in the periphyton attached to reeds, corresponded with the changes in numbers of these organisms in the periphyton (of various age) attached to the slides. The above regularity was very clearly expressed for *Oligochaeta*, *Tendipedidae* and *Nematoda*, whereas for total amount of periphyton it was not so clearly expressed (Fig. 7).

In further consideration, the composition of species and the dominance relations among some of them, besides the numbers of organisms, were analyzed.

Similarly to the situation described for numbers of organisms of the groups examined, the structure of dominance of periphyton algae on the experimental substrates usually resembled that in the surrounding environment at a given period of time (Tab. IX). In periphyton of various age, attached to the slides, the same species predominated as in the periphyton attached to reeds in vicinity. It was found that the period of one month of submergence was insufficient to complete settling by certain species, which resembles the situation described for total amounts of periphyton. *Epithemia argus*, for instance, during its mass occurrence formed the bloom in shape of a crust covering

⁵ The chemical analysis of water was made by Hydrobiological Station Polish Academy of Sciences, at Mikołajki.

Occurrence of dominant species of algae on reeds and glass slides in various periods of vegetation season, Lake Mikołajskie, 1961

Tab. IX

Time of sampling	Periphyton attached to reeds	Periphyton attached to glass slides				
		Time when slides were set up				
		May	June	July	August	September
June	<i>Cymbella ventricosa</i> <i>Epithemia argus</i>	<i>Cymbella ventricosa</i> <i>Epithemia argus</i> <i>Lyngbya limnetica</i>	—	—	—	—
July	<i>Epithemia argus</i> <i>Cymbella aspera</i>	<u><i>Epithemia argus</i></u> <i>Cymbella</i> sp. <i>Cymbella aspera</i>	<u><i>Epithemia argus</i></u> <i>Cymbella</i> sp. <i>Cymbella aspera</i>	—	—	—
August	<u><i>Epithemia argus</i></u> <i>Lyngbya limnetica</i>	<u><i>Epithemia argus</i></u> <i>Cymbella</i> sp. <i>Cymbella aspera</i> <i>Lyngbya limnetica</i>	<u><i>Epithemia argus</i></u> <i>Cymbella</i> sp. <i>Lyngbya limnetica</i> <i>Navicula</i> sp.	<i>Epithemia argus</i> <i>Lyngbya limnetica</i> <i>Cymbella aspera</i> <i>Cymbella</i> sp. <i>Navicula</i> sp.	—	—
September	<u><i>Epithemia argus</i></u> <i>Lyngbya limnetica</i> <i>Navicula</i> sp.	<u><i>Epithemia argus</i></u> <i>Lyngbya limnetica</i> <i>Navicula</i> sp. <i>Cymbella aspera</i>	<u><i>Epithemia argus</i></u> <i>Lyngbya limnetica</i> <i>Navicula</i> sp.	<u><i>Epithemia argus</i></u> <i>Lyngbya limnetica</i> <i>Rhopalodia gibba</i> <i>Navicula</i> sp.	<i>Lyngbya limnetica</i> <i>Epithemia argus</i> <i>Rhopalodia gibba</i> <i>Navicula</i> sp.	—
October	<u><i>Epithemia argus</i></u> <u><i>Navicula</i></u> sp.	<u><i>Epithemia argus</i></u> <u><i>Navicula</i></u> sp.	<u><i>Epithemia argus</i></u> <u><i>Navicula</i></u> sp.	<u><i>Epithemia argus</i></u> <u><i>Navicula</i></u> sp. <i>Lyngbya limnetica</i>	<i>Epithemia argus</i> <i>Navicula</i> sp.	<i>Navicula</i> sp. <i>Epithemia argus</i> <i>Diatoma vulgare</i>

The species of mass occurrence have been underlined.

thoroughly the glass slides. Although during its dominance period on reeds it prevailed also on all the slides, its numbers found in periphyton of one month of submergence period were much lower than those in older periphyton (it has not developed the crust yet). In the periphyton of the submergence period of one month the preponderance of a dominant is not so clearly expressed as in older periphyton. This last observation corresponds with the Duplakov (1933) and Wysocka's (1952) data; according to them, the initial period of colonization involves the accumulation of species; and the clear dominance is characteristic for later periods of periphyton development. Further, it was found that in periphyton of the submergence period of one month, the species which had just appeared in the environment was the dominant as, for example, *Lyngbya linmetica* in August and September, and *Navicula* sp. in October. It seems probable that a species which is new to a substrate, i.e., has just appeared on it, has a better chance to develop on a free substrate than on substrate which has been occupied by periphyton.

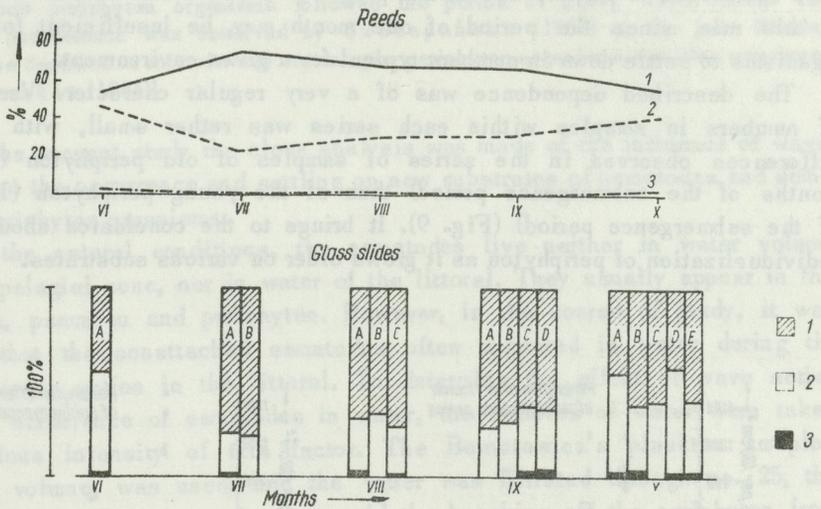


Fig. 8 – Dominance structure in groupings of periphyton nematodes on reeds and on glass slides in various periods of vegetation season

1 – *Prochromadorella bioculata*, 2 – *Punctodora ratzeburgensis*, 3 – Other *Nematoda*. A – after 1 month of submergence period E – after 5 months of submergence period

The clear dominance of *Prochromadorella bioculata* and *Punctodora ratzeburgensis* was characteristic for the groupings of periphyton nematodes. During the whole period of investigation, only minor changes in dominance patterns of nematodes appearing on reeds were observed, but even these changes had some bearing on the dominance structure of nematodes settling down in periphyton of new substrates. However, no regular difference was

observed between the periphyton of the submergence period of one month and the older periphyton (Fig. 8).

Newcombe (1950), Sladeczkova (1960) and Castenholtz (1961) have mentioned the different intensity of the settling process of periphyton organisms during various seasons of the year, but since no observation was made on periphyton in surrounding environments, there was no material for comparison of the data. Among them, only Castenholtz (1961) wrote that the species composition of algae in the periphyton attached to various substrates was identical with that of periphyton of surrounding environments.

In general, it can be stated that periphyton organisms settling down on the new substrates varied with time as to their numbers, species composition and dominance structure. In most of instances, these changes corresponded with relations found in the periphyton of surrounding environment, which was the source of colonization.

It was found that the character of occurrence of periphyton organisms did not depend on the age of periphyton (the time during which the substrates were submerged in water). The initial period of colonization is the exception to this rule, since the period of one month may be insufficient for some organisms to settle down in numbers typical for a given environment.

The described dependence was of a very regular character. Variability of numbers in samples within each series was rather small, with greater differences observed in the series of samples of old periphyton (several months of the submergence period) than of the young periphyton (1 month of the submergence period) (Fig. 9). It brings to the conclusion about some individualization of periphyton as it grows older on various substrates.

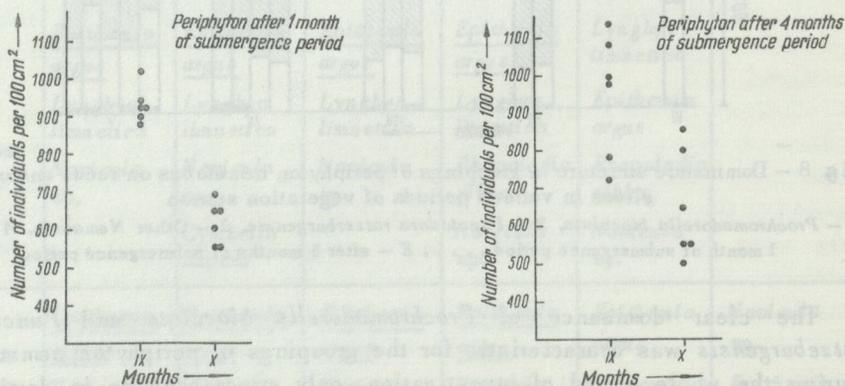


Fig. 9 — Differentiation in numbers of nematodes in series of samples taken from old and young periphyton attached to glass slides

B. The role of wave action

Only fragmentary information on the influence of wave action on the occurrence of periphyton organisms can be found in the literature. In majority of cases it consists of opinions unsupported by the material studies.

Micoletzky (1925) and Hyman (1951) have emphasized the fact that wave action is of a great importance for periphyton organisms, since it is responsible for airing of water. And as it has been mentioned earlier, the high oxygen requirements are characteristic for the dominant species of nematodes belonging to the *Chromadoridae* family.

Ruttner (1953) and Kann (1959) have reported that the intensity of wave action was one of main factors influencing the differentiation of occurrence of periphyton organisms.

Young (1945) and Welch (1952) have pointed out that smaller amounts of periphyton appeared in these zones of the reservoir that were subdued to a strong wave action.

Young (1945) has observed the destructive effect of wave action on periphyton organisms in Michigan lake. He has found that a considerable reduction in numbers of various periphyton organisms followed the period of heavy wave action. The similar phenomenon was observed by Szczepańska (1958) on the lake Mikołajskie. The destructive role of wave action upon periphyton organisms was also mentioned by Meschkat (1934).

In the present study the close analysis was made of the influence of wave action on the occurrence and settling on new substrates of nematodes and some other periphyton organisms.

In the natural conditions, the nematodes live neither in water volume of the pelagial zone, nor in water of the littoral. They usually appear in the benthos, psammon and periphyton. However, in the course of study, it was found that the nonattached nematodes often appeared in water during the heavy wave action in the littoral. To determine the effect of wave action on the occurrence of nematodes in water, the samples of water were taken at various intensity of this factor. The Bematowicz's plankton sampler, 5 l of volume, was used, and the water was filtrated through no. 25, the bolting cloth. Care was taken to avoid the knocking off the periphyton from plants during the sampling. Samples with some parts of substrates covered with periphyton, which got into them casually, were discarded and excluded from the analysis. Each time, the whole sample was searched for nematodes.

The materials were collected from the lake Mikołajskie and, less extensively, from the lakes Śniardwy and Tałtowisko. The intensity of wave action was defined on the lake Mikołajskie. The data come from Hydrobiological Station, Polish Academy of Sciences. For wave action measurements the Szczepański's recorder was used (Szczepański in litt.).

The positive correlation was found between numbers of nematodes present in water and the intensity of wave action (Tab. X, Fig. 10).

Dependence between intensity of wave action and numbers of nematodes in free water

Tab. X

	No wave action	Weak wave action	Heavy wave action
Quantity of water filtrated (l)	320	150	250
Numbers of nematodes per 100 l of water	0.4	6.6	210.3

The materials were collected at various time from the lakes Mikołajskie, Śniardwy and Tałtowisko.

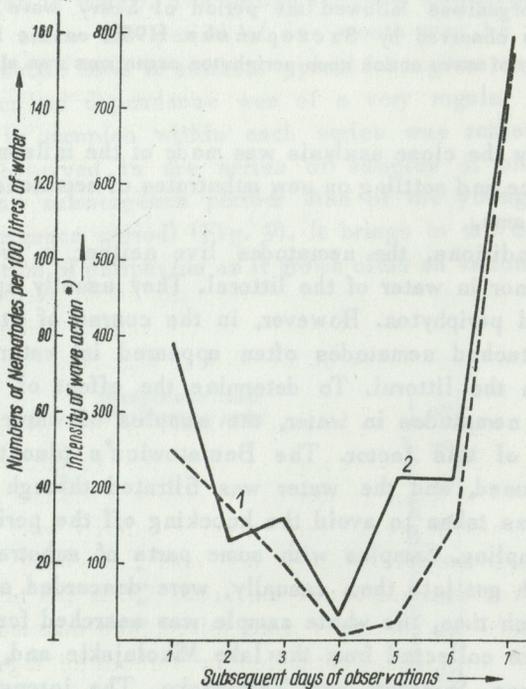


Fig. 10 - Dependence of numbers of nematodes present in the water volume from the intensity of wave action

1 - Numbers of nematodes, 2 - wave action

* In conventional units (from Szczepanski's data, in litt.).

The analysis of the species composition of nematodes found in water showed a clear preponderance of the species dominating in periphyton: *Prochromadorella bioculata* and *Punctodora ratzeburgensis*. In the samples of water these species formed 67% of the total number of nematodes, whereas at the same time in periphyton the percentage was as high as 89%. In the samples of water the typically bottom species such as *Dorylaimus helveticus*, *Monhystera dispar*, *Monhystera paludicola*, *Monhystera vulgaris*, and *Tobrilus gracilis* were also encountered in relatively high percentage (about 20%). These species were considerably less abundant in periphyton (6%). This may indicate that the species living in periphyton and those inhabiting the bottom, though in smaller numbers, get into water due to the wave action. Thus, the washing out of nematodes from the bottom can be considered as the way through which the bottom species get into periphyton, where, indeed, they always occur, although in minimal numbers. That such an interpretation is true, one can infer from the fact that no difference was observed in the incidence of the bottom nematodes appearing in periphyton separated from the bottom (attached to the plates suspended on floats) and in that connected with the bottom (attached to plants and the plates driven into the bottom).

The dependence between the intensity of washing out of periphyton organisms due to wave action and the age of periphyton was also analyzed.

An experiment concerning this problem was carried out in the laboratory. The plates covered with periphyton were placed into an apparatus (Szczeński, unpublished data), where waves were induced artificially. Prior to this, the periphyton was removed from one side of each plate in order to obtain the control sample. The periphyton of various age was exposed to wave action of the known intensity for a certain, always the same, period of time. To get more conspicuous results, unshielded with the natural differentiation of numbers of organisms on both sides of the slides, very heavy wave movements were induced.

The results of this experiment cannot be related directly to the natural conditions. Their interpretation can comprise only the comparison of the degrees of washing out of various groups of organisms from the periphyton of various age. As to this respect, very clear regularity was observed. Various periphyton organisms were washed out from the young periphyton to a greater extent than from the old periphyton (Tab. XI). It can be supposed that periphyton, as it develops, becomes more felted, and this may explain why the washing out of organisms entangled in threads of algae, organic particles, etc., becomes more difficult.

As for algae, it was found that their planktonic forms are more susceptible to wave action than the typically sedentary ones. For example, *Lyngbya limnetica* – the planktonic species – was washed out in 48% from the periphyton of 60 days of submergence period, whereas *Epithemia argus* – the sedentary

Percentage of chosen groups of periphyton organisms washed from periphyton attached to glass slides, due to wave action

Tab. XI

Submergence period (days)	Total periphyton	<i>Nematoda</i>	<i>Oligochaeta</i>	<i>Tendipedidae</i>
18	29.2	90.8	82.8	100.0
30	26.5	88.8	79.4	97.2
60	8.4	62.4	73.7	85.0
90	8.4	63.7	75.0	40.0
120	8.2	47.1	57.8	63.2

form – only in 9%. In the described experiment, only small numbers of algae were generally washed out, probably due to the fact that the algal flora mainly consisted of *Epithemia argus*, the species mentioned above, which formed the compact crust adhesive to the surface of substrates.

Higher degree of washing out of algae was observed in the experiment carried out in the spring, when there was no blooming of the adhesive to the substrate diatoms in periphyton.

In other variants of the experiment, when the periphyton exposed to wave action consisted mostly of *Cladophora* sp. overgrown with diatoms, considerably lower numbers of animals were washed out from it. *Cladophora* sp. formed a better hiding than the flat crust of *Epithemia argus* for these organisms. Conspicuous differences were found in the degree of washing out of organisms from periphyton of different age. For example, from the young periphyton (10 days of submergence period) 36% of the total number of nematodes were washed out, and from older periphyton (60 days of submergence period) – 12%.

Wave action, causing removal of nematodes from periphyton, can be considered as a factor which renders for these, usually attached to a substrate, organisms a possibility of dispersal and, through this, colonization of new substrates.

However, a question arises to what an extent the nematodes are being washed out in the natural conditions at an average intensity of wave action. Whether wave action should be considered as a destructive factor for periphyton biocenose, besides its positive role, depends on the answer to this question.

To explain this problem, special observations were made in the littoral zone, 1 m deep, covered with the uniform belt of reeds. On the basis of large

series of samples, numbers of nematodes were estimated for all reeds in 1 m^3 of water volume. Then, the samples of water were taken at this spot of the littoral, and numbers of nematodes per 1 m^3 of water estimated. The samples from reeds were collected when the water was still, whereas the samples of water — at an average intensity of wave action, 10 hrs later from the beginning of wave movements. In the periphyton on reeds, as many as 185,200 individuals of nematodes were found (on the total area of $9,000 \text{ cm}^2$ of the substrate). In the water, the numbers of nematodes amounted to 2,080 individuals in 1 m^3 of water. From this, it was calculated that 1.1% of nematodes have been washed out from the periphyton. Considering the fact that relatively high numbers of the bottom nematodes were present in the samples of water, the estimated percentage was even smaller than that.

In such a situation, bearing in mind the positive role of wave action in dispersal of the attached organisms, such a small percentage of organisms washed out from periphyton cannot be considered as harmful for the periphyton biocenose.

It should be added that during the periods following wave action no reduction in numbers of the investigated organisms (*Nematoda*, *Oligochaeta*, *Tendipedidae*) was found in periphyton.

Wave action, as any environmental factor, has a positive role within certain limits only. At very heavy and long lasting wave action, although the washed out organisms in water make colonization of new areas potentially possible, the settling of them on new substrates is more difficult. Several times lower rate of colonization of new substrates was observed at a period of stormy weather. For example, during a period of heavy wave action, the amount of 0.5 cm^3 of periphyton per 100 cm^2 of substrate was attained after 6 days of accumulation period, whereas on the same substrate, when the wave movements were slight, this amount of periphyton has been accumulated after 3 days.

On the lakes examined the direction of waves is often constant for several subsequent days. A question arises whether this directional wave action evokes any differences in colonization of substrates situated differently to the direction of waves.

In the lake Mikołajskie the process of colonization of glass plates located at different angles to wave motion was examined. The plates were set in shallow (about 60 cm deep) and in deeper (about 1.5 m deep) parts of the littoral zone.

In the shallow parts, with a great deal of replications made, no difference was observed in amount of periphyton as well as in numbers of nematodes found on the plates situated differently towards the direction of waves. However, inconsiderable differences were observed in the deeper parts of the littoral. The plates situated perpendicularly to the direction of waves were colonized in a smaller extent than the others. From this, it can be supposed

that wave action directly retards the process of settling of organisms. The above results are comprehensible in the light of differences in water circulation between the shallow and deeper parts of the littoral. Since in the shallow parts both the splash of waves and the thorough circulation of water take place, no directional water motion can be maintained, whereas in the deeper parts of the littoral the directional motion of water is possible.

To summarize up the results of the investigations on the effect of wave action on the occurrence of periphyton organisms, it may be said that due to wave action only small proportion of organisms is washed out from the well-shaped periphyton, therefore, one should not consider it as the detrimental factor for periphyton.

Some facts of the devastating effect of wave action on periphyton, as known in the literature, usually relate to very heavy wave action. It seems possible that smaller amounts of periphyton observed by several authors in the parts of littoral which were more exposed to wave action can be explained not only by the mechanical devastation of periphyton, but also by different environmental requirements of the species examined.

The role of wave action in colonization of new substrates is rather complex one. The wave action enables the attached organisms to disperse and, by this, makes the colonization of new substrates possible, but, on the other hand, too heavy wave action delays the process of colonization through washing the organisms from the newly formed periphyton.

VI. SUMMARY OF RESULTS AND DISCUSSION

Periphyton nematodes, with which this paper mainly deals, of the lake environments examined occur in masses in periphyton. Their number amount to several thousands of individuals per 100 cm² of the substrate surface. As it appears from both the literature data and the author's own observations described in the paper, the dominant species: *Prochromadorella bioculata* and *Punctodora ratzeburgensis* show a high degree of attachment to a substrate, due to the secretion of an adhesive substance from their caudal glands and to their ability to entangle among colonies of algae.

The specific seasonal changes in numbers of periphyton nematodes have been described, for which one, very clearly marked, peak in numbers in the vernal period is characteristic. During the other seasons of the year the nematodes occur in smaller, more or less equal, numbers. The vernal maximum is brought about by mass reproduction of the dominant species, which reproduce also, though not so intensely, during the whole year.

In the subsequent years, the vernal peak in numbers can vary with time. The variations are closely related with the temperature of water and with the duration of the icing period on the lake.

In conditions of the lake examined, which can be considered as typical for many lake environments, colonization of the natural substrates takes place twice a year: 1) directly after the icing period – colonization of the substrates on which periphyton has been destroyed by ice and 2) during the vernal season – colonization of young shoots of higher aquatic plants.

During the icing period periphyton undergoes the destruction partially, on those parts of the substrates which are covered with ice, whereas under the ice cover well-developed periphyton occurs. Reduction in numbers of nematodes and algae occurs in the periphyton covered with ice due to the higher death rates of these organisms.

During the time following the thaw vast areas of the littoral were void of periphyton. The habitats, periphyton of which has been destroyed in the icing period, were colonized by periphyton similar to that occurring in the close vicinity, as to numbers of organisms and the species composition. The differences between the new and old periphyton disappear during 4–6 weeks following the thaw.

Also, the young plants appearing on the lake in spring are colonized by the species of algae and of nematodes which occur in the vicinity. The growth of the plants coincides with the maximum of numbers of periphyton nematodes. Initially, the nematodes settle down on the young reeds in smaller numbers than those actually present in the periphyton of old reeds. Equalization of the numbers takes place in late July and early August, and is achieved by reduction in numbers of nematodes on the old reeds. It is the most probable that the reduction is brought about by termination of the mass reproduction period as well as by dispersal of nematodes from the old reeds onto the young ones.

As based on observations on the process of colonization by the nematodes, both the natural and artificial substrates experimentally introduced into the reservoir, it was found that, at the first days of colonization, the nematodes appear in small numbers. Then, their numbers increase rapidly, after one month reaching the level which is characteristic for the given conditions.

That is the compensatory colonization of new substrates by nematodes, and not the multiplication of the initially settled forms, which causes an increase in their numbers. From the initial period of colonization up to the stabilization of numbers at a certain, characteristic for the given conditions, level, the compensatory colonization plays a decisive role in the process of colonization of new substrates by nematodes. From that time on, the numbers of nematodes can maintain their constant level without any further compensatory settling.

The above stated regularity (that in the process of colonization of a new substrate, an increase in numbers is achieved mainly through the further compensatory settling and not through multiplication of the forms initially settled) seems to hold for other groups of periphyton organisms; especially for all the

organisms with a long life cycle, which appear on a new substrate rapidly and in large numbers. On the contrary, the species with short life cycles and high reproduction rates can supposedly occupy a new substrate through the intense multiplication of their forms initially settled.

Of the similar opinion was Duplakov (1933), who has reported that the species with the vegetative reproduction often appeared on the substrates submerged in the pelagial zone (that is, at a considerable distance from the sources of colonization). Such species can colonized a new substrate easily starting with small number of the initially (even by chance) settled forms.

In the paper, the analysis has been made of the role of factors responsible for the course of the colonization process.

Dealing with this problem, the paper by Spodniewska and Pieczyńska (1963), concerning the problem of the differentiating effect of the type of substrate on occurrence and colonization by periphyton organisms, should be discussed first.

A deal of authors tend to accept the view that the type of substrate is the main factor responsible for occurrence of periphyton organisms (Willer 1923, Karsinkin 1925, Duplakov 1933, Young 1945, Ruttner 1953, Gorbunow 1955).

In the study mentioned above no differentiating effect of the type of substrate on the occurrence of periphyton organisms was found. A great similarity in occurrence and settling process of periphyton organisms was observed among various types of substrates, provided that the substrates were located in the same environment (the same spot of the littoral). On the contrary, considerable differences in occurrence and in settling process were found on the same type of substrate, but located in different lakes or in various parts of one lake.

Cooke (1956) and Castenholtz (1960, 1961) have also suggested that there is no differentiating effect of the type of substrate on occurrence of periphyton organisms. Bohr (1962), working on sociology of periphyton has noted that the type of substrate is a secondary factor for the occurrence of periphyton organisms.

In the present paper, the effect of the periphyton occurring in the nearest proximity as a source of colonization, on the process of settling of periphyton organisms on new substrates, was also analyzed.

Numbers, species composition and dominance structure of the periphyton organisms appearing on a new substrate were dependant from the character of the periphyton that was the source of colonization. It was also found that numbers of periphyton organisms settling on new substrates varied with time accordingly to the changes in numbers of the organisms present in close vicinity. The periphyton of the surrounding environment has the decisive role upon the numbers and dominance patterns of organisms occurring in periphyton which develops on a new substrate, irrespectively to the age of periphyton (duration of the submergence period).

The analysis of the influence of wave action on the occurrence of periphyton organisms was also made in the paper.

It was found that due to wave action only inconsiderable numbers of organisms were washed out from the well-developed periphyton, therefore, wave action cannot be considered as a detrimental factor for periphyton.

The role of wave action in colonization of new environments is very composed. Wave action enables the dispersal of the attached organisms and, through this, makes colonization of new substrates possible, but, on the other hand, too heavy action delays the process of colonization, making settling of organisms more difficult by constant washing them from the young periphyton. It has been observed that the degree of washing of the organisms depended on the structure and age of periphyton. Considerably more organisms were washed from the young periphyton than from the old one.

The fact that the organisms are washed out from the young periphyton more intensely than from the old periphyton accounts for the described differences in the role of the compensatory settling of organisms between the young and old periphyton. The young periphyton, being washed out more easily, has to be filled up more intensely with new organisms to compensate the loss due to wave action, and to enable further increase in numbers. On the other hand, the old periphyton, with numbers of organisms characteristic for the given conditions, being washed out to much lesser extent, does not need such an intense compensatory settling of organisms to secure its normal existence.

The washing of organisms from periphyton due to wave action counterbalanced by the compensatory settling — the constantly recurring loss of organisms and its compensation — bring about a kind of "exchange" within periphyton biocenose.

This exchangeability allows to understand the regularities, some of which have been described in the present paper, and some — in the earlier works, in the occurrence of periphyton organisms. Thus, it can render an explanation for the considerable similarities, which have been reported in the earlier paper (Pieczyńska 1961), in the character of groupings of periphyton nematodes (as for their numbers and dominance structure) living on the plants which grow in one place of the littoral. It can also refer to the discussed above semblance of periphyton organisms occurring on the different substrates, located in one site of the reservoir (Pieczyńska and Spodniewska 1963).

Consequently, it can be said that, although some spatial isolation exists in the periphyton appearing on various substrates, considerable uniformity in occurrence of periphyton can be characteristic for rather vast areas of the littoral zone. This uniformity is achieved mainly by the removal of some organisms from periphyton due to wave action, and settling down of other organisms.

As it has been discussed earlier in the paper, greater variability was found in the old periphyton than in the young periphyton collected both from the natural and the experimental substrates.

The "exchangability" of periphyton biocenose can also explain the fact of colonization of new environments (natural and experimental ones) by periphyton organisms in numbers and, with the dominance patterns similar to those in the vicinity. The above regularity can result from the fact that the colonization takes place through the passive dispersal (or passive migration) of periphyton organisms from the nearest substrates.

If such an explanation is to be accepted, one should expect a greater similarity in the dispersion patterns of the organisms that are less connected with a substrate, than in those, closely attached to it. In the earlier study (Pieczyńska and Spodniewska 1963) a greater differentiation was observed in the occurrence of algae than in that of periphyton nematodes, with the highest differentiation found for the permanently attached algae: *Gleotrichia pismus* and *Cladophora* sp.. Undoubtedly, the degree of attachment to a substrate is only one of many factors which regulate the occurrence of periphyton organisms. Consequently, no direct and close dependence should be expected between the degree of attachment of certain species and the differentiation of their dispersion. Other factors may be also decisive for the dispersion of these organisms. For instance, the differentiation in occurrence of the forms permanently attached to a substrate brings about, in turn, changes in living conditions for other organisms. The environmental differentiation of the littoral is another factor which is responsible for the uneven occurrence of periphyton organisms.

Wave action enables to a certain degree some contacts between periphyton biocenose and other aquatic biocenoses. The closest relationship exists between periphyton and plankton. The organisms washed from periphyton live temporarily in plankton, and the planktonic organisms, as it has been reported in the introduction to this paper when discussing the literature data, occur in masses in periphyton. Some contacts, although of a lesser degree, were also observed between periphyton and benthos, to which some authors include the periphyton. Some bottom species of nematodes, evidently due to wave action, were encountered in periphyton.

In spite of a certain degree of exchangability, periphyton represents a grouping of organisms closely connected with the defined environments of water reservoirs. The constant colonization of new substrates, the defined organization, and the presence of the species which do not occur in other groupings, are characteristic for this grouping.

Thus, it seems reasonable to consider periphyton as the self-existing ecological unit, which is a part of the total biocenose of a whole reservoir.

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BADANIA NAD ZASIEDLANIEM NOWYCH ŚRODOWISK PRZEZ NICIENIE (*NEMATODA*) I NIEKTÓRE INNE ORGANIZMY PERIFITONOWE

Streszczenie

Tenatem pracy jest charakterystyka prawidłowości zasiedlania nowych środowisk przez organizmy perifitonowe w warunkach litoralu jeziornego oraz próba określenia mechanizmów tego procesu i warunkujących go czynników. Badaniami objęto zasiedlanie podłoża naturalnych (głównie trzciny *Phragmites communis* Trin.), jak też podłoża eksperymentalnie wprowadzonych do zbiornika (różne rodzaje płytek szklanych). Przeprowadzono również szereg eksperymentów terenowych i laboratoryjnych.

Główny obiekt badań stanowiły wolno żyjące nicienie (*Nematoda*), które są stałym i liczny składnikiem perifitonu; w badanych środowiskach osiągają liczebność kilkunastu tysięcy osobników na 100 cm² powierzchni podłoża. Poza nicieniami przy opracowywaniu niektórych zagadnień uwzględniano również glony, *Tendipedidae* i *Oligochaeta*.

Badania prowadzono w latach 1960–1962 na kilku jeziorach Pojezierza Mazurskiego.

Analizy ilościowe materiału prowadzono w oparciu o serie prób perifitonu zeskrobwanego z określonej powierzchni badanego podłoża.

Przeprowadzono szereg obserwacji nad biologią nicieni, koniecznych dla interpretacji osiedlania się tych organizmów w nowych środowiskach. Badania dotyczyły dominujących w analizowanym materiale (około 90% wszystkich nicieni) gatunków *Prochromadorella bioculata* (M. Schultze) i *Punctodora ratzeburgensis* (v. Linstow). Określono stopień ich osiadłości, długość cyklu życiowego oraz intensywność rozmnażania w różnych okresach roku.

Opisano charakterystyczną dynamikę liczebności nicieni w cyklu rocznym, cechującą się jednym bardzo wyraźnym szczytem liczebności w okresie wiosennym, spowodowanym masowym rozmnażaniem się dominujących gatunków.

W kolejnych latach wiosenny szczyt liczebności występował w nieco różnym czasie, co wiązało się ściśle z temperaturą wody i okresem zlodzenia.

W okresie zimowym obserwowano częściowe zniszczenie perifitonu na tych partiach podłoża, które znajdowały się w pokrywie lodowej (pod lodem występował nonnalnie rozwinięty perifiton). Stwierdzono, że redukcja liczebności glonów i nicieni w perifitonie podłoża wmarzniętych w lód spowodowana była głównie ich zwiększoną śmiertelnością.

Wykazano, że w badanych warunkach zasiedlanie środowisk naturalnych na skalę masową zachodzi dwukrotnie: 1) bezpośrednio po zejściu lodów – zasiedlanie podłoża na których perifiton został zniszczony na skutek wmarznięcia w lód, i 2) w okresie wiosennym – zasiedlanie wzrastającej wyższej roślinności wodnej.

W obu przypadkach badane organizmy osiedlały się na nowych podłożach w liczebności i składzie gatunkowym podobnym do występującego w najbliższym sąsiedztwie.

Podłoża pozbawione perifitonu w okresie zlodzenia, zasiedlone zostały w ciągu czterech do sześciu tygodni po zejściu lodów. Przy tym zasiedlanie głębszych partii litoralu zachodziło szybciej, niż płytkich. Wynika to z tego, że w partiach głębszych następowało tylko dosiedlanie górnych części łodyg roślin, podczas gdy w partiach przybrzeżnych (przemarzających do dna) musiała nastąpić całkowita odbudowa perifitonu.

Młoda wzrastająca roślinność (trzciny) zostaje zasiedlona przez gatunki reku-

tujące się z występujących w perifitonie porastającym rośliny z ubiegłego roku. Wyrównanie liczebności następuje na przełomie lipca i sierpnia.

Badając szczegółowo przebieg procesu zasiedlania nowych środowisk przez nicienie stwierdzono eksperymentalnie, że główną drogą wzrostu ich liczebności na nowych terenach jest dosiedlanie, a nie rozmnożenie form początkowo osiadłych. Dosiedlanie gra decydującą rolę w procesie zasiedlania nowych środowisk od okresów początkowych aż do ustalenia się liczebności na poziomie charakterystycznym dla danych warunków. Od tego momentu liczebność nicieni może być utrzymana na stałym poziomie bez udziału dalszego dosiedlania.

Powyższą prawidłowość można odnieść również do wielu innych organizmów bytujących w perifitonie. Przede wszystkim do tych wszystkich gatunków, które mają długi cykl życiowy, a szybko i licznie pojawiają się na nowych podłożach. Natomiast gatunki o krótkim cyklu życiowym i szybkiej reprodukcji mogą opanować nowe środowiska głównie poprzez intensywne rozmnożenie się form początkowo osiadłych.

Przeprowadzono badania mające określić rolę różnych czynników warunkujących zasiedlanie nowych środowisk przez organizmy perifitonowe. Stwierdzono zależność liczebności składu gatunkowego i struktury dominacji organizmów perifitonowych, pojawiających się na nowym podłożu, od charakteru ich występowania w perifitonie będącym źródłem zasiedlenia. Ustalono, że badane grupy organizmów zasiedlały nowe środowiska w różnych okresach czasu w zmiennych ilościach, odpowiadających aktualnej liczebności w otaczającym środowisku. Perifiton otaczającego środowiska decyduje o liczebności i stosunkach dominacji organizmów w perifitonie rozwijającym się na nowym podłożu, niezależnie od jego wieku (czasu pozostawiania podłoża eksperymentalnych w zbiorniku).

W ramach analizy mechanizmów zasiedlania nowych środowisk przez organizmy perifitonowe, zbadano wpływ falowania na przebieg tego procesu. Obserwowano wielokrotnie pojawianie się nicieni w wolnej wodzie litoralu w okresach silnego falowania. Liczebność nicieni w wodzie zależna była od intensywności falowania — zwiększała się wraz z jego wzrostem. Jak stwierdzono, do wody dostają się osobniki nicieni, które zostały wypłukane przez fale głównie z perifitonu, ale również (choć w mniejszym stopniu) z bentosu.

W eksperymencie laboratoryjnym wykazano, że stopień wypłukania różnych grup organizmów zależy od struktury perifitonu i jego wieku. Z perifitonu „młodego” wypłukuje się znacznie więcej organizmów, niż z perifitonu „starego”.

Na przykładzie nicieni stwierdzono, że falowanie wymywa z perifitonu niewielką liczbę osobników. I tak np. po 10 godz. falowania (o średniej dla badanego zbiornika intensywności) wypłukuje się z perifitonu 1,1% nicieni. Nie można zatem traktować falowania jako czynnika niszczącego biocenozę perifitonową.

Pozytywna dla organizmów perifitonowych rola falowania polega na umożliwieniu rozprzestrzeniania się (na skutek biernej migracji) tym, w dużym stopniu osiadłym gatunkom.

Rola falowania w procesie zasiedlania jest bardzo złożona. Z jednej strony falowanie umożliwia zajmowanie nowych środowisk, z drugiej jednak strony, zbyt silne falowanie opóźnia sam proces zasiedlania, utrudniając osiedlenie się organizmów i wypłukując je z młodego organizującego się perifitonu. Wypłukiwanie organizmów z perifitonu na skutek falowania i równoważące je dosiedlanie, stałe odchodzenie i dochodzenie różnych osobników powoduje pewien stopień „wymienności” biocenozy perifitonowej.

„Wymienność” ta sprawia, że: 1) istnieje prosta zależność liczebności, składu gatunkowego i struktury dominacji organizmów perifitonowych pojawiających się na nowych podłożach od stosunków panujących w perifitonie otaczającego środowiska,

2) różne podłoża, o ile są usytuowane w jednym punkcie zbiornika, zasiedlone są przez perifiton podobny pod względem liczebności i składu gatunkowego organizmów, 3) występuje duża jednolitość perifitonu na znacznych przestrzeniach litoralu.

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