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THE NEMATODES OF THE ROOT REGION OF AQUATIC MACROPHYTES, WITH SPECIAL CONSIDERATION OF NEMATODE GROUPINGS PENETRATING THE TISSUES OF ROOTS AND RHIZOMES*

ABSTRACT: A specific grouping of nematodes associated with the root region of macrophytes was found in the lake littoral. Nematodes penetrating the tissues of underground parts of pondweeds may contribute to their dying. There were much higher numbers of nematodes belonging to genera *Hirschmanniella*, *Chrysonemoides*, *Dorylaimoides*, *Dorylaimus* and *Mesodorylaimus* in the decomposing fragments of rhizomes than in their fresh fragments.

Contents

1. INTRODUCTION

The lake littoral forms differentiated habitats for nematodes. These habitats differ not only in their spatial structure (bottom sediments, surfaces of macrophytes, tissues of macrophytes, their root region), but also in their abiotic and biotic conditions.

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The nematodes of the littoral of Mikołajskie Lake were studied in various habitats by different authors: in periphyton (Pieczyńska 1961, 1964, Pieczyńska and Spodniewska 1963), in eulittoral (Wasilewska 1973), in bottom sediments (Prejs 1970), in rhizosphere and in tissues of roots and rhizomes of *Potamogeton lucens* L. and *Potamogeton perfoliatus* L. (Prejs 1973, Prejs and Wiktorzak 1976). The above studies have shown that nematodes are a numerous group of invertebrates often dominating the meiofauna of these habitats. Nematodes form specific groupings which differ by, among the others, species composition and dominance structure.

The analysis of numbers of benthic nematodes in habitats overgrown by macrophytes have shown that these numbers were much higher than in sediments lacking the growth of macrophytes (sand or mud) (Prejs 1976).

Much higher numbers of nematodes in bottom sediments of littoral overgrown by macrophytes as compared with places without them were also found by Schiemer, Löffler and Dollfuss (1969) in lake Neusiedler (Austria) and by Witkowski and Gutowska (1970) in lake Jeziorak. Unfortunately there is still no comparable data on nematodes of the root region of aquatic macrophytes. This paper aimed at the studies of numbers and dominance structure of groupings of benthic littoral nematodes with special consideration of nematodes of the root region of aquatic macrophytes. The nematodes occurring within the tissues of roots and rhizomes of chosen species of macrophytes were analysed in detail.

2. AREA AND METHODS

The studies were performed in the littoral of Mikołajskie Lake. This is an eutrophic, holomictic lake with an area of 460 ha, maximum depth 27.8 m and mean depth 11.0 m. The littoral occupies 87.8 ha, i.e., 19% of the lake area. The submerged macrophytes overgrow 55% of the littoral area.

Samples in the littoral of Mikołajskie Lake were collected from spring till late autumn in monthly intervals from 9 sampling sites at the depths of 0.3 to 2.5 m in 1972–1973 (Table I).

Samples of bottom sediments with fragments of underground parts of macrophytes were collected from the root region of macrophytes for the estimation of nematode species composition and numbers there. The control samples were collected in the neighbourhood of investigated macrophytes or in places without any. Apart from that 5–10 samples (10–15 g of fresh weight each) of the underground parts of macrophytes were collected at each sampling site. The underground parts of *Potamogeton perfoliatus* and *P. lucens* were the main object of studies, *Nuphar luteum* (L.) and *Sagittaria sagittifolia* L. were studied less extensively. The underground parts of macrophytes were collected by gentle pulling out the roots and rhizomes together with mud. Each sample was immediately rinsed of sediments in order to separate the root region fauna. Roots and rhizomes were weighed, then the nematodes were isolated from them by the incubation method of Young (1954) during 4–5 days. As not all nematodes were getting out during the incubation, the rhizomes were cut and after some time placed in 4% formalin. Number of nematodes was reffered to 1 g of fresh weight of plant or to 1 cm^3 (it was assumed that 1 g of fresh weight equals 1 cm^3 of tissue).

Samples of bottom sediments in the zone overgrown by macrophytes and in places lacking them were collected with the help of a plastic tube of 3.8 cm^2 area. The surface 4–5 cm layer was analysed.

Table I. Characteristics of sampling sites in the littoral of Mikołajskie Lake

Site	Species of macrophytes	Substrate	Depth (m)	Waves
I–IV	*Potamogeton perfoliatus* *P. lucens* *P. pectinatus* L. *P. compressus* L. *P. crispus* L. *Myriophyllum spicatum* L.	mud with sand or sandy	0.5–0.7	strong
V	*P. perfoliatus* *P. lucens* *P. pectinatus* *Chara* sp. *Sagittaria sagittifolia*	mud	0.3–0.5	weak
VI–VIII	*P. perfoliatus* *Ceratophyllum demersum* L. *Myriophyllum spicatum* *Elodea canadensis* Rich. *Chara* sp. *Nitella* sp.	mud with sand	1.5–2.5	weak
IX	*Nuphar luteum* *Elodea canadensis* *Stratiotes aloides* L.	mud with gravel	0.5–0.7	weak

Samples were preserved with 4% formalin. Sediments were sieved through nylon sieves with the mesh size 45 μ and 75 μ. The studied fractions were checked in glass chambers under the binocular microscope to isolate all found nematodes. These were placed in glycerin solution, left to evaporate, and their species were determined if possible.

The distribution of nematodes in particular parts of plants was studied by partitioning the rhizomes from roots or stems and by incubating the samples separately. The same was applied when determining the distribution of nematodes in decomposing and fresh rhizomes.

The contribution of underground parts of macrophytes in the total plant biomass was determined. In the case of *P. perfoliatus* and *P. lucens* 10 plants of each species (whole rhizomes with an apical bud and the aboveground parts) were carefully pulled out from each of the sampling sites. The biomass of aboveground parts and of roots and rhizomes was determined separately. The biomass of *Sagittaria sagittifolia* was determined on the basis of 7 plants gathered on one site, 3 *Nuphar luteum* plants were used.

3. RESULTS

3.1. Composition, numbers and dominance structure of nematodes associated with underground parts of macrophytes

All studied plants are perennials wintering as rhizomes. In the case of *P. perfoliatus* the aboveground parts occur from April till November. The contribution of underground parts in

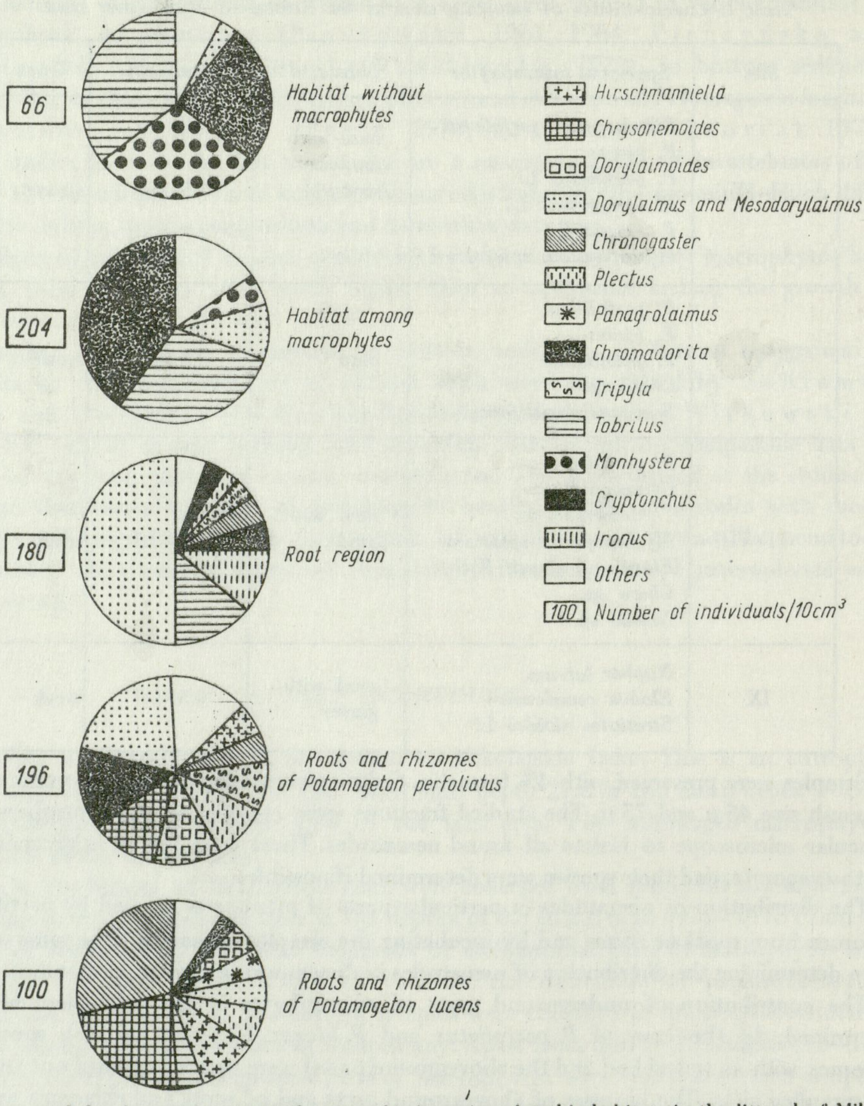

Fig. 1. Numbers and dominance structure of nematodes in various benthic habitats in the littoral of Mikołajskie Lake (data for July 1973)

the total plant biomass at the height of the vegetation season is on the average 39%. This species forms dense stands with 100–400 stems on 1 m^2 at the depth of 0.4–0.7 m, at the depth of 1.0–1.5 m there is not more than 100 of them per 1 m^2, and at the depth 1.5–3.0 m occur single plants only (T. Ozimek, A. Prejs and K. Prejs 1976).

The aboveground parts of *P. lucens* occur from April till November. The contribution of underground parts in the total plant biomass at the height of vegetation season is on the average 49%. This species occurs less frequently in the studied lake than the previous one and is not found below 1.5 m. Its greatest density – 45 aboveground shoots per 1 m^2 occurs at the depth of 0.5 m (T. Ozimek, A. Prejs and K. Prejs 1976).

Table II. Species composition of benthic nematodes of the zone of submerged macrophytes in the littoral of Mikołajskie Lake (data for the whole material)

Family	Species
Hoplolaimidae	*Hirschmanniella gracilis* (de Man)
Rhabditidae	*Rhabditis* sp.
Panagrolaimidae	*Panagrolaimus* sp.
Teratocephalidae	*Teratocephalus demani* Stefański
	Chronogaster typicus (de Man)
	Plectus cirratus Bastian
	P. parietinus Bastian
	P. rhizophilus de Man
Plectidae	*P. parvus* Bastian
	P. granulosus Bastian
	P. longicaudatus Bütschli
	Plectus sp.
	Anonchus mirabilis (Hofmänner et Menzel)
Camacolaimidae	*Aphanolaimus attentus* de Man
	Monhystera vulgaris de Man
Monhysteridae	*M. paludicola* de Man
	M. dispar Bastian
	Prismatolaimus intermedius (Bütschli)
	Chromadorita leuckarti (de Man)
Chromadoridae	*Prochromadorella viridis* (v. Linstov)
	P. bioculata (Schultze)
	Punctodora ratzeburgensis (v. Linstov)
	Prodesmodora circulata (Micoletzky)
Cyatholaimidae	*Achromadora terricola* (de Man)
	Ethmolaimus pratensis de Man
	Tripyla cornuta Skwarra
	T. affinis de Man
	T. monohystera de Man
	Tobrilus medius (G. Schneider)
	T. gracilis (Bastian)
Tripylidae	*T. husmanni* (Altherr)
	T. stefanskii (Micoletzky)
	T. grandipapillatus (Brakenhoff)
	T. longus (Leidy)
	T. pellucidus (Bastian)
	T. steineri (Micoletzky)
	Ironus ignavus Bastian
Ironidae	*I. tenuicaudatus* de Man
	Cryptonchus tristis (Ditlevsen)

Table II (contd)

Family	Species
Dorylaimidae	*Mesodorylaimus filiformis* (Bastian) *M. proximus* (Thorne et Swanger) *M. agilis* (de Man) *Dorylaimus helveticus* Steiner *D. montanus* Stefański *D. holsaticus* Schneider *D. stagnalis* Dujardin *D. flavomaculatus* v. Linstov *Eudorylaimus* sp. *Actinolaimus* sp.
Nygolaimidae	*Nygolaimus* sp.
Leptonchidae	*Dorylaimoides ditlevseni* Micoletzky
*Chrysonematidae**	*Chrysonemoides limigenus* Siddiqi
Mononchidae	*Mononchus truncatus* Bastian

*New family acc. to Siddiqi (1969).

The contribution of roots and rhizomes in the total biomass of *Sagittaria sagittifolia* is about 25%, and for *Nuphar luteum* – about 55%.

The species composition, numbers and dominance structure of nematode fauna were analysed within the root region, in tissues of roots and rhizomes of pondweeds, in sediments among the plants and in habitats lacking the macrophytes (treated as control ones).

The comparison of nematode groupings in the distinguished habitats was made on the basis of a large series of samples (15–20 in each repetition), collected at one time in July 1973 (Fig. 1).

Totally 53 species of nematodes belonging to 16 families (taxonomy acc. to Goodey 1963) were found (Table II).

The lowest number of nematodes was found in bottom sediments lacking the growth of macrophytes (Fig. 1).

The dominance structure was different in particular habitats. In the sediments without the macrophyte growth nematodes of three genera dominated: *Tobrilus*, *Monhystera* and *Chromadorita*; in sediments among the macrophytes the most numerous were *Chromadorita leuckarti* and *Tobrilus* spp., also numerous were the nematodes of the genera *Dorylaimus* and *Mesodorylaimus*, which are distinct dominants in the root region. In the latter habitat a significant contribution was also made by *Tobrilus* spp., *Ironus* spp. and *Chromadorita leuckarti*, apart from *Dorylaimidae*. The nematodes belonging to genera *Chronogaster*, *Tripyla*, *Plectus* and *Cryptonchus* were numerous in the root region but scarce in sediments among the plants or in places without them. Nearly all species occurring in the root region penetrated roots and rhizomes of pondweeds, but dominance structure within their tissues was different than in sediments. The participation of *Dorylaimus* and *Mesodorylaimus* was slightly lower (20% in tissues of *P. perfoliatus* and only 6% – in *P. lucens*), but contribution of species scarce or sporadic in other habitats, i.e., of *Chrysonemoides limigenus*, *Hirschmanniella gracilis*, *Dorylaimoides ditlevseni*, *Chronogaster typicus* and *Panagrolaimus* sp. was higher within the tissues. Only *Chromadorita leuckarti* was numerous in all habitats.

A similar dominance structure of benthic nematodes living closer or farther from the root system of plants was observed also on some other sites of studied lake (Prejs 1973, Prejs and Wiktorzak 1976). All these data confirm the existence of a specific grouping of nematodes inhabiting the root region and the tissues of underground parts of aquatic macrophytes. This grouping differs from other ones not only by its numbers but also by the species composition and the dominance structure.

3.2. The nematodes penetrating the tissues of roots and rhizomes

3.2.1. General characteristics

The numbers and dominance structure of nematode grouping penetrating the tissues of roots and rhizomes of *P. perfoliatus* and *P. lucens* were analysed. These studies were carried out at several sampling sites in the littoral of Mikołajskie Lake during the two consequent years. Tables III and IV contain the average data for period June-August, when samples were collected from all sampling sites.

Numbers of nematodes penetrating the underground parts of *P. perfoliatus* were generally higher than in the case of *P. lucens* (Tables III, IV). This was found on sites I–IV which were similar in many ways, and also on site V, different from former ones (Table I).

The species composition of nematode grouping inhabiting the tissues of roots and rhizomes of both species of pondweeds did not differ significantly.

Hirschmanniella gracilis occurred irregularly, amounting to 1–33% of all individuals. The highest number of this species (94 individuals per 10 g of fresh weight) was found in tissue of *P. perfoliatus* on site II in August (Fig. 2).

Table III. The dominance structure (in per cent) and numbers of nematodes in roots and rhizomes of *P. perfoliatus* during the two consequent years of study in the littoral of Mikołajskie Lake (average for period June-August)

Genus	1972			1973		
	site					
	I–IV	V	VI–VIII	I–IV	V	VI–VIII
Hirschmanniella	32.7	1.6	3.5	8.4	3.6	2.3
Chrysonemoides	8.2	10.4	16.0	6.3	7.3	4.4
Dorylaimoides	0.1	31.1	0.7	0.7	34.4	6.3
Dorylaimus and *Mesodorylaimus*	15.0	43.3	13.0	21.2	22.4	12.5
Chronogaster	8.0	1.0	12.4	6.4	4.4	10.0
Plectus	7.0	0.7	2.0	10.7	0.2	10.0
Panagrolaimus	7.3		2.6	6.0		8.7
Chromadorita	10.1		4.1	16.0	0.1	10.4
Tripyla	1.0	1.5	25.5	6.1	4.2	18.7
Tobrilus	2.6	0.7	2.3	4.5	1.7	2.2
Others	8.0	9.7	18.0	13.7	21.6	14.5
Average number (individuals in 10 g of fresh weight) and 95% confidence limit	180 ± 80	185 ± 68	118 ± 35	122 ± 53	413 ± 195	39 ± 10

Table IV. The dominance structure (in per cent) and numbers of nematodes in roots and rhizomes of *P. lucens* during the two consequent years of study in the littoral of Mikołajskie Lake (average for period June-August)

Genus	1972		1973	
	site			
	I–IV	V	I–IV	V
Hirschmanniella	5.6	4.0	4.8	1.0
Chrysonemoides	12.6	10.8	8.3	4.0
Dorylaimoides	0.6	50.7	0.9	23.0
Dorylaimus and *Mesodorylaimus*	5.6	18.7	20.1	3.0
Chronogaster	12.1	5.5	8.0	31.6
Plectus	20.6	0.9	6.0	21.5
Panagrolaimus	20.0		2.0	
Chromadorita	6.8		33.0	1.2
Tripyla	3.3	1.8	3.2	1.6
Tobrilus	0.6		2.4	
Others	12.2	7.6	11.2	13.0
Average number (individuals in 10 g of fresh weight) and 95% confidence limit	54 ± 19	106 ± 22	62 ± 18	70 ± 23

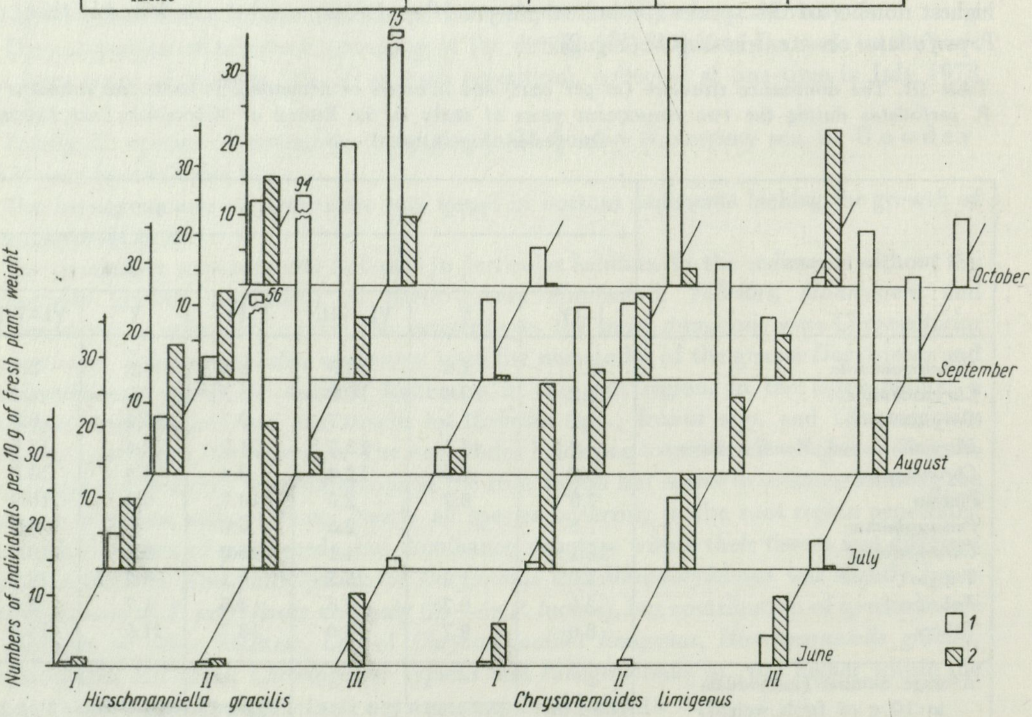

Fig. 2. The occurrence of *Hirschmanniella gracilis* and *Chrysonemoides limigenus* in roots and rhizomes of *P. perfoliatus* (*1*) and *P. lucens* (*2*) at chosen sampling sites (I–III) (1973 data)

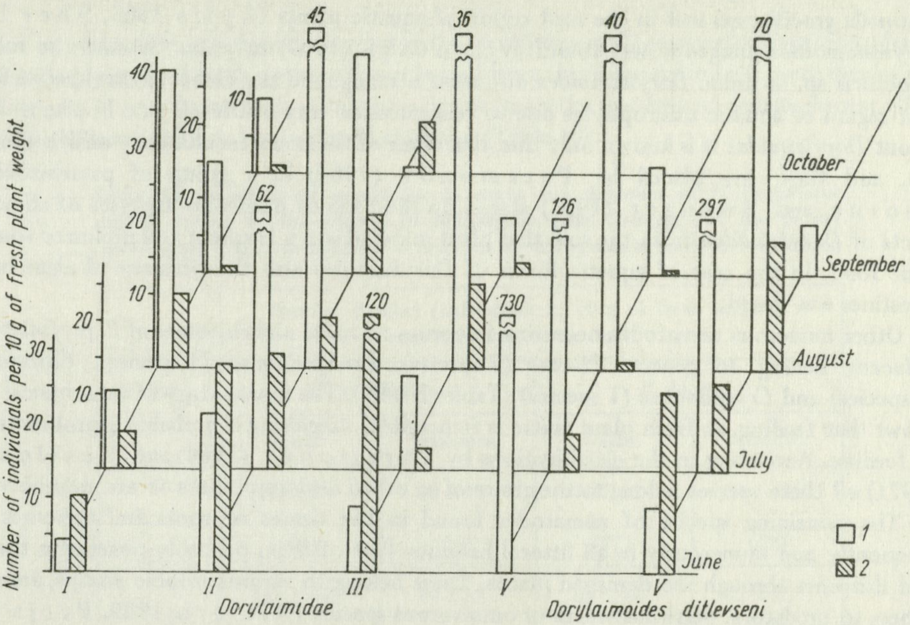

Fig. 3. The occurrence of *Dorylaimidae* and *Dorylaimoides ditlevseni* in roots and rhizomes of *P. perfoliatus* (*1*) and *P. lucens* (*2*) at chosen sampling sites (I–III, V) (1973 data)

Chrysonemoides limigenus occurred in numbers attaining 4 to 16% of the total number of nematodes (Tables III, IV). The maximum number of this species (62 individuals per 10 g of fresh weight) was found in roots and rhizomes of *P. perfoliatus* on site IV in August.

The contribution of *Dorylaimoides ditlevseni* varied at particular sites from 0.1 to 50% of all nematodes. This species was the most important at site V, where it accounted for from 34% (*P. perfoliatus*) to 50% (*P. lucens*) of the total number. At other sites the contribution of this species was low (Tables III, IV). The maximum number of *Dorylaimoides ditlevseni* (297 individuals in 10 g of fresh weight) was found in the roots and rhizomes of *P. perfoliatus* in August (Fig. 3).

The species belonging to genera *Dorylaimus* and *Mesodorylaimus* amounted to 12–43% in the underground parts of *P. perfoliatus*, and in the case of *P. lucens* – to 3–20% of the total number of nematodes. The maximum number of *Dorylaimidae* (126 individuals in 10 g of fresh weight) was found in tissues of underground parts of *P. perfoliatus* in July at site II (Fig. 3).

The numbers of particular species of nematodes did not change regularly with time (Figs. 2, 3). The fact that studied macrophytes are perennials, and thus the nematodes can penetrate their tissues all year round (especially the rhizomes) and move to other places during the plant growth, makes it very difficult to find any regularities of the number dynamics of nematodes inhabiting the underground parts of plants. However, it could be noticed that in the majority of cases the maximum numbers of these nematodes was higher in July and August than in the other periods of studies.

There is not much information on the biology of discussed species of nematodes. All of them have a hollow stylet permitting to pierce the tissue and suck out the cell content.

Nematodes of the genus *Hirschmanniella* are known as rice parasites (S h e r 1968); *Hirschmanniella gracilis* was met in the root region of aquatic plants (L y l i s 1965, S h e r 1968). *Chrysonemoides limigenus* was found by S i d d i q i (1969) in water around the roots of *Eleocharis* sp. in India. *Dorylaimoides ditlevseni* is recognised as a characteristic species for the root region of aquatic macrophytes due to semi-parasitic way of life (C a l o l i c h i n 1972). About *Dorylaimidae* it is known only this, that some of them can facultatively utilize the plant sap, and they are placed by P a r a m o n o v (1964) in a group of pararhizobionts. T h o r n e and S w a n g e r (1957) stated on the basis of numerous analyses of alimentary tracts of *Dorylaimidae* from the soil, that plant material was a frequent and preferred source of their food. In the case of aquatic forms of *Dorylaimidae* also the presence of algae in their intestines was found.

Other numerous nematodes occurring in tissues of roots and rhizomes of *P. perfoliatus* and *P. lucens* belong to genera: *Plectus* (7 species), *Panagrolaimus* (1 species), *Chronogaster* (1 species) and *Cryptonchus* (1 species) (Tables III, IV). The morphology of their buccal cavity shows that feeding on fresh plant tissue is impossible, suggesting a probable saprobiontic type of feeding. According to the classifications by P a r a m o n o v (1964) and W a s i l e w s k a (1971) all these species belong to the group of so called devisaprobionts or are microbivorous.

The remaining species of nematodes found in the tissues of roots and rhizomes occur frequently and numerously in all littoral habitats. Part of them probably penetrates the roots and rhizomes through the damaged places. These belong to various trophic groups, among the others to predators, detritus-feeders or omnivorous species (N i e l s e n 1949, P r e j s 1970, W a s i l e w s k a 1971, Y e a t e s 1971, B r z e s k i and S a n d n e r 1974).

Table V. The dominance structure (in per cent) and numbers of nematodes in roots and rhizomes of *Nuphar luteum* and *Sagittaria sagittifolia* in the littoral of Mikołajskie Lake (average for the period June-August 1973)

Genus	*N. luteum*	*S. sagittifolia*
Chrysonemoides	11.7	3.8
Dorylaimoides	5.8	5.7
Dorylaimus and *Mesodorylaimus*	41.0	69.2
Chronogaster	5.8	0.5
Plectus	4.7	1.9
Tripyla	11.7	0.5
Tobrilus	8.2	1.1
Chromadorita	1.1	
Others	10.0	17.3
Number of individuals in 10 g of fresh weight of plants	17	52

The species composition and numbers of nematodes inhabiting the roots and rhizomes of *Nuphar luteum* and *Sagittaria sagittifolia* were also studied in the Mikołajskie Lake (Table V). Very low numbers were found for *Nuphar luteum* (17 individuals in 10 g of fresh weight on the average). This is probably due to difficult access for nematodes to roots and rhizomes of this plant. Hard and healthy rhizomes were in general without the nematodes, which occurred in decomposing fragments. The number of nematodes in roots and rhizomes of *Sagittaria sagittifolia* equalled to the lowest numbers of nematodes from tissues of pondweeds.

3.2.2. Distribution of nematodes in roots and rhizomes

For an estimation which part of plant is the most intensively penetrated by nematodes, the roots and rhizomes of both species of pondweeds from the Mikołajskie Lake were incubated in separate jars. It was found that in the majority of cases the numbers of nematodes per 10 g of fresh weight were higher in roots than in rhizomes (Table VI).

Table VI. Numbers of nematodes in roots and rhizomes of *P. perfoliatus* and *P. lucens* in the littoral of Mikołajskie Lake (average for the period June-August 1972; in brackets – per cent of individuals in roots and rhizomes)

Site	Average number (individuals in 10 g of fresh weight) and 95% confidence limit			
	P. perfoliatus		*P. lucens*	
	roots	rhizomes	roots	rhizomes
I–IV	166 ± 36 (65)	88 ± 42 (35)	79 ± 21 (77)	23 ± 9.7 (23)
V	203 ± 100 (72)	79 ± 29 (28)	88 ± 24 (68)	42 ± 25 (32)

Analyses have shown that numbers of nematodes in decomposing fragments of rhizomes were much higher than in fresh ones (Table VII). Numbers in dying tissues of both species of pondweeds were much higher than the average number of nematodes for the whole material from underground parts (Tables III, IV); numbers in fresh fragments of rhizomes were usually lower than the above average (Table VII).

Table VII. The occurrence of nematodes in fresh (*1*) and dying (*2*) fragments of rhizomes of *P. perfoliatus* and *P. lucens* in the shallow littoral of Mikołajskie Lake (data for August 1974)

Species	Number* (individuals in 10 g of fresh weight)		Percentage contribution of dominants	
	1	2	*1*	2
P. perfoliatus	66 (0–200)	9.430 (650–41,800)	*Chrysonemoides* – 25 *Hirschmanniella* – 10	*Hischmanniella* – 38 *Dorylaimidae* – 23 *Chrysonemoides* – 19
P. lucens	9 (0–33)	1,095 (480–1.850)	*Prodesmodora* – 60 *Chronogaster* – 40	*Chrysonemoides* – 35 *Dorylaimidae* – 30

*Number – average and limits.

The much higher numbers of nematodes in decomposing fragments of tissues could suggest that the nematodes are the cause of rhizomes destruction. However, it can be assumed that these high numbers are the cause and the result of damages of rhizomes. On the basis of a large series of August samples of underground parts of *P. perfoliatus* and *P. lucens* it was found, that necroses occurred the most often in places mechanically damaged by larvae of *Donacia* sp. (*Chrysomelidae*) fastening to the surfaces of rhizomes. These larvae were frequently noted in large numbers, up to 31 individuals in 100 g of fresh weight of roots and rhizomes (Prejs and Wiktorzak 1976). The presence of plant tissue was found in the alimentary tracts of *Donacia* sp. larvae.

However, the activity of *Donacia* sp. larvae surely is not the only cause of rhizome damages. Within the dying fragments of rhizomes lacking the surface holes, mechanical damages or losses, very large numbers of nematodes were found (maximum 41,800 in 10 g of fresh weight). In all decomposing fragments of rhizomes, also in these with damages caused by *Donacia* sp., the number of nematodes was high (Table VII).

The data on the pest species of plant nematodes for terrestrial habitats (Giebel 1971) show that the majority of parasitic species digest the food outside their body and sucks it in after the digestion. It was found, that number of enzymes excreted by nematodes causes destruction of plant cells, necrosis of whole tissues, and decomposition of plants. This subject was not studied for nematodes penetrating the tissues of aquatic plants, but indirect data can suggest the destructive influence of nematodes on macrophytes. In the case of maximum numbers of nematodes and of significant destruction of tissues *Hirschmanniella gracilis* dominated (80%). In many other cases among the nematodes found in damaged tissues *Chrysonemoides limigenus* and *Dorylaimidae* were numerous apart from *Hirschmanniella gracilis* (Table VII). High numbers of larval forms in these groupings can suggest the presence of conditions convenient to complete the whole life cycle within the plant.

Nematodes of the genera *Plectus*, *Chronogaster* and *Panagrolaimus* were also quite numerous in tissues of dying fragments of rhizomes. Paramonov (1964) and Wasilewska (1971) stated that in grouping of soil nematodes the species belonging to the group of the so called devisaprobionts or to microbivorous species, although they do not act as direct parasites, can be of a negative influence on plants by making possible the invasion of bacteria and viruses.

A similar situation can be expected in waters. It is possible that nematodes invading the tissues first (parasites), change their habitat in a way which makes possible the penetration by other nematodes and bacteria which cause further destruction of tissues.

It can be supposed that stems of pondweeds are also penetrated by nematodes. However, numbers of nematodes isolated from few stems of *P. perfoliatus* and *P. lucens* were much lower than in roots and rhizomes (only 5–10 individuals in 10 g of fresh weight of stems).

3.2.3. Process of invading the rhizomes by nematodes

For gathering the information on movements of nematodes in rhizomes the plants from a field experiment (T. Ozimek, A. Prejs and K. Prejs 1976) were used. The experiment relied on transplanting of single plants of *P. perfoliatus* and *P. lucens*, and on estimating the growth increments and losses of rhizomes after a short period. From the "old" rhizomes (previously transplanted) and their fragments which grew up during the experiment ("new" ones) the nematodes were isolated. In the case of *P. perfoliatus* the comparison of numbers of nematodes isolated from "old" and "new" fragments have shown, that after just 15 days these numbers were equal (Table VIII). But for *P. lucens*, even after 25 days the number of nematodes in "new" rhizomes was only 24% of the total number in the whole

Table VIII. Numbers (individuals in 10 g of fresh weight of plants) and percentage contribution (in brackets) of nematodes in "old" rhizomes and in newly grown ones of two species of pondweeds in the littoral of Mikołajskie Lake

Species	Old rhizomes	New rhizomes	Time of experiment (days)
P. perfoliatus	164 (48.5)	174 (51.4)	15
P. lucens	202 (75.7)	65 (24.3)	25

rhizomes. The slower spreading of nematodes in rhizomes of *P. lucens* can be related with slower rate of destruction of "old" rhizomes of this species as compared with ones of *P. perfoliatus* during the beginning of the experiment (T. Ozimek, A. Prejs and K. Prejs 1976). This difference, considering the usually higher numbers of nematodes in tissues of *P. perfoliatus* than in *P. lucens* (Tables III, IV),could result also from other difficult to estimate presently differences in life conditions in rhizomes of these species.

The spreading of nematodes within the rhizomes from "old" to "new" parts seams to be confirmed by similar species composition of nematodes in both parts, and by lack of mechanical damages in "new" parts, which could make possible the invasion from outside.

The rate of invasion the rhizomes of *P. perfoliatus* by nematodes was studied experimentally. Nematodes from the genera *Chrysonemoides*, *Hirschmanniella*, *Dorylaimoides* and *Dorylaimus* were placed in 5–10 ml chambers of inverted microscope with fresh or decomposed fragments of rhizomes. It was found that *Hirschmanniella*, *Chrysonemoides* and *Dorylaimoides* penetrate the rhizomes in the shortest time (already after a day); these attack mainly fresh rhizomes with some damages making the penetration easier. *Dorylaimidae* penetrated the rhizomes to the smallest degree (to 15% of analysed individuals) and slowly, attacking mainly parts of dead rhizomes. In the majority of cases *Dorylaimidae* stayed by the surface of rhizomes or grouped in places with decomposing or damaged tissue.

4. CONCLUSIONS

1. A specific grouping of nematodes associated with the root system of aquatic plants occurs in the lake littoral. This grouping when compared with one inhabiting littoral sediments lacking the vegetation shows higher numbers, different species composition and dominance structure.

2. The most numerous and permanent components of this grouping are nematodes belonging to the following genera: *Hirschmanniella*, *Chrysonemoides*, *Dorylaimoides*, *Dorylaimus*, *Mesodorylaimus*, *Plectus*, *Panagrolaimus*, *Chronogaster* and *Chromadorita*. The occurrence of larvae and mature individuals in the root and rhizome system of aquatic plants shows, that these nematodes go there through a complete life cycle.

3. Of all the nematode species inhabiting the roots and rhizomes of aquatic macrophytes only these belonging to genera *Hirschmanniella*, *Chrysonemoides*, *Dorylaimoides*, *Dorylaimus*

and *Mesodorylaimus* can feed on the plant tissue directly. Other species occurring there belong to various trophic groups (microbivorous, detritus-feeders, predators or omnivorous).

4. In decomposing rhizomes and in their fragments with necrotic spots high numbers of *Hirschmanniella gracilis*, *Chrysonemoides limigenus*, *Dorylaimoides ditlevseni* and nematodes from the family *Dorylaimidae*, many times greater than in fresh rhizomes, were found.

5. It can be supposed that nematodes invade the plants by penetrating through various kinds of surface damages, and that they spread inside the rhizomes from older parts to young, growing parts.

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5. SUMMARY

The investigations were performed in the littoral of Mikołajskie Lake in 1972–1974. The paper aimed at an analysis of groupings of littoral nematodes with special consideration of these inhabiting the root region and penetrating the roots and rhizomes of aquatic macrophytes. Four species of plants were investigated: *Potamogeton perfoliatus*, *P. lucens*, *Sagittaria sagittifolia* and *Nuphar luteum*. The contribution of underground parts to the total biomass of these macrophytes was estimated.

It was found that there is a specific grouping of nematodes associated with the root region of littoral macrophytes. Nematodes from genera *Hirschmanniella*, *Chrysonemoides*, *Dorylaimoides*, *Dorylaimus*, *Mesodorylaimus*, *Plectus*, *Panagrolaimus*, *Chronogaster* and *Chromadorita* are the most numerous and permanent inhabitants of root and rhizome tissues (fig. 1).

The average number of nematodes penetrating the tissues of roots and rhizomes was 39–413 individuals in 10 g of fresh weight of plants for *P. perfoliatus*, and 54–106 for *P. lucens* (Tables III, IV).

On the basis of the buccal cavity structure (hollow stylet), own observations and scarce literature data it can be supposed that of all species inhabiting roots and rhizomes only species from genera *Hirschmanniella*, *Chrysonemoides*, *Dorylaimoides*, *Dorylaimus* and *Mesodorylaimus* utilize plant tissues as a direct food. Other species occurring in tissues belong to other trophic groups.

In decomposing rhizomes and in their fragments with necrotic spots, high numbers of *Hirschmanniella gracilis*, *Chrysonemoides limigenus*, *Dorylaimoides ditlevseni* and members of the family *Dorylaimidae* were found, many times higher than in fresh rhizomes (Table VIII).

It can be supposed that nematodes invade the plants through various surface damages caused by mechanical destruction of the surface of roots and rhizomes, and that these animals spread actively from old to newly growing parts of rhizomes.

6. POLISH SUMMARY (STRESZCZENIE)

Badania prowadzono w latach 1972–1974 w litoralu Jeziora Mikołajskiego. Celem pracy była analiza zgrupowań nicieni litoralowych, ze szczególnym uwzględnieniem nicieni strefy korzeniowej i nicieni penetrujących tkankę korzeni i kłączy makrofitów. Badano cztery gatunki roślin: *Potamogeton perfoliatus*, *P. lucens*, *Sagittaria sagittifolia* i *Nuphar luteum*. Określono udział części podziemnych w biomasie całej rośliny badanych makrofitów.

Stwierdzono, że w litoralu jeziornym występuje specyficzne zgrupowanie nicieni związanych z systemem korzeniowym roślin. Najliczniejszymi stałymi mieszkańcami tkanek korzeni i kłączy są nicienie z rodzajów *Hirschmanniella*, *Chrysonemoides*, *Dorylaimoides*, *Dorylaimus*, *Mesodorylaimus*, *Plectus*, *Panagrolaimus*, *Chronogaster* i *Chromadorita* (fig. 1).

Średnia liczebność nicieni penetrujących tkanki korzeni i kłączy makrofitów wynosiła 39–413 osobników w 10 g świeżej masy roślin u *P. perfoliatus* i 54–106 osobników w 10 g świeżej masy u *P. lucens* (tab. III, IV).

Na podstawie wiadomości o budowie torebki gębowej (drożny sztylecik), obserwacji własnych a także nielicznych danych z literatury, można sądzić, że w zgrupowaniu nicieni zasiedlających korzenie i kłącza

makrofitów tylko gatunki z rodzajów *Hirschmanniella, Chrysonemoides, Dorylaimoides, Dorylaimus* i *Mesodorylaimus* wykorzystują tkankę roślinną w sposób bezpośredni jako pokarm. Pozostałe gatunki spotykane w tkankach należą do różnych grup troficznych.

W kłączach obumierających i ich fragmentach pokrytych plamami nekrotycznymi stwierdzono duże, często wielokrotnie wyższe niż w kłączach świeżych, liczebności *Hirschmanniella gracilis, Chrysonemoides limigenus, Dorylaimoides ditlevseni* i przedstawicieli rodziny *Dorylaimidae* (tab. VIII).

Można sądzić, że nicienie zasiedlają rośliny przez wnikanie do wnętrza różnego rodzaju otworami powstałymi przez mechaniczne zniszczenie powierzchni korzeni i kłączy, a także aktywnie się przemieszczają z części kłączy „starych" do świeżo przyrastających.

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