KOMITET EKOLOGICZNY – POLSKA AKADEMIA NAUK

EKOLOGIA POLSKA – SERIA A

Tom XII Warszawa 1964 Nr 35

Eligiusz PIECZYŃSKI

ANALYSIS OF NUMBERS, ACTIVITY, AND DISTRIBUTION OF WATER MITES (*HYDRACARINA*), AND OF SOME OTHER AQUATIC INVERTEBRATES IN THE LAKE LITTORAL AND SUBLITTORAL*

The ecological and fauna characteristics of the environments examined are given. A discussion is made of the regularities in abundance, of trappability, within the annual cycle, and the 24-hour activity cycle, as exemplified by water mites and other invertebrates. Activity of various components of the invertebrate fauna is compared. Depending on the abundance and activity criteria, an estimation is given of the role of various groups of invertebrates in the littoral environment, and the dependence between abundance and activity is analysed. The final section of the paper deals with the regularities in spatial distribution (clumping, vertical distribution – the degree of connection with the bottom, occurrence in the littoral and sublittoral, micro-differentiations in occurrence in the littoral). On the basis of the results obtained, a thesis is put forward that water mites play an important role in the lake ecosystem, the role being negative from the aspect of fishery by depleting a stream of energy that flows from the invertebrate fauna to fish.

I. AIM OF THE WORK, STUDY AREA AND METHODS

The aim of the present paper was to analyse some chosen problems concerning numbers, activity and distribution of water mites in lake environments. The above analysis was carried out in two aspects: 1) through comparing the water mites with other groups of invertebrates (primarily *Ostracoda*, but also *Ephemeroptera*, *Tendipedidae*, *Trichoptera*, *Corixidae*, etc.), represented numerously in the environments examined, and 2) by exploring the ecological properties of various species of water mites.

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*From the Institute of Ecology, Polish Academy of Sciences, Warszawa.

Mikołajskie Lake, situated in the Masurian Lake District in Poland, was selected as a study area. The lake is an eutrophic reservoir, with surface of 470.0 ha, and the mean depth of 11.3 m.

Three stations were chosen, 2 of them in the littoral and 1 in the sublittoral. Their characteristics are as follows:

Littoral I – a compact belt of reeds (*Phragmites communis* Trin.) at the south-west shore of the lake. The sandy bottom covered with mud and a large quantity of decaying reeds. Submerged plants missing. The depth of 20 to 50 cm.

Littoral II – a great abundance of bulrush (*Schoenoplectus lacustris* (L.) Palla) growing densely also at the south-west shore, surrounded by reeds. The sandy-mud bottom. Of the submerged plants, *Potamogeton* was found. The depth of about 50 cm. At this station, the investigation has been carried out recently on numbers, sex ratio, and fecundity of several species of water mites (Pieczyński 1961a).

Sublittoral – a heap of empty shells of *Dreissena polymorpha* Pall., off the belt of reeds. The depth of about 5.5 m. This station was in proximity of littoral I.

Besides these three main stations, an analysis was also made of the occurrence of water mites in the upper profundal of Mikołajskie Lake (at a depth of 11.5 m) and, for comparison purpose, also of the material collected in the central part of lake Śniardwy (at a depth of 7.5 m, 1.5–2.0 km far from the nearest shore).

The material was gathered in the years 1960–1962.

To solve the problems which have been chosen for the aim of this paper, different methods were used. Samples were taken by various means: using traps, a dipper, a tube bottom sampler of the Lastočkin-Ulomski's type, a plankton sampler of the Bernatowicz type, and also samples of plants and samples of water taken by a pump.

1. Traps

The type of traps which were used was that described earlier by the author (Pieczyński 1961b). The trap consisted of 2 connected parts: a glass funnel and a jar. The funnels were relatively large, 15 cm in diameter, for, as it has been found earlier (Pieczyński – unpublished data), small funnels caused some deviation in the obtained results. These artifacts were noticed when analysing both the abundance and the dominance relations. As a rule, the traps were exposed for 24 hrs, although in some instances, the exposure time was shorter or longer. A total of 1,054 trap samples were collected from all the stations (the profundal station included).

When using this method, a problem of adequate interpretation of obtained data arises, since two elements will contribute to a catch: mobility of animals and their abundance. Hence, from the theoretical point of view, it is possible to obtain the same number of captured individuals of any two species, one of which is twice as numerous as the other, but its activity being two times lower.

In the ecological literature, there are some examples of investigations, in which traps were used to estimate numbers of organisms, but there are also some papers in which trap methods were used to estimate activity of organisms. Even the same authors have often applied a trapping method to serve both the purposes. The investigations by Geiler (1956) on *Carabidae* of field cultures, can be included to the first type of papers. This author, using a trapping method, has estimated numbers of dominant species and their seasonal changes in various cultures. Skuhravy (1957) has also shown the usefulness of this method in estimating the abundance of *Carabidae*, but he suggested to mark specimens as well. Estimates of numbers of organisms occurring in aquatic environments based on trapping methods were given by Štepanek and Chalupa (1958), and by Štepanek and Havlik (1960). Using the modified Borucki's apparatus, they described abundance and its seasonal changes of various groups of organisms (also *Hydracarina*) occurring in the "littoral" zone of the dam reservoir.

The second approach, i.e., to evaluate activity of organisms rather than their abundance on the basis of trapping methods, is represented by Vlijm, Hartsuijker and Richter (1961). These authors, inferring from differences in trappability of various species of *Carabidae*, described the 24-hour activity cycle of these species. They also analysed the dependence of trappability from temperature and rainfall. Skuhravy (1957) has emphasized the usefulness of trapping methods to evaluate 24-hour cycles in activity of *Carabidae*. Using trap methods, M. Kaczmarek (1960) has described the dependence between activity of *Collembola* and temperature.

In estimating abundance or activity of organisms from trapping methods, one has to be conscious of a specifity of these methods. It is possible to estimate the abundance of some organisms only in this case, when no major changes are expected to occur in their activity, such as those brought about by changing temperature during the investigated period. On the contrary, when analysing activity of some organisms, one can rely on trap materials only after exclusion was made of the possibility of changes in their abundance, and when the external factors do affect the activity of animals, as for example in the 24-hour cycle.

There is also another way to estimate activity which would allow to eliminate the effect of abundance on numbers of individuals captured in traps. To reach this purpose, the abundance should be estimated with the use of some other method, besides trapping. Then, dividing numerical data obtained from traps by those meant to measure abundance, one can obtain a conventional index of activity. Such an index was used by Chapman in 1926, (after Grüm 1959) in ecological investigations on insects; and by Hamilton in 1937, in investigations on rodents (after Grüm 1959). M. Kaczmarek and W. Kaczmarek (1956) also reported on the possibility to employ this index when comparing mobility of various groups of the soil fauna.

It is quite obvious that by such an approach one obtains data concerning not the individual or physiological activity, but rather the "ecological" activity, which is a kind of measurement of intensity of penetration in an environment.

In the present paper, it was accepted to term the results obtained from traps as trappability. Thus, trappability will mean a number of individuals that were caught in the trap during the unit time. The concept of trappability comprises both abundance and activity, and these are unestimated elements. since we do not know to what an extent abundance or activity are responsible for the obtained result. To estimate abundance, other kind of measurement was taken (mainly that from the dipper). Activity was mainly estimated by using the index already mentioned, calculated from the relation of trappability to abundance. In some instances, however, activity was estimated directly from changes in trappability. For example, when defining activity during the 24-hour cycle, an assumption was made that the abundance of organisms did not show any considerable changes within such a short interval, and, therefore, the activity estimates were calculated from changes in trappability. The material from traps served also to estimate a spatial distribution, or to compare the dominant species in various environments.

2. Dipper

Samples were taken by means of a dipper similar to that used in previous investigations (Pieczyński 1959, 1960a, 1960b, 1961a, 1963). It consisted of a metal ring 10 cm in diameter with the bolting silk cloth sack attached to it, mesh dimentions being 0.25 × 0.25 mm. The ring was fastened to a wooden pole. Sampling depended on swift sweeping movements of the dipper in water, among plants and over the bottom. Twenty such sweepings formed one sample. A total of 310 samples were taken at 2 littoral stations.

3. Tube bottom sampler of the Lastočkin-Ulomski's type

The apparatus covered 10 cm^2 of the bottom surface. To prevent small organisms from escaping from a sample, the whole contents of the sampler were placed, without washing on a sieve, into bottles, and then sorted in the laboratory. Samples were collected from the littoral stations. A total of 400 samples were taken by means of this apparatus.

4. Plankton sampler of the Bernatowicz's type

The 5 litre content sampler was used, and the water was filtrated through a plankton gauze with mesh dimensions 0.25 × 0.25 mm. A total of 400 samples were collected from the both littoral stations.

5. Samples of plants

The following procedure was employed: a metal tube 3 cm in diameter, 80 cm long, was put on a stalk of reed or bulrush, and then the plant was cut off at its roots with the garden scissors. Before the plant was removed from water, the lower openning of the tube had been screened with a small dipper 5 cm in diameter of the bolting cloth (with mesh dimentions given above). The piece of plant, collected in the above described way, was placed into a bottle and then searched in the laboratory. Such samples render some information on the fauna occurring on plants. The plant samples were gathered from the two littoral stations. A total of 380 samples were collected.

6. Pump

Samples were taken by placing one end of a rubber hose close to the bottom of lake and by pumping of the water. Ten litres of water formed one sample. The water was filtrated through a plankton gauze of mesh dimentions 0.25 × ×0,25 mm. A total of 100 such samples were collected from littoral I and from the sublittoral.

The material collected by all these methods was immediately sorted, without preserving. Only water mites were later preserved in the Koenike's liquid for further specification, other groups of invertebrates being counted and then discarded.

In general, a total of 2,644 samples of all sorts were collected supplying with a material of 14,130 specimens of water mites.

II. ECOLOGICAL AND FAUNA CHARACTERISTICS OF THE EXAMINED ENVIRONMENTS

Data concerning the species composition and numbers of water mites captured are shown in Table I.

A total of 42 species of water mites were found to occur in Mikołajskie Lake, 31 of which in littoral I, 37 – in littoral II, 25 – in the sublittoral, and 2 – in the upper profundal. In the central part of lake Śniardwy, 11 species were found.

To illustrate the extent of similarity between the water mite fauna occurring in the littoral and sublittoral environments, a simple phytosociological index was used, namely, the Sörensen's species similitude index:

$$P = \frac{2c \cdot 100}{a + b},$$

where c is the number of species common for both the compared environments, a – the number of species in one environment, and b – the number of species in another environment.

High and uniform values of the index were obtained, being an evidence of a considerable similarity of species composition of water mites in the explored

A list of species of water mites and number of specimens captured in the explored environments

Tab. I

Species	Mikołajskie Lake												Śniardwy Lake		
	littoral I			littoral II			sublittoral			profundal			central part		
	A	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*
Hydrachna globosa (Geer 1778)	–	1	1												
Eylais rimosa Piersing 1899 (?)	22	–	22	2	–	2									
Hydrodroma despiciens (Müller 1776)	807	158	965	249	27	276	261	1	262						
Lebertia sp.	222	119	341	70	54	124	3	2	5						
Frontipoda musculus (Müller 1776)	1	1	2	13	6	19	1	3	4						
Oxus ovalis (Müller 1776)	4	1	5	6	–	6									
Limnesia maculata (Müller 1776)	841	228	1069	397	199	596	30	57	87						
L. fulgida Koch 1836													4	–	4
L. undulata (Müller 1776)	7	–	7	202	295	497	6	–	6						
L. polonica Schechtel 1910				1	–	1									
Hygrobates longipalpis (Herman 1804)	115	84	199	64	37	101	19	13	32						
H. nigromaculatus Lebert 1879	167	137	304	79	9	88									
Atractides ovalis Koenike 1883	3	–	3												
Unionicola aculeata (Koenike 1890)	1	–	1	4	–	4	44	–	44	4	–	4			
U. crassipes (Müller 1776)	54	264	318	119	106	225	292	481	773				3	–	3
Neumania callosa (Koenike 1895)							1	–	1				6	1	7
N. deltoides (Piersig 1894)				3	–	3	93	–	93						
N. spinipes (Müller 1776)	4	–	4												
N. vernalis (Müller 1776)	1	–	1	11	–	11	37	–	37						
Neumania sp.				–	13	13	–	53	53						
Hydrochoreutes krameri Piersig 1896	1	3	4	9	8	17	2	2	4						
H. ungulatus (Koch 1836)													1	–	1
Pionopsis lutescens (Herman 1804)	6	–	6	5	–	5									

Piona clavicornis (Müller 1776)				1	–	1									
P. coccinea (Koch 1836)	115	117	232	194	493	687	58	130	188				5	9	14
P. conglobata (Koch 1836)	290	156	446	8	–	8	1	–	1						
P. discrepans (Koenike 1895)				7	–	7									
P. disparilis (Koenike 1895)							3	–	3						
P. longipalpis (Krendowskij 1878)	34	1	35	4	–	4									
P. neumani (Koenike 1883)	7	–	7	49	–	49	1	–	1						
P. rotunda (Kramer 1879)	18	–	18	47	–	47	34	–	34				48	–	48
P. variabilis (Koch 1836)	1	–	1	116	–	116									
Piona sp.	–	34	34	–	236	236	–	42	42	–	1	1	–	7	7
Forelia liliacea (Müller 1776)	336	42	378	268	9	277	324	64	388				78	–	78
F. variegator (Koch 1836)	37	–	37	13	–	13	5	–	5						
Brachypoda versicolor (Müller 1776)	1149	1081	2230	584	293	877	160	56	216						
Mideopsis orbicularis (Müller 1776)	46	5	51	77	3	80	74	11	85				1	–	1
Arrenurus albator (Müller 1776)	36	–	36	10	–	10	5	–	5						
A. bicuspidator Berlese 1885				1	–	1									
A. crassicaudatus Kramer 1875	10	–	10	14	–	14	1	–	1						
A. maculator (Müller 1776)				1	–	1									
A. nobilis Neuman 1880													8	–	8
A. tricuspidator (Müller 1776)				1	–	1									
A. latus Barrois et Moniez 1887				1	–	1									
A. globator (Müller 1776)	21	–	21	60	–	60							1	–	1
A. sinuator (Müller 1776)	2	–	2	8	–	8	12	–	12				2	–	2
A. biscissus (Lebert 1879)				1	–	1	2	–	2						
Arrenurus sp.	150	4	154	29	5	34	5	9	14				–	88	88
Total	4508	2436	6944	2728	1793	4521	1474	924	2398	4	1	5	157	105	262

A – adults, *B* – nymphs, *C* – adults and nymphs global.

environments. They amounted to: 79.4% for littoral I and littoral II, 75.0% for littoral I and sublittoral, and 74.2% for littoral II and sublittoral.

Brachypoda versicolor was the most numerous species in littoral I, forming 32.1% of all the water mites captured in this environment. Next to this were consecutively: *Limnesia maculata* (15.4%), *Hydrodroma despiciens* (13.9%), *Piona conglobata* (6.4%), and *Forelia liliacea* (5.4%). Totally, these most numerous species formed 73.2% of all the water mites found in this environment.

In littoral II, *Brachypoda versicolor* was also the most numerous species (19,4%), and next to it were: *Piona coccinea* (15.2%), *Limnesia maculata* (13.2%), *Limnesia undulata* (11.0%), *Forelia liliacea* and *Hydrodroma despiciens* (6.1% each). Totally, they formed 64.9% of all the water mites captured in this environment.

In the sublittoral, *Unionicola crassipes* was the most numerous species (32.4%), next to it were: *Forelia liliacea* (16.3%), *Hydrodroma despiciens* (11.0%), *Brachypoda versicolor* (9.1%), and *Piona coccinea* (7.9%). All these species formed a total of 76.7% of all the individuals captured in this environment.

This presentation leads to a conclusion that no greater differences occur between the littoral and sublittoral in the water mite fauna. In general, the same species were found to be most numerous in both the environments. The sublittoral, however, is an environment less differentiated in the water mite fauna. It is expressed by smaller numbers of species of water mites found in this environment. As many as 17 species noted in the littoral were missing in the sublittoral, namely: *Hydrachna globosa*, *Eylais rimosa*, *Oxus ovalis*, *Limnesia polonica*, *Hygrobates nigromaculatus*, *Atractides ovalis*, *Neumania spinipes*, *Pionopsis lutescens*, *Piona clavicornis*, *P. discrepans*, *P. longipalpis*, *P. variabilis*, *Arrenurus bicuspidator*, *A. maculator*, *A. tricuspidator*, *A. latus*, and *A. globator*. Some of these, such as *H. nigromaculatus*, *P. variabilis*, and *A. globator* occurred rather abundantly in the littoral. Reversely, of the species noted in the sublittoral, only two were missing in the littoral, namely, *Neumania callosa* and *Piona disparilis*, both belonging to species very scarcely occurring in lakes.

The upper profundal of Mikołajskie Lake is very scarcely populated by water mites, both in numbers of species and numbers of individuals. Only two species were found to occur in this zone, in spite of the fact that light traps were used, which, as it has been found for the littoral and sublittoral environments, should increase numbers of captured individuals by many times (Pieczyński 1962). The central part of lake Śniardwy, as opposite to Mikołajskie Lake, showed an abundance of fauna. Eleven species were found, of which *Forelia liliacea* and *Piona rotunda* were most numerous.

The most numerous species of water mites found in the littoral of Mikołajskie Lake are the commonest components of the water mite fauna of the Masurian lakes. To give an example, the following species were the most numerously represented and distributed in the complex of 41 lakes in the Krutynia river basin: *Hydrodroma despiciens*, *Limnesia maculata*, *Unionicola crassipes*, *Piona conglobata*, and *Brachypoda versicolor* (Pieczyński 1963).

III. REGULARITIES IN ABUNDANCE, TRAPPABILITY AND ACTIVITY

1. Seasonal changes in abundance and trappability

Analyses of seasonal changes in numbers and trappability of water mites and other groups of invertebrates were carried out for littoral I and sublittoral (in the latter, only changes in trappability were traced). Observations were

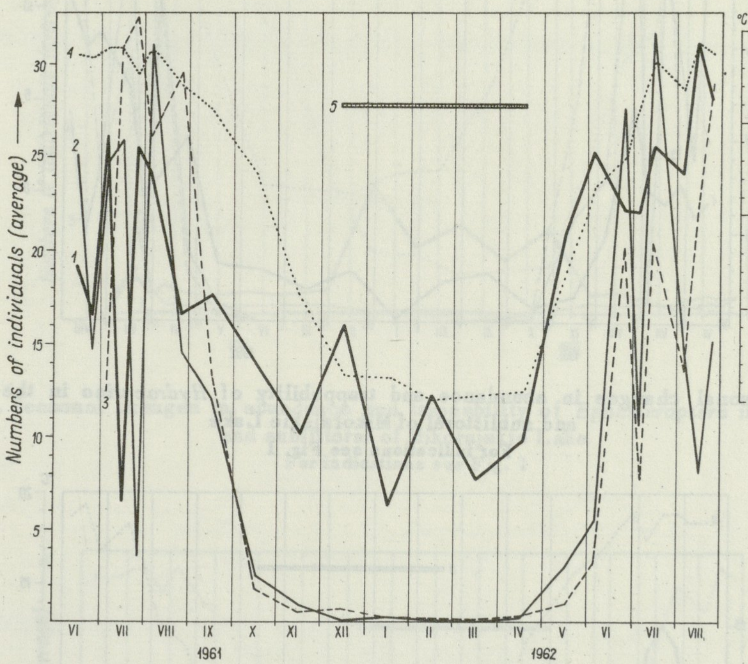

Fig. 1. Seasonal changes in abundance and trappability of invertebrates (all groups totaled) in the littoral and sublittoral of Mikołajskie Lake

1 — abundance in the littoral (mean numbers per dipper), *2* — trappability in the littoral (mean numbers per trap), *3* — trappability in the sublittoral (mean numbers per trap), *4* — temperature of water at the surface, *5* — duration of ice cover on the lake

conducted over the period from June 1961 to August 1962. To grasp changes in abundance of fauna in the littoral, series of 10 samples each were taken by means of the dipper (in the summer 1961, such series consisted of 20 samples each). Simultaneously, traps were set in for 24 hours intervals, also in series, first of 20 traps, and later on of 10 traps. The dipper samples were taken twice or three times a month, in the summer, and in the remaining seasons — once a month. In the sublittoral, series of 10 traps each were set in at the analogical periods for the same intervals.

Results are shown in Figures 1–8. Changes in numbers and trappability are plotted against the course of temperature of water[1] at the surface in Mikołajskie Lake, and the period when the lake was icebound is also marked on the graphs.

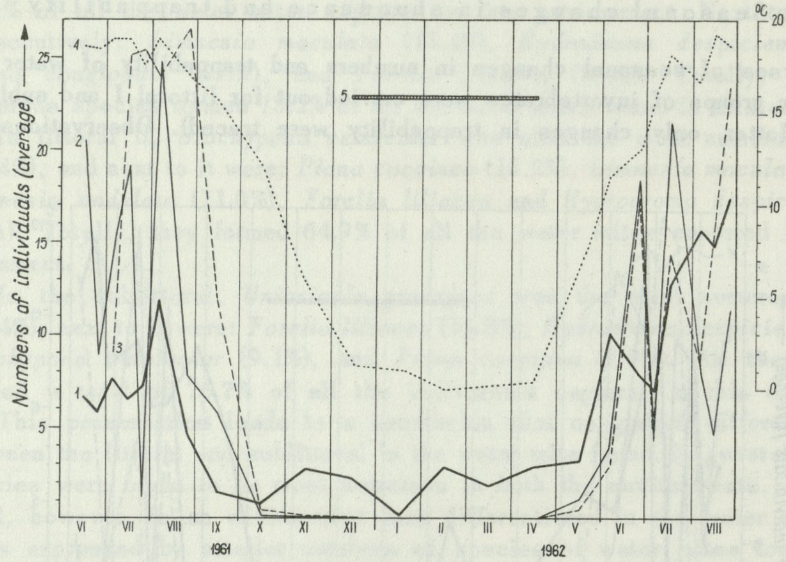

Fig. 2. Seasonal changes in abundance and trappability of *Hydracarina* in the littoral and sublittoral of Mikołajskie Lake

For indications see Fig. 1

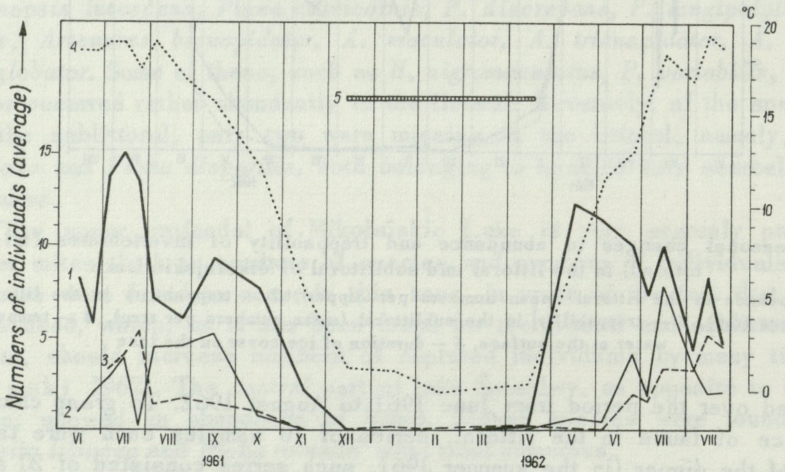

Fig. 3. Seasonal changes in abundance and trappability of *Ostracoda* in the littoral and sublittoral of Mikołajskie Lake

For indications see Fig. 1

[1] Data concerning water temperature of Mikołajskie Lake were supplied by the PIHM Observatory at Mikołajki.

Tracing seasonal changes in numbers and trappability of the invertebrate groups considered together, one can perceive the following regularity: the highest levels of abundance and trappability are observed in summer. In autumn, winter and spring, numbers are lower. A decrease in trappability is even more clearly

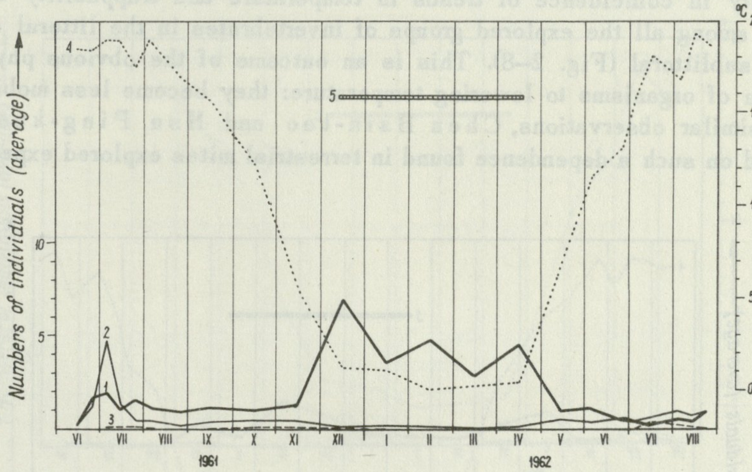

Fig. 4. Seasonal changes in abundance and trappability of *Ephemeroptera* in the littoral and sublittoral of Mikołajskie Lake

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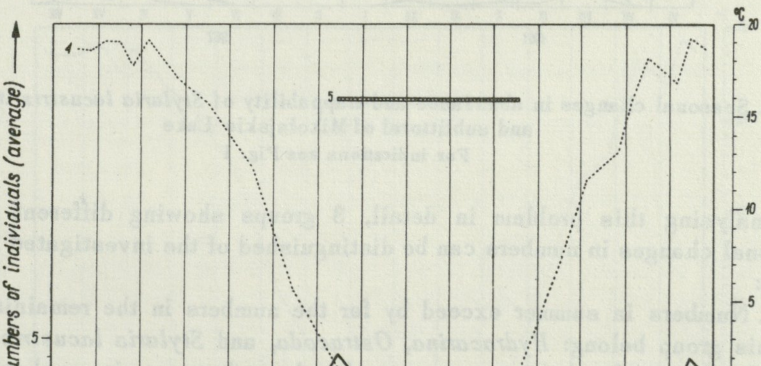

Fig. 5. Seasonal changes in abundance and trappability of *Tendipedidae* in the littoral and sublittoral of Mikołajskie Lake

For indications see Fig. 1

expressed for those periods, and is probably brought about by lowering water temperature. The period, when the water temperature fell down below 14°C, coincided with a conspicuous decrease in trappability; later on, trappability ceased almost completely. In early summer, when temperature of water went up to 15°C (June), a clearly marked increase in trappability was observed. The regularity in coincidence of trends in temperature and trappability can be observed among all the explored groups of invertebrates in the littoral as well as in the sublittoral (Fig. 2–8). This is an outcome of the obvious physiological reaction of organisms to lowering temperature: they become less mobile. Among other similar observations, Chen Hsin-tao and Hsu Ping-kuen (1962) reported on such a dependence found in terrestrial mites explored experimentally.

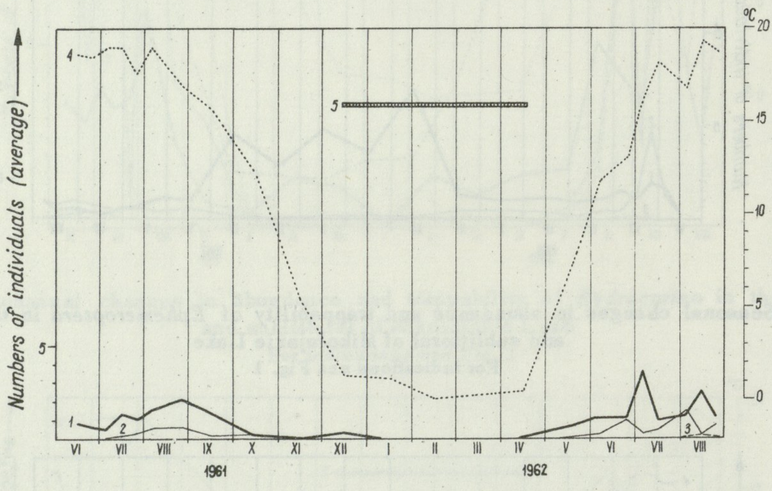

Fig. 6. Seasonal changes in abundance and trappability of *Stylaria lacustris* in the littoral and sublittoral of Mikołajskie Lake

For indications see Fig. 1

Analysing this problem in detail, 3 groups showing different patterns of seasonal changes in numbers can be distinguished of the investigated invertebrate fauna:

1. Numbers in summer exceed by far the numbers in the remaining seasons. To this group belong: *Hydracarina*, *Ostracoda*, and *Stylaria lacustris* (Fig. 2, 3, and 6); *Ostracoda* showing an extremely sharp decrease in numbers in winter.

2. More or less equal numbers are observed in summer and in the remaining seasons. This group includes *Tendipedidae* and *Asellus aquaticus* (Fig. 5 and 8).

3. Higher numbers in winter than in summer. To this group belong: *Ephemeroptera* and *Trichoptera* (Fig. 4 and 7).

The examined groups of invertebrates revealed different patterns also in trappability, but this will be a subject of further analysis. Here, it is enough to say that the coincidence of trends in temperature and trappability was reaffirmed. This, of course, pertains only to major changes within the annual cycle (between summer and autumn, and spring and summer). However, a considerable and rapid changes in trappability may also occur in summer and, in this case, it cannot be explained by changes in temperature.

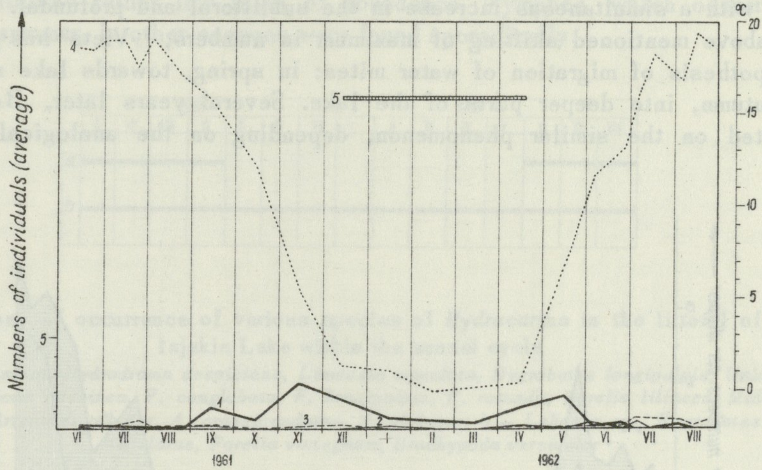

Fig. 7. Seasonal changes in abundance and trappability of *Trichoptera* in the littoral and sublittoral of Mikołajskie Lake

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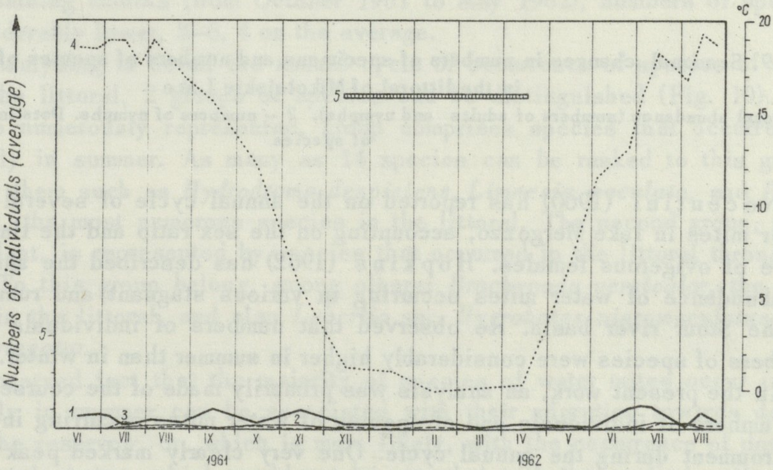

Fig. 8. Seasonal changes in abundance and trappability of *Asellus aquaticus* in the littoral and sublittoral of Mikołajskie Lake

For indications see Fig. 1

Little is known in the literature on the problem of quantitative occurrence of water mites in the littoral. Among other authors, Viets (1930) dealt with this problem, analysing abundance of water mites in the littoral, sublittoral, and profundal environments during various seasons. He described an interesting phenomenon that, in summer, water mites occurred most numerously in the littoral, but during the remaining seasons their numbers decreased in this environment with a simultaneous increase in the sublittoral and profundal. Relying on the above mentioned shifting of maximum in numbers, Viets has put forward a hypothesis of migration of water mites: in spring, towards lake shores, and in autumn, into deeper parts of the lake. Several years later, Berg (1938) reported on the similar phenomenon, depending on the analogical materials.

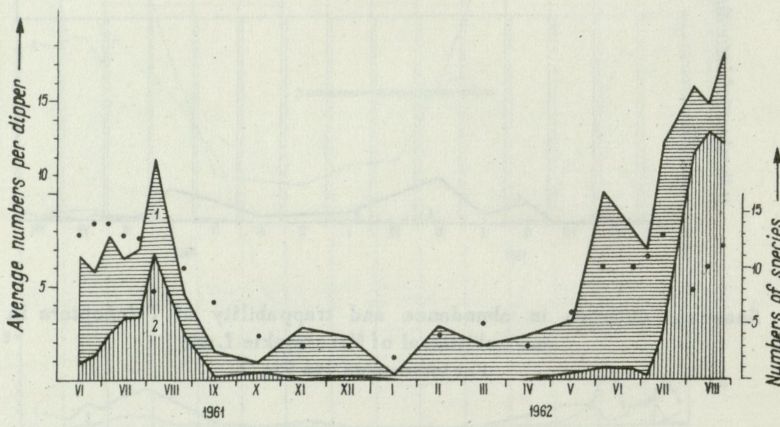

Fig. 9. Seasonal changes in numbers of specimens and numbers of species of *Hydracarina* in the littoral of Mikołajskie Lake

1 — total abundance (numbers of adults and nymphs), *2* — numbers of nymphs. Dots indicate number of species

Nocentini (1960) has reported on the annual cycle of several species of water mites in lake Mergozzo, accounting on the sex ratio and the time of occurrence of ovigerous females. Hopkins (1962) has described the annual cycles of abundance of water mites occurring in various stagnant and running waters in the Stour river basin. He observed that numbers of individuals as well as numbers of species were considerably higher in summer than in winter.

In the present work, an analysis was primarily made of the course of changes in numbers of individuals and of species of water mites occurring in the littoral environment during the annual cycle. One very clearly marked peak in numbers in August is characteristic for the annual cycle of water mites in the littoral of Mikołajskie Lake (Fig. 9). Such peak was observed for both years of study, but it was somewhat delayed in 1962 (the second half of August), as compared with that in 1961 (the first half of August). The peak coincided with a mass occurrence of nymphs. Apart from this peak, a minor peak in numbers was observed at the beginning of June 1962. It is interesting that this peak neither coincided, nor was preceded by any mass occurrence of nymphs. It appears, then, that this peak was probably brought about by immigration of water mites to the littoral from other environments. Besides the summer seasons, numbers of water mites maintained rather low level of abundance. Nymphes, which occurred in masses in summer, in other seasons were found sporadically.

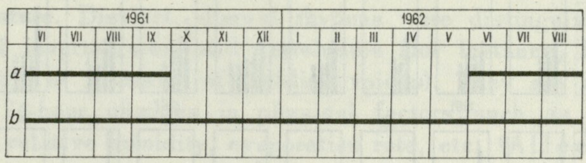

Fig. 10. Types of occurrence of various species of *Hydracarina* in the littoral of Mikołajskie Lake within the annual cycle

a — *Eylais rimosa, Hydrodroma despiciens, Limnesia maculata, Hygrobates longipalpis, Unionicola crassipes, Piona coccinea, P. conglobata, P. longipalpis, P. rotunda, Forelia liliacea, Mideopsis orbicularis, Arrenurus albator, A. crassicaudatus, A. globator*; *b* — *Lebertia* sp., *Hygrobates nigromaculatus, Forelia variegator, Brachypoda versicolor*

Analogical changes were also observed in numbers of species, which attained much higher level in summer than in the remaining seasons (Fig. 9). It follows that 7 to 14 species, 11 on the average, were found in series of samples collected in the summer 1961; and 8 to 13, also 11 on the average, in the summer 1962. In the remaining months (from October 1961 to May 1962), numbers of species were considerably lower, 2–6, 4 on the average.

When analysing in detail the annual cycle of occurrence of species of water mites in the littoral, 2 groups of species can be distinguished (Fig. 10). The first, more numerously represented, group comprises species that occurred in littoral only in summer. As many as 14 species can be ranked to this group, and among them such as *Hydrodroma despiciens, Limnesia maculata*, and *Piona conglobata*, the most numerous species in the littoral. The second group, much less abundant, is represented by species that occurred in the littoral throughout the year. To this group belong, among others: *Brachypoda versicolor*, the most numerous in the littoral, and also *Lebertia* sp., *Hygrobates nigromaculatus*, and *Forelia variegator*.

The observed fact that the majority of species of water mites occur in the littoral only in summer can be associated with their migration towards deeper zones of the reservoir, or, which is more likely, with the occurrence of dormant developmental stages, which could not be recorded with the applied methods of sampling. The latter possibility was also considered by Hopkins (1962).

Further analysis concerned the dominance relationships among *Hydracarina* within the course of year. Differences in this respect were found among seasons as well as between the two subsequent years (Fig. 11). In the summer 1961 (June – September), 3 species were dominating alternately: *Piona conglobata*, *Limnesia maculata* and *Brachypoda versicolor*. The level of dominance was not very high one, within the limits of 22–40%. Later on, from November 1961

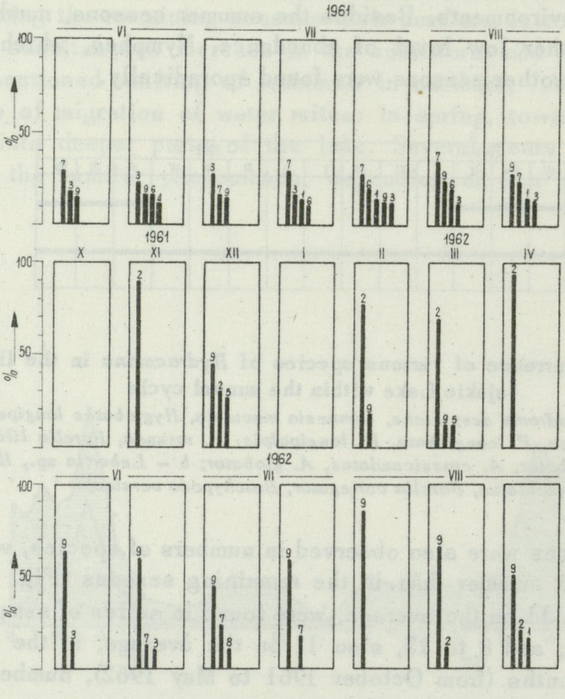

Fig. 11. Seasonal changes in dominance relationships among *Hydracarina* in the littoral of Mikołajskie Lake (as based on dipper samples)

1 – Hydrodroma despiciens, 2 – Lebertia sp., 3 – Limnesia maculata, 4 – Hygrobates longipalpis, 5 – H. nigromaculatus, 6 – Unionicola crassipes, 7 – Piona conglobata, 8 – Forelia liliacea, 9 – Brachypoda versicolor

until April 1962, *Lebertia* sp. was the almost exclusive dominant (only in December, *Brachypoda versicolor* was more numerous). During this period, the dominance level was much higher, within the limits of 44–92%. This period corresponded more or less with duration of the ice cover on the lake and, in general, with typical winter conditions of living. The increase in the dominance level, as compared with that of summer season, coincided with a decrease in numbers of species (Fig. 9). Later on, i.e., in the summer 1962, *Brachypoda versicolor* was the most numerous species, which dominated throughout the whole summer, maintaining very high dominance level (44–84%). The high dominance level in this period corresponded with increasing numbers of species, as compared with those of the winter season (Fig. 9).

To summarize up, it can be said that distinct differences in the dominance do appear in various periods of the same year as well as between the same seasons (summers) of the two subsequent years. One can assume that the latter fact is an expression of changes that happen in the littoral environment and in its fauna during consecutive years.

2. Activity in 24-hour cycle

A problem of 24-hour activity of terrestrial animals is rather well known in the literature. Distinct, diurnal rhythms were distinguished in activity of a number of invertebrates and vertebrates (for instance, by analysing locomotor activity, or intensity of yielding voices). They are connected with the rhythmical, 24-hour changes in physical factors such as intensity of light, temperature, relative humidity, evaporation rate, etc. (Allee and others 1958). Twenty four-hour cycles are well known and described in insects. Černyšev (1963), for instance, has distinguished 12 types of 24-hour activity, reporting that primitive insects show full 24-hour activity, while insects highly organized – "broken" activity restricted to some defined hours of the diurnal cycle.

Much less is known about 24-hour activity in aquatic animals. Existing data pertain almost exclusively to vertical movements of planktonic invertebrates (mainly Crustaceans). These movements are connected directly or indirectly with periodicity of light (Allee and others 1958).

In the present paper, when analysing this problem, the author inferred about changes in activity from those in trappability. Preliminary findings on activity of aquatic animals by daytime and at night, as based on the trapping method, were reported earlier (Pieczyński 1961b). It was found that *Hydracarina* and *Ostracoda* have higher activity during the daytime, and *Ephemeroptera* and *Coleoptera* – at night. At present, the problem of 24-hour activity has been analysed more thoroughly.

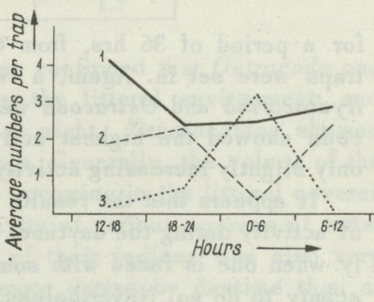

Fig. 12. The 24-hour cycle of activity of *Hydracarina*, *Ostracoda*, and *Ephemeroptera* in the littoral of Mikołajskie Lake

1 – Hydracarina, 2 – Ostracoda, 3 – Ephemeroptera

Four 24-hour cycles were traced, 3 of which in the littoral and 1 in the sublittoral, in July and August, 1961.

A series of 10 traps was used for the first cycle explored, and the captured fauna was removed from the traps every 6 hrs, thus, obtaining data in 4 intervals, namely, 12–18, 18–24, 0–6, 6–12. The material allowed to make the following statements (Fig. 12), which are in accordance with the results obtained earlier (Pieczyński 1961b): *Hydracarina* and *Ostracoda* show higher activity by daytime, and *Ephemeroptera* – much higher at night. In *Ostracoda*, the activity during daytime remains more or less unchanged, but in *Hydracarina*, the maximum of activity comes in P.M. hours (12–18).

In the second of the investigated cycles, carried out also in the littoral, traps were emptied more often, i.e. every 3 hrs. The observations have lasted

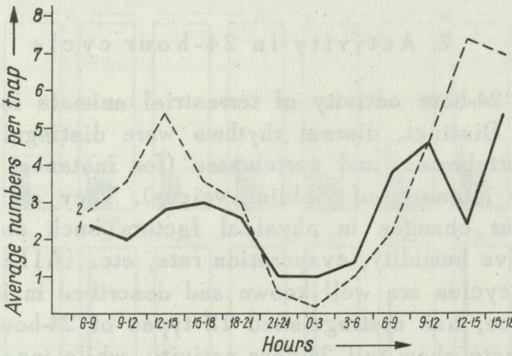

Fig. 13. The 24-hour cycle of activity of *Hydracarina* and *Ostracoda* in the littoral of Mikołajskie Lake
1 – Hydracarina, 2 – Ostracoda

for a period of 36 hrs, from 6 o'clock of one day to 18 of the next one. Five traps were set in. Again, a very regular and remarkable decrease in activity of *Hydracarina* and *Ostracoda* was observed at night (Fig. 13). By daytime, *Ostracoda* showed the highest activity between 12 and 15, and *Hydracarina* showed only slightly increasing activity in P.M. hours.

It appears that the results of these two diurnal cycles, concerning the course of activity during the daytime, do not allow to make any generalizations (especially when one is faced with some incongruities between them); the material is too scanty to do so. Nevertheless, one fact is beyond any doubt that there are clear differences in activity of the examined groups of invertebrates between daytime and night.

Further attention was given to activity during the daytime and night in the littoral and sublittoral. Activity of different groups of invertebrates and of species of water mites was compared. The analysis was based on two 24-hour cycles. In the littoral, a series of 20 traps was set in for 2 subsequent 24-hour periods; and in the sublittoral – a series of 10 traps for one 24-hour period. The captured fauna was removed from traps at 5 o'clock in the morning and at 20 in the evening. To illustrate differences in activity, a simple index was used, calculated from the ratio of numbers captured during the daytime to numbers captured at night (related to 1-hour period). For example, a value of the index higher than one indicates how many times the activity by daytime is higher than that at night. Results of the above analysis are shown in Table II.

Comparison between activity by daytime and at night of various invertebrate groups and of species of water mites in the littoral and sublittoral of Mikołajskie Lake (Index of 24-hour activity: relation of abundance in traps by daytime to abundance in traps at night)

Tab. II

Groups of invertebrates	The 24-hour activity index	
	littoral	sublittoral
Ostracoda	4.0	0.9
Hydracarina	3.2	1.2
Tendipedidae	0.9	0.1
Ephemeroptera	0.4	–
Stylaria lacustris	0.1	–
Species of *Hydracarina*		
Piona coccinea	9.9	0.9
Brachypoda versicolor	7.0	1.8
Hygrobates longipalpis	4.2	1.2
Forelia liliacea	1.8	0.6
Limnesia maculata	1.5	–
Hydrodroma despiciens	0.7	1.6
Unionicola crassipes	0.6	1.7

Once again, the described previously fact was confirmed that *Ostracoda* and *Hydracarina* show higher activity by daytime in the littoral environment, and *Ephemeroptera* and also *Stylaria lacustris* – at night. *Tendipedidae* showed more or less even activity within the 24-hour cycle. Generally, the values of the activity index for various groups of invertebrates occurring in the littoral covered very broad limits. It was also the case with activity of various species of water mites in this environment (Tab. II). The range of their indices was also very broad. There are some species that are much more active by daytime than at night (*Piona coccinea*, *Brachypoda versicolor*, and *Hygrobates longipalpis*), species with slightly higher activity by daytime (*Forelia liliacea* and *Limnesia maculata*), and also species with somewhat higher activity at night (*Hydrodroma despiciens* and *Unionicola crassipes*).

A thoroughly different situation was observed in the sublittoral. The activity indices of groups of invertebrates as well as these of species of water mites are much less differentiated (Tab. II); their range is smaller and the obtained values concentrate around 1. For example, *Ostracoda* and *Hydracarina*, which in the littoral showed considerably higher activity by daytime, in the sublittoral, they revealed rather uniform activity within 24-hour cycle. The same can be said about such species of water mites as *Piona coccinea*, *Brachypoda versicolor*, and others. Some deviation from the described regularity was observed in *Tendipedidae*.

From the above analysis, one can infer that differences in activity of invertebrates occurring in the sublittoral are, in general, smaller than those in the littoral. It seems probable that different rank of changes in insolation of both the environments can play a decisive role in this case. In the sublittoral, differences in insolation between the day and night periods, at depths higher than 5 m, certainly are much smaller than those in a shallow, 20 cm deep, layer of water in the littoral.

3. "Ecological" activity

Estimates were made of the so-called "ecological" activity in order to compare intensity in which the groups of invertebrates and species of water mites penetrate the littoral environment. The index discussed elsewhere in the paper was applied, as calculated from the ratio of trappability (traps) and abundance (dipper). The materials chosen for the analysis were restricted to those for the summer periods only, when no higher changes were observed in trappability, as might be brought about by eventual changes in water temperature. A total of 220 dipper samples, and 220 captures in traps were considered.

Activity of various groups of invertebrates in the littoral is shown in Table III, the groups being arranged according to their decreasing activity. Mainly *Coleoptera* (adults), but also *Corixidae* and *Argulus foliaceus* are the forms of very high activity. The high activity is also characteristic for *Heleidae* and *Hydracarina*. On the other hand, low activity was found in *Trichoptera*, *Ostracoda* and *Tendipedidae*. A relatively high position of *Gastropoda*, and the exceedingly low position of *Asellus aquaticus*, are of some interest. It appears that the selective operation of the traps caused some deformations of the results obtained for these groups. The glass funnels used in the traps could form an attractive substrate for *Gastropoda*. Their trappability was high, which accounted for the high values of the index. *Asellus aquaticus*, on the contrary, seem to avoid the glass substrate, which, in consequence, diminished its trappability, and caused artificial lowering the values of the activity index.

A similar analysis was also carried out to describe activity of species of water mites. The obtained data showed rather high differentiation in their activity (Tab. III). To the most active forms, one can include such species as *Hygrobates nigromaculatus*, *Hydrodroma despiciens*, *Limnesia maculata*, *Forelia liliacea*, and *Piona longipalpis*. On the other hand, low activity is characteristic for such species as *Piona conglobata*, *Unionicola crassipes*, *Brachypoda versicolor*, and others.

References can be found in the literature on the motion differentiation in water mites, but these data are based on quite a different, since morphological criterion, i.e., the shape of legs, and especially the number of swimming hairs on legs. Schwoerbel (1959) has distinguished 6 locomotor types of water mites, namely, 1. creepers (Die Kriecher), 2. climbers (Die Kletterer), 3. runners (Die Läufer), 4. those which burrow (Die Wühler), 5. swimmers (Die Schwimmer), and 6. gliders (Die Schweber).

Comparison of activity of various groups of invertebrates and of species of water mites in the littoral of Mikołajskie Lake during the summer

Tab. III

Groups of invertebrates	Activity index	Species of water mites	Activity index
Coleoptera	9.28	*Hygrobates nigromaculatus*	11.54
Corixidae	3.73	*Hydrodroma despiciens*	6.28
Argulus foliaceus L.	3.00	*Limnesia maculata*	3.47
Heleidae	1.55	*Forelia variegator*	3.17
Hydracarina	1.54	*F. liliacea*	2.86
Ephemeroptera	1.00	*Piona longipalpis*	2.83
Hirudinea	0.84	*Arrenurus albator*	2.13
Gastropoda	0.71	*Piona coccinea*	1.72
Trichoptera	0.37	*Hygrobates longipalpis*	1.24
Ostracoda	0.36	*Lebertia* sp.	1.08
Stylaria lacustris L.	0.25	*Brachypoda versicolor*	0.86
Tendipedidae	0.14	*Unionicola crassipes*	0.73
Asellus aquaticus L.	0.11	*Mideopsis orbicularis*	0.61
		Piona conglobata	0.27

Of the lake forms, *Limnochares aquatica* was included to creepers, species of the genus *Lebertia* – to climbers, the genera *Hygrobates* and *Atractides* – to runners, the genera *Eylais, Hydrachna, Piona,* and *Arrenurus* – to swimmers; finally, the genera *Unionicola, Neumania,* and *Hydrochoreutes* – to gliders. The same author (Schwoerbel 1961), reporting on the fauna of water mites in brooks, took an adventage of morphological criterion in defining the gradient in incidence of swimming and non-swimming forms, along the course of the brook: from its source to the lowest part.

Böttger (1962), working on biology and ethology of 3 species: *Arrenurus globator, Piona nodata nodata,* and *Eylais infundibulifera meridionalis,* reported, among other problems, on the type of locomotion of these species. He found *Eylais infundibulifera* being the best swimmer, *Arrenurus globator* – the worst one, and *Piona nodata* – a mediocre swimmer.

The results of the present work, as compared with the literature data, allow to conclude that the species with high "ecological" activity are those defined by Schwoerbel (1959) as swimmers (*Piona longipalpis*), or runners (*Hygrobates nigromaculatus*); and the species with low "ecological" activity – defined as climbers (*Lebertia* sp.), or gliders (*Unionicola crassipes*).

4. Degree of prevalence in environment[2]

Indices of abundance or biomass, related to a given surface or volume, are commonly used to define the role which a species or a group of species plays in an environment. This usually results in obtaining some information about the dominant forms in this environment. An estimation of such a role given in the present paper is based not on one criterion, but on two, namely, on abundance and activity (expressed in trappability). It can be assumed that these two elements together deside upon the number of contacts or encounters among individuals of one or of several species. Once, it can be an encounter between males and females, which will be associated with the reproduction rate of population; the other time, contacts between individuals with the same environmental requirements will decide upon intensity of intra- or interspecies competition. Finally, it can be an encounter between predators and their prey, which will result in a given intensity of prey-predator relationship. The more frequent the contacts, the higher intensity of the phenomena mentioned. In consequence, the frequency of contacts, depending on both the abundance and activity of animals, will decide upon the role of a given group in an environment. A species, or a group of species showing high abundance and possessing high activity will play a more important role in an environment than another species or a group of species less abundant or with lower activity.

To evaluate the role, conceived in the above given way, of a group of invertebrates in the littoral environment, point estimates were made of the degree of prevalence in this environment. Computed indices are the products of abundance and trappability. For convenience purpose, ranges of abundance and trappability were divided into 5 classes, starting from very low values to very high ones. To these classes, the points were ascribed from 1 to 5, respectively. Later on, after multiplication of figures, numerical values were obtained which served to characterize the degree of prevalence in the environment of various groups of invertebrates. The above described indices were computed for the summer season and for the remaining seasons of the annual cycle, separately. The results are presented in Table IV.

In summer, the highest degree of prevalence in the environment was observed in *Hydracarina*. Both the very high abundance and very high trappability composed it. The index reached its highest value. Next to *Hydracarina*, were *Ostracoda*, characterized by also very high abundance and high trappability. Further went *Ephemeroptera* and *Stylaria lacustris*, both showing high abundance and hight trappability. Then, there was a distinct gap behind these 4 groups followed by *Tendipedidae* (high abundance, low trappability) and others. *Trichoptera*, *Heleidae*, and *Argulus foliaceus* were the last.

In the remaining seasons treated together, a considerable total decrease was

[2] The author wishes to understand under the term "prevalence" the combined effect of abundance and activity. The other possible term would be "a degree of getting hold of an environment" which being a little awkward has been rejected.

Degree of prevalence in the littoral environment of various groups of invertebrates (point estimation)

Tab. IV

Groups of invertebrates	Summer period			Autumn – winter – spring period		
	abundance A	trappability T	degree of prevalence in the environment $A \times T$	abundance A	trappability T	degree of prevalence in the environment $A \times T$
Hydracarina	5	5	25	4	2	8
Ostracoda	5	4	20	4	2	8
Ephemeroptera	4	4	16	4	2	8
Stylaria lacustris	4	4	16	2	1	2
Tendipedidae	4	2	8	4	2	8
Corixidae	2	3	6	1	1	1
Hirudinea	2	2	4	1	1	1
Gastropoda	2	2	4	2	1	2
Coleoptera	1	3	3	1	1	1
Asellus aquaticus	3	1	3	3	1	3
Trichoptera	2	1	2	4	1	4
Heleidae	1	1	1	1	1	1
Argulus foliaceus	1	1	1	–	–	–

Abundance or trappability: very low (< 0.1 for dipper or trap) – 1 point
low (0.1 – 0.2) – 2 points
average (0.3 – 0.9) – 3 points
high (1.0 – 4.0) – 4 points
very high (> 4.0) – 5 points

observed in the degree of prevalence in the environment. It mostly resulted from the conspicuous lowering in trappability (Tab. IV), brought about by a decrease in temperature of water. Values of the index, which in summer had amounted from 1 to 25 for various groups, in these periods became restricted to the limits 1–8. Generally, the degree of prevalence in the environment of all the groups together became twice as low as in summer. Such a decrease was not observed in those groups of invertebrates in which the degree of prevalence depended mostly on their abundance, their trappability being low. To these belonged *Tendipedidae* and *Trichoptera*. The highest and also uniform values of the index were found in *Hydracarina*, *Ostracoda*, *Ephemeroptera*, and *Tendipedidae* for the discussed periods.

The above analysis leads to a conclusion that water mites play an important and specific role in the littoral environment, as compared with the other groups of invertebrates.

5. Activity versus abundance

The above problem has been approached by searching for a dependence between trappability and abundance, and then, between activity (as defined by the index described earlier in the paper) and abundance.

Considering annual cycles of abundance and trappability of various groups of invertebrates, one can perceive that, in summer, variations in numbers are generally smaller than those in trappability (see Fig. 1 and 2). For better illustration of the above stated regularity, a coefficient of variation was computed by dividing variation values by the means. Variations in abundance and trappability in the littoral, and of trappability in the sublittoral, were compared for some chosen groups of invertebrates. The summer seasons, 1961 and 1962, were considered. Results are presented in Table V, which includes the way of computing the coefficient and the obtained values.

From these data, it becomes evident that the lowest variation is found in abundance of the examined groups in the littoral; the coefficient attains an average value of 1.0, with the limits 0.5–1.5. On the other hand, the highest variation was observed in trappability, the average value of the coefficient being much higher, 3.9, with the limits 1.0–6.0. Trappability in the sublittoral showed an intermediary variation, higher than that of abundance in the littoral, but lower than that of trappability in the littoral. The average value of the coefficient was 2.9, with the limits 0.9–4.8. Higher changes in trappability in the littoral than those in the sublittoral one can probably explain by greater astatic conditions in the former environment. The littoral undergoes sharp changes in such factors as temperature, insolation, or wave movements.

It is most interesting to compare variations in abundance and trappability of *Hydracarina* and *Ostracoda* (Tab. V). With similar variations in abundance of both these groups, *Hydracarina* showed much higher variation in trappability in both the environments explored. It can be related with higher activity, ascer-

Comparison of variations in abundance and trappability of the chosen groups of invertebrates in the littoral and sublittoral of Mikołajskie Lake using the coefficient of variation

Tab. V

	Littoral				Sublittoral	
	abundance		trappability		trappability	
	a	*b*	*a*	*b*	*a*	*b*
Total of all groups	0.8	0.5	4.6	6.0	3.2	4.8
Hydracarina	1.2	1.4	5.2	4.9	2.9	4.3
Ostracoda	1.5	0.9	1.0	1.8	0.9	1.1

a – summer 1961, *b* – summer 1962.

Coeficient variation: $\delta = \frac{\sigma^2}{\bar{x}}$, where σ^2 = variation, $\bar{x}$ = arithmetical mean.

Variation was calculated from the formula: $\sigma^2 = \frac{1}{n-1}\sum_{k=1}(x_k - \bar{x})^2$ where x_k $(k = 1,2 \ldots n)$ – arithmetic means from series of samples, n = number of series of samples.

tained previously for this group (Tab. III). Factors interfering with trappability seem to affect much more the organisms showing high activity than the others.

Further analysis aimed at finding out whether changes in trappability were correlated with changes in abundance. The course of trappability of water mites was traced in detail in littoral I for the period: July 9 – August 18, 1962, by placing one trap in this environment and collecting the captured material in 24-hour intervals. The obtained curve of trappability (smoothed by means of the moving average) was compared with the course of abundance (data from 5 series of 10 dipper samples each), and of temperature of water at the surface layer. The comparison of curves (Fig. 14) allowed to make the following statement: there is no correlation between trappability and temperature of water, but there is rather clearly marked, negative correlation between trappability and abundance. The temperature of water oscillated within the limits of 16–17°C, then increased somewhat. These changes, however, being of the minute rank, did not correspond with changes in trappability. The abundance showed a constant increasing tendency in the course of observations, whereas trappability, being at first high (July, 10–26), later on, decreased considerably (July 27–August 18).

To elucidate the observed regularity: a decrease in trappability with increasing abundance of water mites, the species composition of *Hydracarina* that were found in the traps was analysed in respect to their activity. Calculations were made to grasp percentage of the most active species found in the captures (8 species of the highest activity, listed in Tab. III), collected in two periods: of high and low trappability. It became evident that during the first period (July, 10–26) the most active species formed 49% of all water mites captured, whereas in the second period (July 27–August 18) their incidence was only of 26%.

Thus, a considerable decrease by 23% in the incidence of more active forms might account for the observed phenomenon of a general decrease in trappability of water mites.

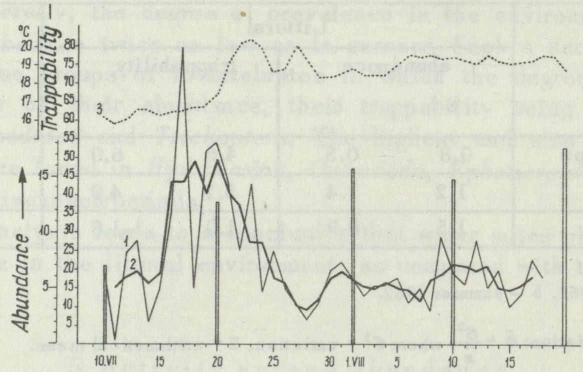

Fig. 14. The course of trappability of water mites in the littoral of Mikołajskie Lake plotted against their abundance and temperature of water

1 — trappability (absolute values), *2* — trappability (three point moving mean), *3* — temperature of water at the surface. Bars indicate an average abundance per dipper

Further attempts were made to find out whether it can be possible to prove the described above negative correlation by a direct comparison between activity (as defined by the proposed index) and abundance. This approach included a comparison carried out between the littoral and sublittoral environments as well as within the littoral environment.

To compare abundance and activity of chosen components of the fauna in the littoral and sublittoral, their trappability was computed on the basis of 60 trap samples, and their abundance — on the basis of 80 samples taken by means of a pump. The following groups were considered: *Ostracoda*, *Tendipedidae*, and *Hydracarina*, and among the latter, 5 most numerous species. The results are presented in Table VI. In general, higher activity of the examined groups was observed in the littoral (in 6 instances of a total of 8), in spite of the fact that in this environment, abundance was often lower than in the sublittoral. And so, *Ostracoda* were less abundant and more active in the littoral. On the other hand, *Hydracarina*, revealing more or less equal level of abundance in the littoral and sublittoral, showed also similar activity in both these environments. Considering species of water mites, one can observed that some of them showed, at the same abundance level, a considerably higher activity in the littoral (*Limnesia maculata*), or somewhat higher activity in the sublittoral (*Hydrodroma despiciens*, *Piona coccinea*).

Usually higher activity in the littoral than in the sublittoral, often independent of the abundance level, is undoubtedly caused by better insolation conditions and higher temperature in the former environment.

Comparison between abundance and activity of selected groups of invertebrates and of species of water mites in the littoral and sublittoral of Mikołajskie Lake

Tab. VI

	Abundance*		Activity**	
	littoral	sublittoral	littoral	sublittoral
Ostracoda	0.6	5.6	5.5	0.6
Tendipedidae	0.2	0.6	0.5	0.3
Hydracarina (total)	2.7	2.8	5.5	4.1
Hydrodroma despiciens	0.1	0.1	15.0	23.0
Limnesia maculata	0.1	0.1	20.0	2.0
Piona coccinea	0.1	0.1	7.0	11.0
Forelia liliacea	0.3	1.3	3.0	2.5
Brachypoda versicolor	1.9	0.4	5.0	2.8

*Mean abundance per pump sample (10 l).

$$**\text{Activity index} = \frac{\bar{x}\,\text{trappability (traps)}}{\text{abundance (pump samples)}}.$$

Further consideration was given to a dependence between activity and abundance of *Ostracoda* and *Hydracarina* in the littoral environment. An advantage was taken of the dipper and trap samples which previously had served to characterize the annual cycle. A total of 220 dipper samples and 220 trap samples, taken in the summer seasons, 1961 and 1962, formed the material for the analysis. Activity was measured using the previously described index, computed from the ratio of trappability to abundance. Calculations were based on series of 10 samples, and in order to arrange the material more uniformly, several series of 20 samples that were taken, in the summer 1961, were each divided into 2 series of 10 samples. To grasp the postulated dependence, all the instances taken for analysis were divided into two groups, namely, these with abundance below 10 individuals per dipper, and those with abundance above 10 individuals per dipper. For both these groups the average values of the activity index were calculated. It turned out that *Ostracoda* as well as *Hydracarina* showed a conspicuously higher activity when their abundance was lower, and vice versa (Tab. VII).

The above stated negative correlation between abundance and activity can be also presented graphically (Fig. 15 and 16). For this purpose, when calculating the index of activity, instead of absolute numbers, relative values were used (per cent by which a given group was represented among all other groups captured by means of a trap or dipper). The obtained picture clearly confirmed the negative correlation between activity and abundance in *Ostracoda* (Fig. 15), and *Hydracarina* (Fig. 16).

Causes of this phenomenon, similarly to the case of negative correlation between trappability and abundance, probably lie in the fact that more active

Dependence between activity and abundance as exemplified by *Ostracoda* and *Hydracarina* occurring in the littoral of Mikołajskie Lake

Tab. VII

	Number of cases explored	Abundance (mean numbers per dipper)	Activity (numerical values of the index)	
			Mean	Limits
Ostracoda	16	< 10	0.7	0.1 – 2.5
	4	> 10	0.2	0.1 – 0.2
Hydracarina	13	< 10	2.2	0.6 – 3.9
	7	> 10	1.1	0.3 – 2.1

forms usually occur less abundantly than forms with high activity. The analysis based on water mite material can be an evidence for it. Two groups were distinguished from all the points present in Figure 16, namely, a group of average

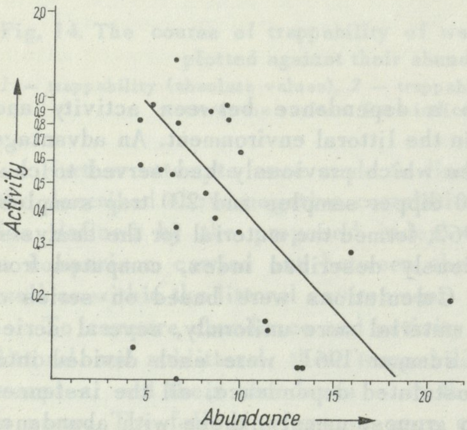

Fig. 15. Dependence between activity and abundance of *Ostracoda* in the littoral of Mikołajskie Lake (activity – numerical values of the index, abundance – mean numbers per dipper)

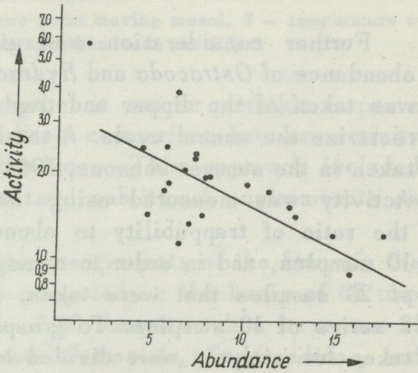

Fig. 16. Dependence between activity and abundance of *Hydracarina* in the littoral of Mikołajskie Lake (activity – numerical values of the index, abundance – mean numbers per dipper)

abundance below 10 individuals per dipper, and that with abundance above this number. Then percentage was calculated of the most active species (8 species with the highest activity, listed in Tab. III) for both the groups distinguished. It was found that a higher per cent of more active forms corresponded with lower abundance, as compared with cases of higher abundance. This holds for both the dipper and trap materials (dipper – 30.2% and 16.9%, traps – 68.3% and 46.8%, respectively). Therefore, it is evident that the changing proportion between species of high activity and those of lower activity is responsible for an increase in activity with the simultaneous decrease in abundance of *Hydracarina*. This is probably the case also in *Ostracoda*. One can assume that this kind of mutual replacement of abundance and activity, i.e., increasing activity with decreasing abundance, and vice versa, will decide upon the fact that a given group can maintain a constant degree of prevalence in an environment. Frequency of contacts, responsible for a number of ecological phenomena, such as competition or prey-predator relationship, can also remain unchanged.

IV. SPATIAL DISTRIBUTION

1. Character of distribution and of penetration in environment

Characterization of distribution and penetration (by defining the extent of clumping tendencies) of the groups of invertebrates was performed by comparing the empirical data with the Poisson distribution using Pearson's statistics χ^2. The materials collected from the littoral (littoral I) and the sublittoral environments in summer were analysed. As many as 220 dipper samples in the littoral, and 50 pump samples in the sublittoral served for calculations to estimate the character of distribution. Penetration characteristics for both these environments were based on trap samples: 200 samples in the littoral and 130 – in the sublittoral.

The results are shown in Table VIII. The "plus" symbols indicate these instances, when values of χ^2 showed a significant deviation from the Poisson distribution, therefore, when clumping tendencies occurred. In these cases, probability that the obtained values for χ^2 were hazardous was usually smaller than 0.001 (in 14 instances $P < 0.001$, in 2 – $P < 0.01$, and in 1 – $P < 0.05$). The "minus" symbols indicate all these situations, when deviation between the empirical data and the Poisson distribution was within the limits of hazard, which proves the random character of distribution or penetration. The obtained values which showed probability level higher than 0.3 (6 cases), $P \geq 0.2$ (1 case), $P > 0.1$ (2 cases), $P > 0.05$ (1 case), $P > 0.02$ (1 case), were considered as hazardous.

The most conspicuous clumping tendencies were observed in *Hydracarina* and *Ostracoda*, both in their distribution and in the character of penetration. In all the analysed instances, significant deviation from the Poisson distribution was found. *Trichoptera*, *Asellus aquaticus* and *Tendipedidae* were the oposite. In majority of cases, they were characterized by lack of clumping tendencies (the deviation from the Poisson distribution was statistically insignificant).

Clumping tendencies in *Hydracarina*, revealed by this analysis, associate with a well-known fact of their biology and behaviour. These usually predacious forms were seen to attact collectively, in a group, a prey (Wesenberg-Lund

Character of distribution and penetration in the environment by various groups of invertebrates

Tab. VIII

Groups of invertebrates	Littoral		Sublittoral	
	distribution	penetration	distribution	penetration
Hydracarina	+	+	+	+
Ostracoda	+	+	+	+
Stylaria lacustris	+	+		
Corixidae	+	+		–
Ephemeroptera	+	+	–	–
Trichoptera	+	–		–
Asellus aquaticus	+	–	–	–
Tendipedidae	+	–	–	–

Distribution or penetration: + clumped, – random.

1939, Kudrinskaja 1952). Perhaps, this is one of the reasons which can explain the obtained clumped distribution and penetration in water mites.

A similar situation can be also observed in *Ostracoda*, some predacious species of this group also show the habits of collective attack on prey (Liperovskaja 1948).

2. Vertical distribution (degree of connection with the bottom)

This problem has been analysed earlier (Pieczyński 1961b). When placing traps on the bottom and, at different levels, over the bottom, higher numbers of water mites were found in the bottom traps. At present, the problem of vertical distribution of the aquatic fauna was explored in detail; the analysis was based on a broader material, which included also other groups of invertebrates, collected in two littoral environments, and also in the sublittoral. The traps that were placed in water were oriented horizontally towards the bottom and suspended at different levels. In the littoral with the depth less than 50 cm, the traps were set at 2 levels: close to the bottom and at the surface of water. In the sublittoral with depth over 5 m, traps were set at 3 levels: close to the bottom, in free water and at the surface. This allowed to compare the distribution of organisms in the bottom and surface layers in the littoral and in sublittoral, besides these two, also in an intermediary layer. A total of 120 captures in littoral I, 60 – in littoral II, and 150 – in the sublittoral served as the material for analysis. To illustrate the pattern of vertical distribution of investigated groups, the per cent index was used. The total number of individuals of species or groups of species captured in all the layers in one of the environments formed a hundred per cent.

Vertical distribution of various groups of invertebrates in the littoral and sublittoral of Mikołajskie Lake (as based on trap samples)

Tab. IX

Groups of invertebrates	Littoral I			Littoral II			Sublittoral			
	N	*A*	*B*	*N*	*A*	*B*	*N*	*A*	B_1	*B*
		per cent			per cent			per cent		
Ostracoda	96	90	10	239	71	29	173	92	2	6
Hydracarina	1196	96	4	1748	81	19	1166	94	4	2
Tendipedidae	109	43	57	4	+	+	30	43	47	10
Corixidae	113	76	24	15	20	80	27	56	–	44
Stylaria lacustris	121	69	31	88	84	16	3	–	+	–
Ephemeroptera	48	88	12	26	46	54	4	+	–	+

N – total number of specimens captured, *A* – bottom layer, *B* – surface layer, B_1 – intermediate layer, + – occurs sporadicaly, – does not occur.

Considering the problem of vertical distribution of various groups of invertebrates, it can be stated that they are very strongly connected with the bottom of the lake (Tab. IX). However, considerable differences can be distinguished as far as various groups and environments are concerned. *Ostracoda* and *Hydracarina* showed the closest connection with the bottom, in the two littoral environments and in the sublittoral. From 71 to 96% of all the individuals of these two groups were found to occur in the bottom layer of water. A strong degree of connection with the bottom was also observed in *Stylaria lacustris*, and, to some extent, in *Ephemeroptera*. On the contrary, *Corixidae* and *Tendipedidae* (probably those living on plants) showed a strong predisposition to a smaller contact with the bottom. The above analysis pertains, of course, only to these forms which can swim. Attention should be drawn to the fact that, in the sublittoral, *Corixidae* were noted in the bottom layer as well as in the surface layer, with no representatives of this group found in the intermediary layer. An emphasis should be also laid over the fact that the degree of connection with the bottom in various groups was, as a rule, higher in littoral I than in littoral II. It can be explained by the fact that vascular, submerged or immerged, plants were by far more abundant in littoral II. This, in a way, might cause vanishing the boundary between the bottom and the water of the littoral, since some plants per se form a substrate for occurrence of animal organisms.

Consideration was also given to the vertical distribution of species of *Hydracarina*. Generally, they showed a very strong connection with the bottom (Tab. X). For instance, in littoral I, the degree of connection of water mites with the bottom exceeded 90%, *Mideopsis orbicularis* being an exception. In littoral II, the degree of connection with the bottom was, as a rule, considerably lower, especially in such species as *Hydrodroma despiciens* and *Limnesia maculata*. In the sublittoral, where the situation was similar to that in littoral I, Vertical distribution of various species of water mites in the littoral and sublittoral of Mikołajskie Lake (as based on trap samples)

Tab. X

Species	Littoral I			Littoral II			Sublittoral			
	N	A	B	N	A	B	N	A	B_1	B
		per cent			per cent			per cent		
Hydrodroma despiciens	221	96	4	87	66	34	68	88	9	3
Limnesia maculata	55	96	4	397	68	32	47	94	2	4
Hygrobates longipalpis	41	98	2	45	98	2	16	100	–	–
Unionicola crassipes	32	100	–	191	73	27	502	98	1	1
Piona coccinea	25	96	4	373	85	15	90	86	11	3
Forelia liliacea	188	98	2	72	87	13	115	100	–	–
Brachypoda versicolor	502	96	4	105	87	13	84	98	2	–
Mideopsis orbicularis	17	83	17	29	100	–	41	96	2	2

N — total number of specimens captured, *A* — bottom layer, *B* — surface layer, B_1 — intermediate layer.

some predispositions to occur in free water were observed in *Piona coccinea* and *Hydrodroma despiciens*.

In general, it can be stated that the analysed species of water mites, e.g., *Brachypoda versicolor* or *Hygrobates longipalpis*, occur mainly in the layer close to the bottom, in the littoral and sublittoral environments. Some predispositions to a lesser contact with the bottom can be observed in *Hydrodroma despiciens*, *Limnesia maculata*, and *Piona coccinea*.

3. Occurrence in littoral and sublittoral

As it was described earlier (while characterizing ecological and fauna features of the environments examined), differences in occurrence of water mites in the littoral and sublittoral were rather of a small rank. Although the number of species was smaller than in the littoral, the index of species similitude between these two environments reached rather high values. It was also reported that the same species were usually the most numerous components of the water mite fauna in both the environments.

As based on the trap material, the analysis was made of the dominance of *Hydracarina* in these two environments during the summer seasons. When analysing, an advantage was taken of the index of dominance similitude by Renkonen. Calculations were made by summing up the smaller percentage values of pairs of species being compared. If, for example, the species composition is as follows:

	Environment I	Environment II
species *A*	70%	40%
species *B*	20%	50%
species *C*	10%	10%,

summation is made of: 40% + 20% + 10%, thus obtaining the value of dominance similitude index = 70%.

The higher are the values of the index, the higher is the dominance similitude, and vice versa.

Results of the above analysis are presented in Table XI, and the list of dominant species is also given there.

Comparison of dominance pattern of *Hydracarina* in the littoral and sublittoral of Mikołajskie Lake (as based on trap samples)

Tab. XI

Dates		Dominant species: littoral	Dominant species: sublittoral	Index of dominance similitude (in per cent)
1961	10. VII	*Hydrodroma despiciens*	*Unionicola crassipes*	42
	19. VII	*Brachypoda versicolor*	*U. crassipes*	27
	10. VIII	*Hydrodroma despiciens*	*U. crassipes*	17
	21. VIII	*Limnesia maculata*	*U. crassipes*	41
	22. IX	*Lebertia* sp.	*Brachypoda versicolor*	29
1962	5. VI	*Limnesia maculata*	*Limnesia maculata*	51
	30. VI	*L. maculata*	*Hydrodroma despiciens*	28
	11. VII	*L. maculata*	*H. despiciens*	31
	21. VII	*Brachypoda versicolor*	*H. despiciens*	40
	2. VIII	*B. versicolor*	*Forelia liliacea*	25
	11. VIII	*B. versicolor*	*Unionicola crassipes*	28
	21. VIII	*B. versicolor*	*U. crassipes*	40

The similarity of domination of water mites in the littoral and sublittoral was of not a very high rank. The values of the index attained the average level of 33.3% with the limits 17–51%. The list of the dominant species of water mites also pointed to differences in their occurrence between these two environments (Tab. XI). Of a total number of 12 instances of dominance which were compared at the same dates, only in one case the same species was most numerous in both the environments. In the littoral, *Brachypoda versicolor* and *Limnesia maculata* were the commonest dominants; and in sublittoral – *Unionicola crassipes* and *Hydrodroma despiciens*.

In general, it can be said that the analysis of dominance among *Hydracarina* showed distinct differences in formation of groupings of water mites in the littoral and in the sublittoral.

4. Micro-differentiations in occurrence in littoral

The littoral environment, as opposed by the pelagial or profundal, forms a highly mosaic biotope with large number of ecological niches. Using differentiated methods of sampling, attempts were made to find out how does this mosaic character of the environment affect the occurrence of the invertebrate fauna, and especially that of water mites? Three spatial elements were distinguished in the littoral environment, namely, free water, plant vegetation and the bottom. To characterize the fauna occurring in the free water stratum, samples were taken by means of a plankton sampler of the Bernatowicz's type. The fauna occurring on plants was characterized by the plant samples taken according to the way described in the chapter on methods. Finally, characteristic of the bottom fauna was based on sanples taken by the tube bottom sampler of the Lastočkin-Ulomski's type. The results of these three methods were compared with those of the dipper; the latter characterized, in a way, the whole environment, slurring however the supposed differences among its spatial elements.

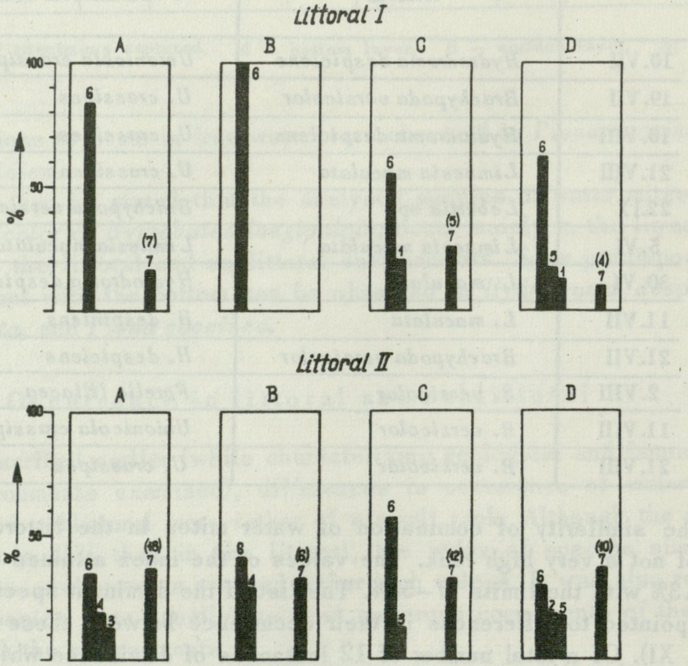

Fig. 17. Dominance structure of *Hydracarina* in various spatial elements of the littoral environment

A – total environment (10 dipper samples), *B* – free water (50 samples by a plankton sampler of the Bernatowicz's type), *C* – plant vegetation (50 samples), *D* – bottom (50 samples by a bottom tube sampler of the Lastočkin-Ulomski's type)

1 – *Lebertia* sp, *2* – *Hygrobates nigromaculatus*, *3* – *Limnesia undulata*, *4* – *Piona coccinea*, *5* – *Forelia liliacea*, *6* – *Brachypoda versicolor*, *7* – remaining species (their number in parentheses)

At the first stage of the analysis, comparison was made of the dominance structure of *Hydracarina* within various spatial elements of littoral I and II. In this respect, no higher differences were found; neither among various elements within one environment, nor between the environments compared (Fig. 17). *Brachypoda versicolor* was the dominant species in all the spatial elements of both the littoral environments. The preponderance of this species over the others is by far greater in littoral I than in II, and can be related with smaller number of species occurring in the former. Since, as it has been already found on the basis of a vast material, a decrease in the dominance level correlated with the increase in number of species (Pieczyński 1963).

Analysing micro-differentiations, attempts were made to distinguish some types of occurrence of various species of *Hydracarina* and also to learn about relationships among these species. This type of analysis was carried out for littoral II, by taking as many as 280 samples of plant vegetation, 300 planktonic and 300 benthic samples. For distinguishing the types of occurrence of water mites the per cents were compared, as related to all the remaining species in various elements of the environment. There were 3 groups distinguished, differing in the type of occurrence in the littoral environment (Fig. 18). Species of the first group showed some predisposition to occur at the bottom. To this group of species belonged: *Lebertia* sp., *Forelia liliacea*, *Brachypoda versicolor*, *Mideopsis orbicularis*, and *Arrenurus globator*. The species of the second group were characterized by predisposition to occur in the free-water layer of the littoral. This group was represented by: *Hydrodroma despiciens* and *Piona coccinea*. Finally, the third group of species, similar to the last one, was characterized by predisposition to occur on plant vegetation, with rather numerous occurrence in the free-water layer. Two species belonged to this group, namely, *Limnesia maculata* and *L. undulata*.

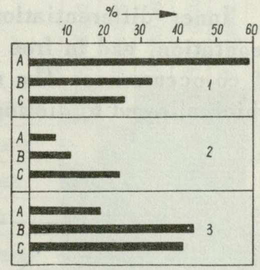

Fig. 18. Types of occurrence of various species of water mites in different spatial elements of the littoral environment
A — bottom, *B* — plant vegetation, *C* — free water
1 — *Lebertia* sp., *Forelia liliacea*, *Brachypoda versicolor*, *Mideopsis orbicularis*, *Arrenurus globator*; 2 — *Hydrodroma despiciens*, *Piona coccinea*; 3 — *Limnesia maculata*, *L. undulata*

In order to learn about links connecting various species in the grouping, an analysis was carried out of the inner differentiation in the water mite grouping, using an index of co-occurrence. It allowed, through estimation of probability of co-occurrence of species in samples, to estimate the extent of overlapping the ecological niches (Tarwid 1960). The index of co-occurrence of any two species, say A and B, is calculated by dividing the number of real encounters (n_{AB}) in samples by the number of theoretical encounters (N_p), according to the formula:

$$S_{AB} = \frac{n_{AB}}{N_p},$$

The theoretical values of encounters are obtained from the formula:

$$N_p = \frac{n_A \cdot n_B}{N},$$

where: n_A – number of samples with species A, n_B – number of samples with species B, N – total number of samples.

When the value of the index equals to 1 (i.e., when the number of real encounters = the number of theoretical encounters), the lack of dependence between these two species is inferred. When the value is > 1 (i.e., when the number of real encounters is higher than that of theoretical ones) one infers about tendency to co-occurrence (coincidence). On the other hand, when the value of the index is < 1, a non-overlapping tendency (diversity) is expected. When calculating, some restrictions in applying the index, as reported by Kajak (1957), and Tarwid (1960), were taken into account.

Inner differentiations in the water mite grouping, at the bottom, on plant vegetation, and in free water, were tested with the use of the above given index of co-occurrence. The results were illustrated using diagrams by Czekanowski, which allowed to distinguish groups of species with overlapping niches.

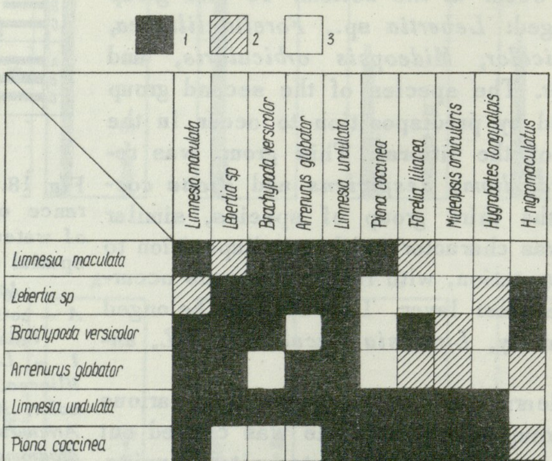

Fig. 19. A diagram illustrating the inner differentiation of the water mite grouping at the littoral bottom of Mikołajskie Lake

1 – index of co-occurrence > 1, *2* – index of co-occurrence = 1, *3* – index of co-occurrence < 1

Two groups of species were distinguished in the water mite grouping at the bottom, connected by *Limnesia undulata*, a "joint" species (Fig. 19). To the first group, besides *Limnesia undulata*, belonged such species as *Limnesia maculata*, *Lebertia* sp., *Brachypoda versicolor*, and *Arrenurus globator*. The second group was represented by: *Piona coccinea*, *Forelia liliacea*, *Mideopsis orbicularis*, and *Hygrobates longipalpis*.

Among the plant vegetation, also two groups were found, though consisting of less numerous species. *Limnesia undulata* also played the role of a "joint" species between these groups (Fig. 20). To the first group belonged: *Hygrobates longipalpis* and *Hydrodroma despiciens*; to the second – *Piona coccinea* and *Brachypoda versicolor*.

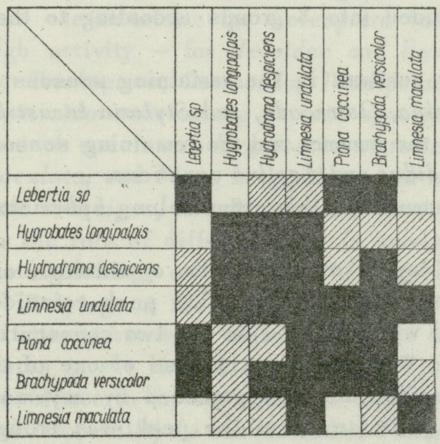

Fig. 20. A diagram illustrating the inner differentiation of the water mite grouping on plant vegetation in the littoral of Mikołajskie Lake
For indications see Fig. 19.

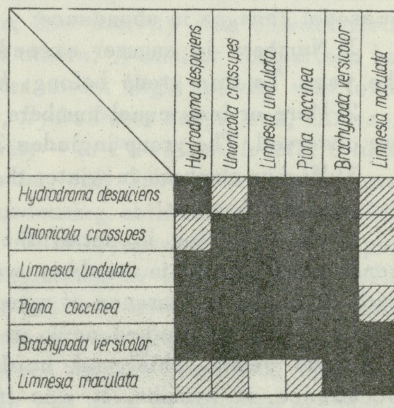

Fig. 21. A diagram illustrating the inner differentiation of the water mite grouping in free water of the littoral of Mikołajskie Lake
For indications see Fig. 19.

In the free-water layer of the littoral, one group was observed of 5 species with convergent niches, namely: *Hydrodroma despiciens*, *Unionicola crassipes*, *Limnesia undulata*, *Piona coccinea*, and *Brachypoda versicolor* (Fig. 21).

Summarizing, it can be stated that in the spatial elements of the littoral environment, species of water mites are connected in various structural systems. *Limnesia undulata* is a species of special importance, playing the role of a "joint" species between various groups, at the bottom and among plant vegetation.

CONCLUSIONS AND DISCUSSION

Chosen problems have been analysed as pertaining to abundance, activity, and the character of spatial distribution of water mites and other invertebrates in the littoral and sublittoral of Mikołajskie Lake. Diverse methods of sampling were used, among them – the special traps (Pieczyński 1961b).

A total of 42 species of water mites were found to occur in Mikołajskie Lake, with 31 and 37 species occurring in the two littoral environments, 25 – in the sublittoral, and 2 – in the upper profundal.

The species composition was similar in both the littoral and sublittoral environments, and the same species were usually most abundant in these environments.

Analysing seasonal changes in numbers and trappability of invertebrates in the littoral and sublittoral, it was found that a rapid autumnal decrease in trappability, which lasted through winter and spring, did not corresponded with changes in abundance, but precisely coincided with lowering of water temperature below 14°C. The invertebrates were divided into 3 groups according to their seasonal changes in abundance:

1) Numbers in summer exceed by far numbers in the remaining seasons of the year. To this group belong; *Hydracarina*, *Ostracoda*, and *Stylaria lacustris*.

2) More or less equal numbers in both the summer and the remaining seasons are observed. The group includes *Tendipedidae* and *Asellus aquaticus*.

3) Higher numbers in winter than in summer. To this group belong *Ephemeroptera* and *Trichoptera*.

When analysing in detail the annual cycle of water mite occurrence, one conspicuous peak in numbers was observed in August. This peak coincided with the mass appearance of nymphs, and was observed for the two consecutive years. The less marked peak in numbers occurred also in June of one of the examined years. This peak neither coincided nor was preceded by any mass occurrence of nymphs. It was inferred, therefore, that the peak was brought about by immigration of water mites from the other environments. The nymphs, besides the summer season, were sporadically found in the littoral throughout the year. Correspondingly to lowering numbers of individuals, a decrease in numbers of species was also observed in the autumn-winter-spring period. In the summer seasons, 7 to 14 species (11 on the average) were noted in series of samples collected from the littoral, while in the remaining seasons, 2 to 6 species (4 on the average) were found. Analysing in detail the occurrence of species of water mites in the littoral, 2 groups were distinguished. The first group, more numerous, included species that occurred in the littoral exclusively in the summer seasons (among other species: *Hydrodroma despiciens*, *Limnesia maculata*, and *Piona conglobata* belonged to this group). The second group was represented by species that occurred in the littoral throughout the whole year (among other species *Brachypoda versicolor* belonged to this group). *B. versicolor* was the species mainly dominating in the littoral in the summer seasons, while *Lebertia* sp. was dominant in the period of icing on the lake. Little is known on the annual cycle of water mites in lakes. Some data on this problem can be found in papers by Viets (1930), Berg (1938), Nocentini (1960), and Hopkins (1962).

The 24-hour activity cycle has been described, and it was found that *Hydracarina* and *Ostracoda* showed higher activity by daytime, and *Ephemeroptera* – at night. When comparing 24-hour activity of various groups of invertebrates and of species of water mites in the littoral and sublittoral, the differences in activity between the day and night were found to be generally smaller in the latter environment. One can relate this fact with smaller changes in intensity of insolation of the bottom stratum in the sublittoral.

To compare the intensity of penetration of various groups of invertebrates in the environments, the so-called "ecological" activity has been estimated. The index of such activity was obtained by dividing the values of trappability (obtained from the traps) by the values of abundance (obtained from the dipper or ancther apparatus estimating abundance). It was found that a very high activity was characteristic for *Coleoptera* (adults), *Corixidae*, and *Argulus foliaceus*, high activity – for *Heleidae* and *Hydracarina*; low activity was characteristic for *Trichoptera*, *Ostracoda*, *Tendipedidae*, and others. A similar comparison has been also made among various species of water mites. High activity was found in such species as *Hygrobates nigromaculatus*, *Hydrodroma despiciens*, *Limnesia maculata*, and *Piona longipalpis*, and low activity – in *Piona conglobata*, *Unionicola crassipes*, and *Brachypoda versicolor*. So far, only Schwoerbel has reported on the role of differentiation in moving and swimming abilities of water mites, distinguishing, on the basis of morphological criteria, several locomotor types.

Relying on the abundance and activity (expressed by trappability) criteria, an attempt has been made to estimate the importance of various groups of invertebrates in the littoral environment. Point estimates were given of the degree of prevalence in the environment. The index computed was the product of abundance and trappability (a conventional, 5-degree scale was used to estimate abundance and trappability). It was found that in summer seasons the highest degree of prevalence in the littoral environment was that observed in *Hydracarina*. Both, very high abundance and very high trappability resulted in the highest possible value of the index. Next to *Hydracarina* were *Ostracoda* (showing very high abundance and high trappability) and then, *Ephemeroptera* and *Stylaria lacustris*. In the other seasons, as the opposite to summer, the degree of prevalence in the environment was much lower (more than twicely) which resulted, first of all, from decreasing trappability caused by lowering the water temperature. The values of the index stayed unchanged in these groups of invertebrates in which the degree of prevalence in the environment was mainly based on their abundance, their trappability being low (e.g., *Tendipedidae* and *Trichoptera*). In the discussed period, *Hydracarina*, *Ostracoda*, *Ephemeroptera*, and *Tendipedidae* showed the highest degree of prevalence in the environment.

When analysing the dependence between activity and abundance, the negative correlation was found of the following type: the lower abundance, the higher activity, and vice versa. Such negative dependence was found in *Ostracoda* and *Hydracarina*. One can assume that due to the mutual compensation of abundance and activity, the degree of prevalence in the environment can be maintained at a constant level by the given group of animals.

When analysing the chosen elements of spatial distribution, it was found that *Hydracarina* and *Ostracoda*, among other groups, showed the highest tendency to clumping, in their distribution as well as in the character of penetration. The well-known, behavioral habit, depending on the group attact on prey, can be one of the causes of revealed tendency to clumped distribution (Wesenberg-Lund 1939, Kudrinskaja 1952, Liperovskaja 1948).

When analysing the vertical distribution in the littoral and sublittoral, a very strong degree of connection with the bottom was found in the majority of groups, especially in *Ostracoda* and *Hydracarina*, which occurred mainly in the water layer close to the bottom. The most clearly marked predisposition to a lesser contact with the bottom was that observed in *Corixidae* and *Tendipedidae* (probably those living on plants). The strongest degree of connection with the bottom was found in most of *Hydracarina* species (e.g., *Brachypoda versicolor* or *Hygrobates longipalpis*); and the weakest connection with the bottom was observed in *Piona coccinea* and *Hydrodroma despiciens*.

When analysing the dominance pattern of *Hydracarina* in the littoral and sublittoral, major differences were found to occur between these two environments, indicating the spatial diversity of the groupings occurring in them. In the littoral, *Brachypoda versicolor* and *Limnesia maculata* were the most common dominants in the summer seasons; and in the sublittoral – *Unionicola crassipes* and *Hydrodroma despiciens*.

Finally, the last part of the work was devoted to micro-differentiations in occurrence of the fauna in the littoral environment. Three spatial elements of the littoral environment have been distinguished, namely, free water, plant vegetation and the bottom. No differentiation was observed between these elements in the dominance pattern of *Hydracarina*. The precise analysis, however, showed that various species of *Hydracarina* occurred in different proportions in these elements of environment. Again, three groups of species were distinguished of the diverse type of occurrence in the littoral environment. The species of the first group showed some predisposition to occur more abundantly at the bottom. To this group belonged: *Lebertia* sp., *Forelia liliacea*, *Brachypoda versicolor*, *Mideopsis orbicularis*, and *Arrenurus globator*. The species of the second group were characterized by predisposition to occur in the free water layer. To these belonged: *Hydrodroma despiciens* and *Piona coccinea*, which is in accordance with the previous observations on their degree of connection with the bottom. Finally, the species of the third group were characterized by predisposition to occur on plant vegetation, besides the common occurrence in the free water. To these belonged: *Limnesia maculata* and *L. undulata*.

Still further, analysis has been made of the inner differentiations of the water mite grouping (using the index of co-occurrence) in order to define the links connecting various species. It was found that, in the spatial elements of the littoral environment, species of *Hydracarina* were connected in various structural systems. Of an utmost importance in the grouping is *Limnesia undulata* playing the role of a "joint" species between various groups of species with overlapping niches at the bottom and among plants.

On the basis of the results obtained in this work as well as on some data found in the literature, one can evaluate the role of water mites in the lake ecosystem. Their significance seems to be unrightly neglected; on the contrary, one can assume that their role is serious one, and negative from the aspect of fishery. The following premises support this view:

1. The findings of the present paper indicate that water mites are very numerous in the fauna both in the littoral and sublittoral environments. They can also attain a considerable abundance in the relatively shallow zones of the central part of a lake. In the littoral, a continuity of their occurrence through the annual cycle is characteristic, although their numbers, besides the summer, are not especially high. Water mites tend to occur mainly at the bottom and in the layer of water close to the bottom, although they can often occur abundantly in other spatial elements of the aquatic environment, such as plants or free water.

2. The second, a very important characteristic of water mites that was found during this study, is their considerable "ecological" activity, which brings about a very intense penetration of the environment. The exceedingly high trappability of water mites, as compared with very high abundance, decides, at least for the summer seasons, upon a high degree of prevalence of water mites in the environment. As the point estimates have shown, this degree is the highest for water mites, of all the invertebrate groups explored.

3. The third feature of water mites deciding of their importance in the ecosystem, is their predaciousness. One can assume that this property, as connected with their high abundance and activity, contributes to a considerable reduction of the invertebrate fauna. The fact that water mites can play an important role in the ecosystem as predators has been shown by Laird (1947) in his experimental study on natural enemies of mosquitoes. He reported on the serious role of water mites in reduction of *Anopheles* and *Culex* (mainly in their primary developmental stages by preying on their eggs and larvae). He gave them the same rank in predaciousnnes with such admitted predators as dragon fly larvae. He also observed a regularity which supported his experimental results that in the reservoirs with mass occurrence of *Hydracarina*, numbers of mosquitoes were rather low. Kudrinskaja (1952), concluding in her study on feeding habits of water mites, reported that they can contribute to reduction of fish, indirectly – through feeding on *Cladocera* and *Copepoda*, or directly – through feeding on roe. This problem, of course, needs further investigation.

4. The fourth property, which has a decisive impact on the role of water mites in the ecosystem, is parasitism of their larval stages. It appears that this phenomenon, occurring frequently, also contributes to the reduction of numbers of the invertebrate fauna. Their parasitism, for instance, can affect decreasingly the fecundity of host species. Crisp (1959) reported on a decreasing fecundity of *Corixidae* caused by parasitism of water mites.

5. Finally, the last property which should be emphasized in estimating the role of water mites in the ecosystem, is the lack of their natural enemies and their high resistance to depletive action of environmental factors. So far, these problems were but little investigated. From the laboratory observations

by Cloudsley-Thompson (1947), it follows that neither invertebrate predators nor fish – even when starved – feed on water mites. This author ascribes an aposematic function to the vivid coloration of water mites. Large, subcutaneous glands, typical for water mites, probably secrete a substance of repelling taste. This probably would account for the observed facts that water mites, when caught by predators, are either released or ejected.

High resistance to environmental factors is a well-accepted feature of water mites, although the data on this problem are also phragmentary. For instance, Lindeman (1940) in his experimental study on the resistance of various organisms to the oxygen starving conditions has found that water mites of the *Limnesia* genus had survived for as long as 90 days in anoxic conditions. A considerable resistance of water mites to desiccation, to high temperature and anoxic conditions was proved experimentally by Hopkins (1962).

From the above data, one can suppose that the reduction in numbers of water mites concerns to a lesser extent the adults, but occurs mainly in earlier stages of their development. Such a suggestion appealed to the author earlier, during his study on numbers and fecundity of several water mite species (Pieczyński 1961a). Efford (1963) has pointed to a considerable reduction of water mites in their larval stages parasiting on insects living in air. The reduction was caused by deaths of these insects far away from the reservoir.

In general, one can say that water mites do play an important role in the ecosystem, the role being negative from the aspect of fishery, since they deplete the stream of energy flowing from the invertebrate fauna to fish.

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ANALIZA LICZEBNOŚCI, AKTYWNOŚCI I ROZMIESZCZENIA WODOPÓJEK (*HYDRACARINA*) ORAZ NIEKTÓRYCH INNYCH BEZKRĘGOWCÓW W LITORALU I SUBLITORALU JEZIORNYM

Streszczenie

Analizowano wybrane zagadnienia dotyczące ekologii wodopójek i niektórych innych bezkręgowców eutroficznego Jeziora Mikołajskiego. Posługiwano się zróżnicowaną metodyką pobierania prób, między innymi specjalnymi pułapkami (Pieczyński 1961b). Ogółem pobrano 2644 prób różnych typów, uzyskując materiał 14130 osobników wodopójek, reprezentowanych przez 42 gatunki. Zarówno w litoralu jak i w sublitoralu skład gatunkowy jest zbliżony, a do najliczniej notowanych należą w zasadzie te same gatunki (tab. I).

Analizując sezonowe zmiany liczebności i łowności różnych bezkręgowców (fig. 1–9) stwierdzono między innymi, że *Hydracarina* osiągają największą liczebność i liczbę gatunków w okresie letnim (fig. 9). Większość gatunków wodopójek występuje w litoralu jedynie w okresie letnim (fig. 10). Na przykładzie wszystkich badanych grup bezkręgowców stwierdzono, że łowność – poza okresami letnimi – kształtuje się na bardzo niskim poziomie. Wiąże się to z obniżeniem się temperatury wody poniżej 14°C. Powyższą zgodność przebiegu temperatur i łowności obserwowano zarówno w litoralu, jak i sublitoralu (fig. 1–8).

Analizując aktywność w cyklu dobowym stwierdzono, że w litoralu *Hydracarina* i *Ostracoda* mają wyższą aktywność w dzień, natomiast *Ephemeroptera* – w nocy (fig. 12 i 13). Z porównania aktywności dobowej różnych grup bezkręgowców i gatunków wodopójek w litoralu i sublitoralu wynikło, że w tym ostatnim środowisku różnice aktywności w dzień i w nocy są na ogół znacznie mniejsze (tab. II). Fakt ten można wiązać, jak się wydaje, z mniej ostro wyrażonymi zmianami przede wszystkim intensywności naświetlenia w przydennej strefie sublitoralu.

Dla porównania intensywności, z jaką poszczególne grupy bezkręgowców penetrują środowisko, oceniano tzw. aktywność „ekologiczną". Wskaźnik tak pojmowanej aktywności wylicza się ze stosunku łowności (dane z pułapek) do liczebności (dane z czerpaka, bądź innego aparatu szacującego liczebność). Stwierdzono, że bardzo wysoką aktywnością odznaczają się między innymi *Coleoptera* (imagines) i *Corixidae*, a wysoką – *Hydracarina* (tab. III). Podobne porównanie aktywności przeprowadzono też dla poszczególnych gatunków wodopójek (tab. III).

W oparciu o kryteria liczebności i aktywności (wyrażonej w postaci łowności) dokonano próby oceny roli, jaką w środowisku litoralnym odgrywają poszczególne bezkręgowce. Przeprowadzono ocenę punktową stopnia opanowania środowiska, który to wskaźnik jest iloczynem liczebności i łowności (ocenianych według szacunkowej, 5-stopniowej skali). Stwierdzono, że w okresie letnim najwyższy stopień opanowania środowiska, na który składa się bardzo wysoka liczebność i bardzo wysoka łowność (wskaźnik osiąga maksymalną wartość liczbową), wykazują *Hydracarina*. Drugie miejsce pod względem wartości wskaźnika zajmują *Ostracoda* (tab. IV). W przeciwieństwie do okresu letniego, w innych okresach obserwuje się ogólnie znacznie niższy (przeszło dwukrotnie) stopień opanowania środowiska, na co wpływa przede wszystkim znaczne obniżenie się łowności na skutek spadku temperatury wody.

Analizując zależność między aktywnością i liczebnością stwierdzono, że ma ona charakter odwrotnie proporcjonalny, tzn. przy niższej liczebności obserwuje się wyższą aktywność i vice versa. Stwierdzono to na przykładzie *Ostracoda* i *Hydracarina* (tab. VII, fig. 15 i 16). Można przypuszczać, że dzięki wzajemnemu, kompensującemu zastępowaniu się liczebności i aktywności, stopień opanowania środowiska przez daną grupę utrzymuje się na stałym poziomie.

Analizując wybrane elementy rozmieszczenia przestrzennego stwierdzono między innymi, że *Hydracarina* i *Ostracoda* wykazują najlepiej wyrażoną tendencję do skupiskowości (tab. VIII). Większość grup bezkręgowców, zarówno w litoralu jak i sublitoralu, wykazuje bardzo silny stopień związania z dnem, a zwłaszcza *Ostracoda* i *Hydracarina*, występujące głównie w naddennej warstwie wody (tab. IX i X). Pod względem przebiegu dominacji *Hydracarina* w litoralu i sublitoralu, stwierdzono znaczne różnice między tymi środowiskami, wskazujące na odrębność zasiedlających je zgrupowań (tab. XI).

Ostatnią część pracy poświęcono analizie mikrozróżnicowań w zasiedleniu przez faunę wodopójek środowiska litoralnego. Wyróżniono trzy elementy przestrzenne środowiska: toń wodną, roślinność i dno. Poszczególne gatunki *Hydracarina* w różny sposób zasiedlają powyższe elementy środowiska. Wyróżniono na tym tle trzy grupy gatunków, o predyspozycji do liczniejszego występowania na dnie, w toni wodnej i na roślinności (fig. 18). W badanych elementach środowiska litoralnego wykształcają się różne układy strukturalne gatunków o zbieżnych niszach (fig. 19, 20 i 21).

Na podstawie uzyskanych w tej pracy wyników oraz pewnych danych z literatury przedyskutowano problem roli wodopójek w ekosystemie jeziora. Opierając się o takie elementy, jak: 1) wysoka liczebność, 2) znaczna aktywność „ekologiczna" i wysoki stopień opanowania środowiska, 3) drapieżny tryb życia, 4) pasożytnictwo larw i 5) brak specyficznych wrogów i duża odporność na działanie czynników środowiskowych, wysunięto tezę, że wodopójki w ekosystemie odgrywają znaczną rolę, negatywną z rybackiego punktu widzenia, uszczuplając strumień energii płynący od fauny bezkręgowej w kierunku ryb.

AUTHOR'S ADDRESS:
Dr. Eligiusz Pieczyński
Institute of Ecology,
Warszawa, ul. Nowy
Świat 72.