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THE LITTORAL AND PROFUNDAL BENTHIC NEMATODES OF LAKES WITH DIFFERENT TROPHY

ABSTRACT: The species diversity and numbers of nematodes in particular zones of three lakes with different trophy were analysed. In an oligotrophic lake (Char) the highest number of profundal nematodes and high species diversity in both profundal and littoral zones were found, in the contrary to data for b-mesotrophic (Żarnowieckie) and eutrophic (Mikołajskie) lakes.

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1. INTRODUCTION

The authors of the majority of papers devoted to the comparison of fauna inhabiting the littoral and profundal of lakes deal mainly with macrobenthos. The data presented in numerous papers (e.g., Lundbeck 1926, 1936, Rzóśka 1935, Berg 1938, Deevey 1941, Eggleton 1952, Ricker 1952, Rawson 1953, Macan 1955, Ökland 1964, Guziur, Lossow and Widuto 1975, Kajak and Dusoge 1975) show, that number of species and biomass of fauna are the highest in the littoral of eutrophic lakes. It was found that at greater depths the macrobenthos is more scarce, there are less species within particular groups of invertebrates, also the whole groups disappear. For an example, Kajak and Dusoge (1975) studying the benthic macrofauna of Mikołajskie Lake found 17 taxonomic groups at the depth of 4 m, 11 at 8 m, 7 at 16 m and only 3 at 24 m. The decrease of the number of *Chironomidae* larvae, dominating in macrobenthos, was marked even better. At 4 m the mentioned authors found 27 species, at 8 m — 10 and only 3 at 24 m. However, it should be underlined, that the intensity of reduction of the number of

macrobenthic groups and species with the increase of depth seems to depend on the trophic type of a lake, there are some indications that this phenomenon is not that strong in oligotrophic as in eutrophic lakes. Rzó ska (1935) studying the benthic fauna of eutrophic Kierskie Lake and oligotrophic Lake Wigry found among the others in the littoral of the former one 23 species of *Chironomidae*, and only 4 at the depth of 20 m. In the oligotrophic Lake Wigry at equivalent depths there were 21 and 10 species, respectively.

The data of B o r n e r (1921) show, that number of nematode species decreased with an increase of depth in mesotrophic St. Mortiz Lake. There were 25 species in the littoral of this lake, 19 in sublittoral and only 8 in profundal, with 2 species only in the deepest parts (22–26 m). Š č e r b a k o v (1955) found a rapid decrease of the number of benthic nematodes with the increase of depth in mesotrophic Glubokoe Lake. A similar situation was found also by S a c h a r o v a (1965, 1970) in eutrophic reservoir Učinskoe.

Significant differences in the numbers and species composition of nematodes in the littoral and profundal were found in the Mikołajskie Lake (P r e j s 1970). In such situation an analysis was undertaken of the species composition and numbers of groupings of benthic nematodes in particular zones of three lakes with different trophic type.

2. AREA AND METHODS

The studies were carried out in three lakes with different trophic type during summers of 1972–1974.

Mikołajskie Lake. It is an eutrophic, holomictic lake of a surface area 460 ha, maximum depth 27.8 m and mean depth 11.0 m. The littoral occupies 87.9 ha, i.e., 19% of the lake area.

The sediment samples were collected from this lake from two transects in July 1974:

Transect 1 – from 0.5, 1.5, 2, 4, 8, 12, 15, 17, 20 and 25 m depth.

Transect 2 – from 0.3, 1, 1.5, 2, 4, 8, 10, 15, 17, 20 and 22 m depth.

Żarnowieckie Lake. It is a b-mesotrophic lake, located in the River Piaśnica drainage basin (Kaszuby District), surface area 1,431 ha, maximum depth 19.4 m, mean depth 8.4 m. The neighbourhood of the sea, and thus frequent strong winds result in good mixing of the lake; the oxygen content in near bottom waters in summer was above 3 mg/l.

The samples were collected in the littoral and profundal from three transects¹. On each of them 1.5, 3, 6, 10 and 16 m depth was sampled.

Char Lake (74° N, Cornwallis Island, Canada)². It is an oligotrophic lake with the area of 52.6 ha, maximum depth 27.5 m and mean depth 10.2 m (R i g l e r 1972). Three bottom zones can be distinguished in this lake:

a. Near-shore rocky zone ("littoral"), 0–4 m deep, occupying 15.5 ha, covered by various size rocks filled among them with silt.

b. Moss zone, 4 to 10–15 m deep (depending on site), occupying 13.6 ha (mainly *Calliergon richardsoni* (Mitten), *Drepanocladus brevifolius* (Lindb.) and *Bryum* sp.).

¹The meiobenthos was collected from Żarnowieckie Lake few times a year, in April, June, August and October. In this paper only the August 1974 data dealing with nematodes were considered.

²This subject was studied as a part of Canadian Committee of the International Biological Programme dealing with production processes and energy flow in an arctic lake (Char Lake Project).

c. Profundal zone below the moss zone, occupying 24.5 ha, with silty bottom.

The lake is covered by ice, about 2.2 m thick, during the nearly whole year. Usually, it is free of ice for 3 weeks starting mid-August. However, during an unusual cold summer of 1972, only 16% of the lake area was free of ice (Welch 1973).

The majority of samples was collected in July 1972. Forty sites were sampled within the profundal zone at depths 12 to 26 m, 20 in the moss zone at depths 4 to 12 m, and 15 in the rocky zone at depths 0.5 to 3.5 m.

The profundal samples of sediments were collected with the help of a tubular sampler (Kajak, Kacprzak and Polkowski 1965) with sampling area of 10 or 20 cm². The upper 4–5 cm of sediments were analysed. The littoral and sublittoral samples were collected with the help of a sampler of Morduchaj-Boltovskoj (1955) with sampling area of 19.6 cm², or with an organic glass tube (area of 3.8, 10 or 20 cm²) pushed into the bottom and stopped, as the former sampler did not work in hard bottom.

In the majority of cases 5 sediment samples were collected from each site while using a 10 cm² sampler, 3 with 20 cm² one, and 10 while using a 3.8 cm² tube. Additional 3 samples of near bottom water for oxygen measurements were collected in Mikołajskie Lake.

Samples were preserved with 4% formalin. Sediments were sieved through 45 and 75 μ net; and all nematodes were isolated within studied fractions from glass chambers under the stereoscopic microscope. In the case of very numerous nematodes, the samples were subsampled as 1/2, 1/5 or 1/10 part of a whole. Nematodes were placed in glycerin solution, left to evaporate, and if possible their species determined under the microscope.

3. RESULTS

Mikołajskie Lake. The highest number of nematodes (538,000 individuals per m²) was found in the shallow littoral at the depth of 0.5 m. A rapid decrease of this number occurred in sublittoral, it rose slightly in shallow profundal, and dropped again at greater depths down to 25 m (Fig. 1).

A gradual decrease of the number of species was observed also, with 52 species in shallow littoral, and 12 in profundal. 27 species occurred in the sublittoral zone (Table I). The dominance structure was different in particular zones. Among the littoral species no dominant one could be distinguished. Three species from family *Chromadoridae* formed jointly 40% of littoral nematodes. Relatively numerous were also *Tobrilus gracilis*, *Prodesmodora circulata*, *Ironus tenuicaudatus*, *Tripyla cornuta*, *Dorylaimus stagnalis* and *Mesodorylaimus filiformis* (5–15%).

Ironus tenuicaudatus dominated in sublittoral (above 30% of the total number of nematodes). The second one was *Chromadorita leuckarti*. *Tobrilus gracilis*, *Monhystera paludicola* and *Dorylaimus stagnalis* did not exceed 15% of the total number of nematodes. The remaining species formed a small per cent.

Tobrilus gracilis dominated in profundal amounting to over 40% of all nematodes. *Tobrilus medius* and *Monhystera paludicola* were also relatively numerous (Table I).

Żarnowieckie Lake. The highest number of nematodes occurred in the littoral, similarly as in previous lake (Fig. 1). There was a rapid decrease of the nematode number in the sublittoral zone, then it decreased down to 16 m, where it was the lowest at all three transects.

Among the 16 species of nematodes found on the most shallow sites only 6 occurred in deep profundal (Table II). *Tobrilus gracilis* dominated in littoral, next in numbers were

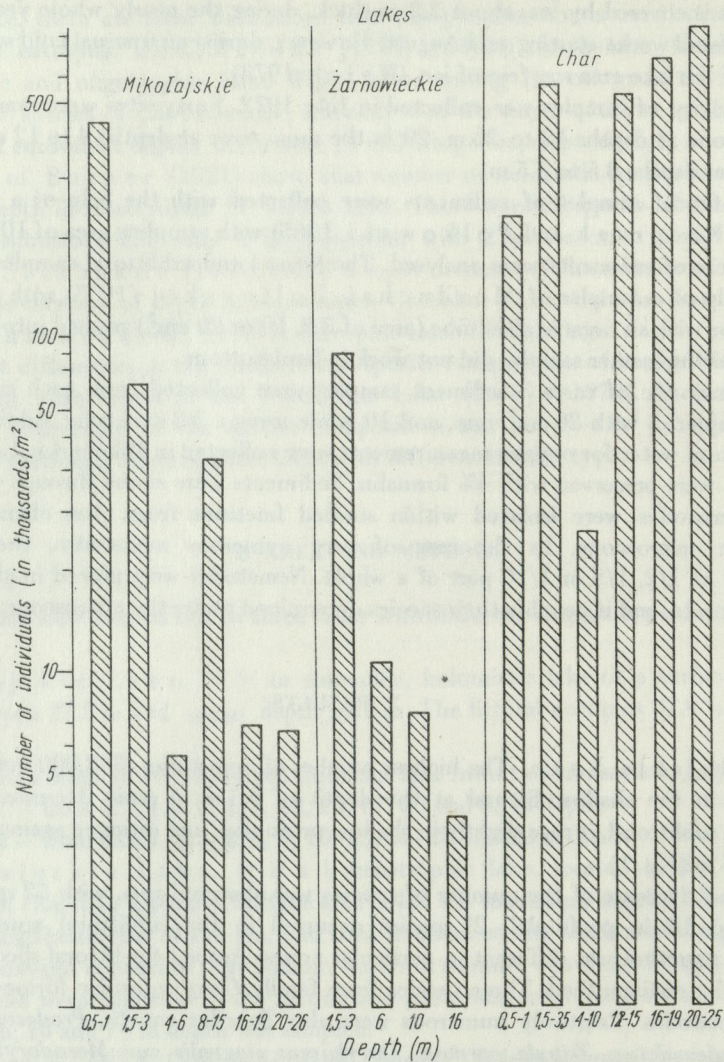


Fig. 1. Changes of the benthic nematode numbers with the increase of depth in three investigated lakes

Ethmolaimus pratensis, *Tripyla cornuta* and *Dorylaimus stagnalis*. The remaining species were not significant. A similar situation was in the sublittoral. Two species were clearly dominating in the shallow profundal: *Tobrilus gracilis* and *Chromadorita leuckarti*; *Monhystera dispar* was a subdominant there. The latter species dominated in the deepest places, also *Tobrilus gracilis* and *Plectus granulatus* were relatively numerous there.

Char Lake. Changes of the nematode number in relation to depth of this oligotrophic lake had a completely different pattern than ones in two lakes previously described. The highest number was found in the deepest part (19–26 m), slightly lower in near shore sediments, and the lowest (over 30 times lower) in sediments of the moss zone at the depth of 4–10 m (Fig. 1).

Table 1. The percentage contribution of particular species of benthic nematodes in various zones of the Mikołajskie Lake (data from the whole material)

+ < 1%, ++ < 5%, +++ 5–15%, ++++ 16–30%, +++++ > 30%

Species	Littoral	Sublittoral	Profundal	
	depth (m)			
	0.5–3	4–5	10–15	17–26
1	2	3	4	5
<i>Tobrilus gracilis</i> (Bastian)	+++	+++	++++	++++
<i>T. medius</i> (G. Schneider)	++	+	+++	+++
<i>Monhystera paludicola</i> de Man	++	+++	+++	+++
<i>Chromadorita leuckarti</i> (de Man)	++++	++++	++	++
<i>Monhystera vulgaris</i> de Man	+	+	++	++
<i>M. dispar</i> Bastian	++	++	+	+
<i>Ethmolaimus pratensis</i> de Man	+	+	++	+
<i>Dorylaimus flavomaculatus</i> v. Linstov	+	+	+	+
<i>Diplogaster rivalis</i> (Leydig)	+	+	+	+
<i>Anonchus mirabilis</i> (Hofmänner et Menzel)	+	+	+	+
<i>Prismatolaimus intermedius</i> (Bütschli)	+	+	+	
<i>Aphanolaimus attentus</i> de Man	+		+	
<i>Ironus tenuicaudatus</i> de Man	+++	++++		
<i>Prochromadorella bioculata</i> (Schultze)	+++	+		
<i>Punctodora ratzeburgensis</i> (v. Linstov)	+++	+		
<i>Prochromadorella viridis</i> (v. Linstov)	+	+		
<i>Prodesmodora circulata</i> (Micoletzky)	+++	++		
<i>Dorylaimus stagnalis</i> Dujardin	+++	+++		
<i>Ironus ignavus</i> Bastian	++	++		
<i>Tripyla cornuta</i> Skwarra	+++	++		
<i>T. affinis</i> de Man	++	++		
<i>Dorylaimus helveticus</i> Steiner	+	++		
<i>Plectus granulatus</i> Bastian	++	+		
<i>Alaimus primitivus</i> de Man	+	+		
<i>Dorylaimus montanus</i> Stefański	+	+		
<i>Tobrilus stefanskii</i> (Micoletzky)	+	+		
<i>T. pellucidus</i> (Bastian)	+	+		
<i>T. longus</i> (Leidy)	+++			
<i>Mesodorylaimus filiformis</i> (Bastian)	+++			
<i>Tobrilus grandipapillatus</i> (Brakenhoff)	++			
<i>Mesodorylaimus proximus</i> (Thorne et Swanger)	++			
<i>Chronogaster typicus</i> (de Man)	++			
<i>Cryptonchus tristis</i> (Ditlevsen)	++			
<i>Plectus cirratus</i> Bastian	++			
<i>P. rhizophilus</i> de Man	++			
<i>Mesodorylaimus agilis</i> (de Man)	+			
<i>Eudorylaimus</i> sp.	+			
<i>Nygolaimus</i> sp.	+			
<i>Actinolaimus</i> sp.	+			
<i>Achromadora terricola</i> (de Man)	+			
<i>Mononchus truncatus</i> Bastian	+			
<i>Tripyla monohystera</i> de Man	+			
<i>Teratocephalus demani</i> Stefański	+			

Table I (contd)

1	2	3	4	5
<i>Rhabditis</i> sp.	+			
<i>Heterodera</i> sp. ♂	+			
<i>Aphelenchoides parietinus</i> (Bastian)	+			
<i>Chrysonemoides limigenus</i> Siddiqi	+			
<i>Hirschmanniella gracilis</i> (de Man)	+			
<i>Dorylaimoides ditlevseni</i> Micoletzky	+			
<i>Plectus parvus</i> Bastian	+			
<i>P. longicaudatus</i> Bütschli	+			
<i>Panagrolaimus</i> sp.	+			
Total number of species	52	27	12	10

Table II. The percentage contribution of particular species of benthic nematodes in various zones of the Żarnowieckie Lake (data from the whole material)
 + < 1%, ++ < 5%, +++ 5–15%, ++++ 16–30%, +++++ > 30%

Species	Littoral	Sublittoral	Profundal	
	depth (m)			
	1.5–3	6	10	16
<i>Tobrilus gracilis</i>	+++++	+++++	+++++	++++
<i>Ethmolaimus pratensis</i>	++++	++++	+	+
<i>Monhystera dispar</i>	+	+	++++	+++++
<i>Chromadorita leuckarti</i>	+	+++	+++++	++
<i>Plectus granulosus</i>	++	+	+	++++
<i>Monhystera paludicola</i>	+	+	+	+
<i>Tripyla cornuta</i>	++++	+++	+	
<i>Dorylaimus</i> sp.	+	++	+	
<i>Aphanolaimus attentus</i>	++	+	+	
<i>Dorylaimus stagnalis</i>	+++	++++	+	
<i>Ironus tenuicaudatus</i>	+	+	+	
<i>Tobrilus</i> sp.	++	++	+	
<i>Plectus rhisophilus</i>	++	+		
<i>Diplogaster rivalis</i>	+	+		
<i>Tobrilus longus</i>	++			
<i>Achromadora terricola</i>	++			
Total number of species	16	14	12	6

There were no significant differences in the species composition in both near shore and profundal zones (Table III). Out of 21 species occurring in the near shore zone, up to 17 were found in profundal. The only 4 species missing in profundal were sporadic in the near shore zone. Only 9 species were present in the moss zone, with comparatively low number of nematodes there. This considerable decrease of the number of nematodes and their species in the moss zone is a phenomenon difficult to explain. Possibly this is related with worsening of the environmental conditions under the moss cover (lower oxygen content in winter, substances released by mosses, etc.).

Table III. The percentage contribution of particular species of benthic nematodes in various zones of the Char Lake (Canada) (July 1972)
 + < 1%, ++ < 5%, +++ 5-15%, ++++ 16-30%, +++++ > 30%

Species	Near shore rocky zone	Moss zone	Profundal		
	depth (m)				
	0.5-1	1.5-3	4-10	11-15	16-26
<i>Chromadorita leuckarti</i>	++++	++++	+++	++++	++++
<i>Ethmolaimus pratensis</i>	+++	++++	+++	++++	++++
<i>Monhystera filiformis</i> Bastian	++	++++	++++	+++	++++
<i>M. vulgaris</i>	++	+++	+++	+++	+++
<i>Microlaimus arcticus</i> Mulvey	++	++	+	++++	+++
<i>Prismatolaimus intermedius</i>	++	+++	+	++	++
<i>Plectus parvus</i>	++	++	+	+	+
<i>Monhystera macramphix</i> Filipjev	++	++	+	+	++
<i>M. similis</i> Bütschli	+	+	+	++	++
<i>Mononchus niddensis</i> Skwarra	+++	++		++	++
<i>Eudorylaimus carteri</i> (Bastian)	++++	++		++	+
<i>Eudorylaimus</i> sp.	++++	+		++	+
<i>Cylindrolaimus melancholicus</i> de Man	++	++		+	+
<i>Tobrilus</i> sp.	+	+		+	+
<i>Hofmaenneria</i> sp.	++	+		+	+
<i>Tobrilus aequiseta</i> (W. Schneider)	+	+		+	+
<i>Tripyla monohystera</i>	+	+		+	
<i>Achromadora terricola</i>	+	+			
<i>Plectus</i> sp.	+	+			
<i>Theristus</i> sp.	+	+			
<i>Aphelenchoides</i> sp.	+				
Total number of species	21	20	9	17	16

No species exceeded 30% of the total number of nematodes on sites 0.5 to 1 m deep. The most numerous were nematodes of the genera *Eudorylaimus* and *Chromadorita*. *Ethmolaimus pratensis* and *Mononchus niddensis* were quite numerous. Other species were scarce.

Chromadorita leuckarti, *Ethmolaimus pratensis* and *Monhystera filiformis* were quite numerous at depths 1.5 to 3 m, achieving up to 30% of the total number of nematodes. A similar situation was found in shallow profundal.

Monhystera filiformis was a decisive dominant in the moss zone; other species did not exceed 15% of the total number.

In the deepest areas *Ethmolaimus pratensis* dominated, next in the dominance structure were *Chromadorita leuckarti* and *Monhystera filiformis*.

It was found while comparing the numbers and species composition of nematodes inhabiting various bottom zones of lakes which differ among the others in their trophic type, that the smallest difference between the littoral and profundal zones existed in Char Lake. The most numerous grouping of nematodes with greatest variety of species was found in the profundal of this oligotrophic lake, in the contrary to eutrophic Mikołajskie Lake and to mesotrophic Żarnowieckie Lake.

The greatest number of species was found in the littoral of Mikołajskie Lake, especially in areas covered by vegetation. High numbers of the littoral groupings of nematodes did not result

from the abundance of a dominant species, but from the contribution of few species occurring in similar numbers. It is worth to notice that few species of the same genus occurred in this grouping (e.g., of genera *Tobrilus*, *Tripyla*, *Dorylaimus*, *Monhystera*, etc.); in Char Lake only *Monhystera* was represented by 4 species, other genera — usually by one species.

Table IV. Values of the Shannon species diversity index (\bar{H}) in the littoral and profundal of lakes with different trophy

Lake	Littoral		Profundal	
	shallow	deep	shallow	deep
Mikołajskie (eutrophic)	2.3	2.4	1.4	0.3
Żarnowieckie (mesotrophic)	—	2.8	2.6	1.7
Char (oligotrophic)	2.7	2.4	2.8	2.6

A Shannon index of species diversity³ was calculated for the littoral and profundal groupings of nematodes (not for sublittoral) in the studied lakes. It was found that in all cases this index was high for littoral groupings (Table IV). The lowest species diversity ($\bar{H} = 0.3$) was found in the deep profundal of Mikołajskie Lake. Its value decreased also with the increase of depth in Żarnowieckie Lake, although it was higher there than in Mikołajskie Lake. The high and only slightly variable species diversity was found in both near shore and profundal zones of Char Lake. Also, a similar number of nematodes occurred in these zones. The highest number of nematodes in Mikołajskie and Żarnowieckie lakes was found in the littoral, it decreased with the increase of depth.

4. DISCUSSION

Usually lower number of nematodes and their species in the profundal of eutrophic lakes as compared with the littoral can certainly be related with worsening of the oxygen conditions at greater depths. The oxygen content in the near bottom waters of Mikołajskie Lake varied in profundal from 9 mg O₂/l at 8 m depth to 0.3 mg O₂/l at 22 m. However, in oligotrophic Char Lake the oxygen content near the bottom at depths below 24 m was 13–14 mg O₂/l during the summer months, and during the whole year it did not drop below 5 mg O₂/l (Schindler et al. 1974).

The dependence of the distribution of nematodes in a lake on the oxygen content in the near bottom waters was already noticed by Schneider (1922), who explained in this way greater abundance of profundal fauna in alpine lakes as compared with eutrophic East-Holstnian lakes.

$${}^3\bar{H} = -\sum \frac{n_i}{N} \ln \frac{n_i}{N}; \quad n_i - \text{number of consequent species, } N - \text{total number.}$$

As far as the differences in the number of species in the littoral and profundal are concerned, data of the same author show that in various types of lakes the ratio of "deep living" species to the number of species in the whole lake is as follows: for oligotrophic Neuenburger Lake (Switzerland) this ratio is 25 : 32, thus number of "deep living" species equals 72% of all species, analogous ratio for oligotrophic Lunzer Lake (Austria) is 20 : 33, thus "deep living" species amounted to 61%. In the case of eutrophic Plöner Lake (Federal Republic of Germany) this ratio was 12 : 36, thus "deep living" species amounted to only 35% (Schneider 1922).

I wish to thank Dr. Frank Rigler for making possible my participation in the Char Lake Project. I am grateful to Dr. Harold Welch and his co-workers for their help in the field work on Char Lake.

5. SUMMARY

The composition and numbers of the benthic nematode groupings were analysed in particular zones of lakes with different trophic types. The studies were carried out during the summer time in the littoral and profundal of eutrophic Mikołajskie Lake, b-mesotrophic Żarnowieckie Lake, and of oligotrophic Char Lake (Canada, Cornwallis Island, 74° N).

The highest number of nematode species (52) was found in the littoral of Mikołajskie Lake, especially in parts overgrown by vegetation. In the littoral of Żarnowieckie and Char lakes there were 16 and 17 species of nematodes, respectively (Tables I–III).

The highest numbers of nematodes (about 700,000 individuals/m²) was found in the oligotrophic Char Lake (Fig. 1). The most numerous and most differentiated qualitatively grouping of nematodes in this lake occurred in profundal, in the contrary to two above mentioned lakes. A gradual decrease of the number of nematode individuals and species with the increasing depth was found in lakes Mikołajskie and Żarnowieckie (Fig. 1, Table IV).

6. POLISH SUMMARY (STRESZCZENIE)

Dokonano analizy składu i liczebności zgrupowań nicieni bentosowych w poszczególnych strefach jezior różniących się typem troficznym. Badania prowadzono w okresie letnim w litoralu i profundalu eutroficznego Jeziora Mikołajskiego, b-mezotroficznego Jeziora Żarnowieckiego i oligotroficznego jeziora Char (Kanada, wyspa Cornwallis, 74° N).

Stwierdzono, że najbogatszym pod względem liczby gatunków nicieni (52) jest litoral Jeziora Mikołajskiego, a zwłaszcza jego partie porośnięte roślinnością. W litoralu jezior Żarnowieckiego i Char stwierdzono odpowiednio 16 i 17 gatunków nicieni (tab. I–III).

Najwyższą liczebność nicieni (ok. 700 000 osobników/m²) notowano w oligotroficznym jeziorze Char (fig. 1). W zbiorniku tym, odwrotnie niż w dwu pozostałych, najliczniejsze i jakościowo bardzo zróżnicowane zgrupowanie nicieni występowało w profundalu. W jeziorze Mikołajskim i Żarnowieckim stwierdzono stopniowe zmniejszanie się liczebności i zróżnicowania gatunkowego nicieni wraz ze wzrostem głębokości (fig. 1, tab. IV).

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