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NEMATODE FEEDING-TYPES AT THE EULITTORAL OF LAKE SAKADAŠ (KOPAČKI RIT NATURE PARK, CROATIA)

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A total of 45 nematode species was found at the investigated sites of the eulittoral of Lake Sakadaš during 1998: 12 deposit-feeders (bacterial feeders), six epistrate-feeders (algal feeders), eight chewers (predators/omnivorous), and 19 suction-feeders (plant feeders/omnivorous). Chewers were the major group of nematofauna at the eulittoral of Lake Sakadaš – they comprised 68.28% of total nematofauna at submerged site A, 70.13% at site B (at the land-water interface), and 54.16% at emerged site C. The highest relative abundance within the chewers group was found in *Brevitobrilus stefanskii*, *Mononchus aquaticus* and *Tobrilus gracilis* at sites A and B, and *B. stefanskii*, *M. aquaticus* and *Paramononchus* sp. at site C. Suction-feeders were the next important nematofauna group: 19.98% at site A, 23.60% at site B, and 36.97% at the site C, followed by deposit-feeders (5.98–11.78%), whereas epistrate-feeders had the lowest abundance (<2%). Irregularities in the water level and the quantity of food available had the major influence on changes in the distribution of nematode feeding-types.

Key words: eulittoral, sediment, freshwater nematodes, feeding-types

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Na istraživanim postajama u eulitoralu Sakadaškog jezera tijekom 1998. godine ukupno je utvrđeno 45 vrsta oblića: 12 »gutača« (bakteriofagnih vrsta), šest »kidača-gutača« (algivornih vrsta), osam »žvakača« (predatora/omnivora) i 19 »isisavača« (fitofaga/omnivora). »Žvakači« su bili osnovna skupina koja je obilježavala faunu oblića u eulitoralu Sakadaškog jezera – činili su 67.28% ukupne nematofaune na submerznoj postaji A, 70.13% na postaji B (na kontaktu vode i kopna) te 54.16% na emerznoj postaji C. Najveća relativna gustoća utvrđena je za »žvakače«: *Brevitobrilus stefanskii*, *Mononchus aquaticus* i *Tobrilus gracilis* na postajama A i B, a na postaji C za *B. stefanskii*, *M. aquaticus* i *Paramononchus* sp. Iduća po značajnosti bila je skupina »isisavača«: 19.98% na postaji A, 23.60% na postaji B te 36.97% na postaji C. Manje su bili zastupljeni »gutači« (5.98–11.78%) i najmanje »kidači-gutači« (<2%). Na promjene u trofičkoj strukturi oblića najveći su utjecaj imali fluktuacije nivoa vode i količina raspoložive hrane u sedimentu.

Ključne riječi: eulitoral, sediment, slatkovodni oblići, trofička struktura

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INTRODUCTION

Nematodes are the most abundant and, in terms of species diversity, the richest group of meiofauna in the benthos of aquatic ecosystems (NICHOLAS, 1975; PEHOFER, 1989; TRAUNSPURGER, 2000; 2002), and their role in the trophic food webs of the benthos is extremely important (SCHIEMER *et al.*, 1969; PREJS, 1970; TUDORANCEA & ZULLINI, 1989; OCANA & PICAZO, 1991; TRAUNSPURGER 1996 a, 2000; VIDAKOVIĆ & BOGUT, 1999; VIDAKOVIĆ *et al.*, 2001).

Free-living aquatic nematodes can ingest a wide spectrum of food (TRAUNSPURGER, 1996 a). Nematodes feed on bacteria, fungi, algae, detritus, suspended organic matter, plants and animal organisms (PREJS, 1970; WETZEL, 1975; JENSEN, 1982, 1987; NICHOLAS *et al.*, 1992; TRAUNSPURGER, 1996 a, 2000). The morphology of the buccal cavity can be a limiting factor for certain types of food (YEATES, 1998). For example, a species with a small buccal cavity and without teeth cannot be a predator. The stylet width of stylet-bearing nematode species is a limiting factor concerning the type of food they eat (YEATES, 1998). YEATES (1987), during his investigations, observed that some nematode species can change the type of food they eat in the process of their development. Likewise, some obligate predators become facultatively bacteriovorous in specific situations (YEATES, 1998). Despite that, the classification of nematodes into feeding categories is a good way for an interpretation of the ecological role of nematodes in the meiobenthos (TRAUNSPURGER, 1996 a).

TRAUNSPURGER (1996a) differentiates deposit-feeders, epistrate-feeders, predators/omnivores and nematodes with stylets, and the same author (1997a), in order to determine more easily the functional role of nematodes in the sediment of an oligotrophic lake, and on the basis of morphological characteristics of the buccal cavity, grouped nematodes into four feeding types: 1) deposit-feeders – »swallowers«, which feed on bacteria and unicellular eucaryotes, 2) epistrate-feeders – »tear-and-swallow feeders«, which feed on bacteria, diatoms and other algae, 3) chewers – predators on protozoa, other nematodes, rotifers and tardigrades, 4) suction-feeders – omnivores (algae, fungi, vascular plants, animals, epidermal cells and root hairs).

TRAUNSPURGER's classification (1997a, 2002) is a modification of systems by WIESER (1953), JENSEN (1987) and YEATES *et al.* (1994), and this classification provides an insight into the special role of nematodes in the trophic food webs of aquatic ecosystems, which we used as a starting point for this paper.

MATERIAL AND METHODS

Site description

Kopački rit Nature Park is a protected flooded area of the Danube in Baranja (NE Croatia), situated in an angle between the Drava and the Danube. The basic ecological characteristic of this complex and specific wetland area is the dynamics of inundation. The whole region depends on flooding intensity. A larger quantity of water flows from the Danube into Kopački rit than from the Drava River (MIHALJEVIĆ *et al.*, 1999; MIHALJEVIĆ & NOVOSELIĆ, 2000).

Lake Sakadaš is the deepest water depression (about seven to eight meters deep during high water level) and it is an important part of the hydrobiological system of Kopački rit. This lake has an oval shape, a relatively steep shore and a surface of about six hectares (VIDAKOVIĆ *et al.*, 2001).

Feeding-types of nematodes were investigated in the period between February and December 1998 at three sites in the eulittoral zone of Lake Sakadaš: in the sandy sediment 15 cm below the water surface (submerged, A), in the transition zone between water and land (the land-water interface, B), and at the lake shore, 110 cm from site B (emerged, C) (BOGUT & VIDAKOVIĆ, 2002).

Sample collection and analysis

Six replicate samples of sediment were collected monthly at each site with the help of a metal hand corer (diameter 4 cm, length 10 cm, area 12.56 cm^2). The sediment layer observed was up to 10 cm deep. The sediment in each corer was fixed with 4% formaldehyde and stained with Rose Bengal (Riedel-de Haën AG). Sediment samples were rinsed in the laboratory with a 60 µm sieve. A net with a mesh size of 60 µm was suitable for the investigation since inspection of the fraction under the sieve during the protozoa analysis did not detect any nematode species. Nematodes were isolated under a stereoscopic microscope (x100), then placed in glycerine solution, prepared on permanent slides (SEINHORST, 1959), and identified to species level under the microscope (oil immersion, x1000).

The abundance of nematodes was analysed using Pearson's coefficient of correlation (PARKER, 1979).

With the purpose of defining the role of aquatic free-living nematodes in the food-webs in the sediment of the eulittoral zone of Lake Sakadaš, the physical and chemical parameters of the habitat were examined: water level fluctuations of the Drava and Danube, and of Lake Sakadaš, granulometic composition of sediment, water temperature, concentration of dissolved oxygen and chemical oxygen demand in the water (APHA, 1985). The quantity of the food available in the sediment was examined simultaneously, involving analyses of the organic matter amount, composition, abundance of bacteria and protozoa. The organic matter in the sediment was determined out of the dry matter of corresponding replicates as a loss that resulted from the glow or as a dry weight of released ash. The sediment samples were homogenised and dried at 105 °C first, then they were heated to glow at 600 °C for 20 minutes (APHA, 1985). Standard indirect microbiological methods (KUZNECOV & DUBININA, 1989) were used to determine: the number of eutrophic bacteria (CFU-E/g sediment), the number of oligotrophic bacteria (CFU-O/g sediment) and the number of aerobic sporogenic bacteria. A modification of the method of UHLIG *et al.* (1973) was used for the analysis of protozoa: a sediment sample was covered with ice and, as a result of the decrease in temperature, protozoa individuals passed through the sieve into a laboratory glass. Protozoa were determined according to STREBLE & KRAUTER (1983) and FOISSNER & BERGER (1996).

RESULTS AND DISCUSSION

The results of the measured physical and chemical parameters and analysed sediment fauna composition – bacteria and protozoa (Tab. 1) in the littoral zone of

Tab. 1. Bacteriological analysis of sediment (number of bacteria x 10^6 / g), and protozoa composition and abundance (ind./100 cm^2) in the sediment of Lake Sakadaš during 1998.

site A	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
No. of eutrophic bacteria (CFU-E) x 10^6 / g	32.310	33.547	32.375	2.165	0.484	2.862	2.180	3.786	1.801	7.968	1.996
No. of oligotrophic bacteria (CFU-O) x 10^6 / g	59.635	16.317	16.900	0.763	0.295	2.642	1.467	2.145	1.742	3.205	4.443
No. of aerobic spores x 10^6 / g	2.206	0.820	1.660	0.008	0.037	0.029	0.118	0.616	0.831	0.209	0.192
Total bacteria x 10^6 / g	94.151	50.684	50.935	2.936	0.816	5.533	3.765	6.547	4.374	11.382	6.631
site B											
No. of eutrophic bacteria (CFU-E) / g	1.426	68.261	25.526	0.579	0.385	1.065	2.632	3.684	2.456	6.415	2.363
No. of oligotrophic bacteria (CFU-O) / g	1.851	113.440	46.330	0.650	0.115	0.966	1.189	1.620	8.035	6.342	2.893
No. of aerobic spores x 10^6 / g	0.113	1.430	3.733	0.011	0.076	0.094	0.126	0.054	0.329	0.465	0.250
Total bacteria x 10^6 / g	3.390	183.131	75.589	1.240	0.576	2.125	3.947	5.358	10.820	13.222	5.506
site C											
No. of eutrophic bacteria (CFU-E) g	3.795	16.661	38.143	0.263	0.208	1.697	1.360	2.795	1.579	8.595	1.200
No. of oligotrophic bacteria (CFU-O) / g	0.405	1.013	91.067	0.740	0.125	2.379	1.176	1.713	3.723	8.526	2.128
No. of aerobic spores x 10^6 / g	0.083	1.535	1.626	0.044	0.020	0.021	0.213	0.031	0.440	0.677	0.201
Total bacteria x 10^6 / g	4.283	19.209	130.836	1.047	0.353	4.097	2.749	4.539	5.742	17.798	3.529
site A											
Ciliata / 100 cm^2	68780	14820	11260	39020	5670	7210	3520	4080	–	7730	2970
Flagellata / 100 cm^2	245880	44490	19000	34640	19540	10510	15230	2660	–	350	10500
Total protozoa / 100 cm^2	314660	59310	30260	73660	25210	17720	18750	6740	–	8080	13470
site B											
Ciliata / 100 cm^2	10910	15440	2320	1320	8240	3490	1820	4970	–	200	320
Flagellata / 100 cm^2	690090	4490	15090	2000	9630	5330	5330	3380	–	0	4260
Total protozoa / 100 cm^2	701000	59930	17410	3320	17870	8820	7150	8350	–	200	4580
site C											
Ciliata / 100 cm^2	2520	4560	3520	3050	4590	1060	1010	1150	–	555	0
Flagellata / 100 cm^2	67310	2565	15940	17050	5350	2440	3580	1170	–	0	0
Total protozoa / 100 cm^2	69830	30210	19460	20100	9940	3500	4590	2320	–	555	0

Tab. 2. Classification of recorded nematode species into feeding types.
Legend: **FT – Feeding types:** DF – deposit feeders, CH – chewers, EF – epistrate feeders, SF – suction feeders; **DS – Data sources:** 1: PREJS (1970), 2: NICHOLAS *et al.* (1992), 3: TRAUNSPURGER (1996 a, b), 4: TRAUNSPURGER (1997 a), 5: VIDAKOVIĆ & BOGUT (1999).

Species	Site	Food sources	FT	DS
Alaimus primitivus de Man 1880	B	bac., unic. Euc.	DF	1, 2
Alaimus sp. de Man 1880	B	bac., unic. Euc.	DF	1, 2
Brevitobrilus stefanskii Tsalolikhin 1981	A, B, C	unic. Euc., prot., Rotat., Nemat., Tard.	CH	2
Chromadorina bioculata Schultze in Carus 1857	B, C	bac., unic. Euc., Diat., other algae	EF	4
Chromadorina viridis (Linstow 1876) Wieser 1954	B	bac., unic. Euc., Diat., other algae	EF	4
Chromadorina sp. Wieser 1954	A	bac., unic. Euc., Diat., other algae	EF	4
Chromadoridae indent.	B	bac., unic. Euc., Diat., other algae	EF	2
Diplogaster rivalis Bütschli 1873	A, B, C	unic. Euc., prot., Rotat., Nemat., Tard.	CH	4
Dorylaimus stagnalis Dujardin 1845	A, B, C	algae, fungi, plants, roots, epid. cells, anim.	SF	2
Dorylaimus sp. 3 Dujardin 1845	B, C	algae, fungi, plants, roots, epid. cells, anim.	SF	2
Dorylaimus sp. 4 Dujardin 1845	B	algae, fungi, plants, roots, epid. cells, anim.	SF	2
Dorylaimus sp. 6 Dujardin 1845	B, C	algae, fungi, plants, roots, epid. cells, anim.	SF	2
Dorylaimus sp. 7 Dujardin 1845	C	algae, fungi, plants, roots, epid. cells, anim.	SF	2
Eudorylaimus sp. (Kreis 1963) Andrássy 1969	A, B, C	algae, fungi, plants, roots, epid. cells, anim.	SF	4
Eudorylaimus obtusicaud. (Kreis 1963) Andrássy 1969	A, B, C	algae, fungi, plants, roots, epid. cells, anim.	SF	2
Eumonhystera filiformis Andrássy 1981	A, B, C	bac., unic. Euc.	DF	3, 4
Eumonhystera sp. 1 Andrássy 1981	A, B, C	bac., unic. Euc.	DF	3
Eumonhystera sp. 2 Andrássy 1981	A	bac., unic. Euc.	DF	3
Ethmolaimus pratensis de Man 1880	A, B	bac., unic. Euc., Diat., other algae	EF	1, 2, 4
Ethmolaimus sp. de Man 1880	C	bac., unic. Euc., Diat., other algae	EF	4
Mesodorylaimus bastiani (Bütschli 1873) Andrássy 1959	A, B, C	algae, fungi, plants, roots, epid. cells, anim.	SF	4

Mesodorylaimus sp. (Bütschli 1873) Andrássy 1959	A, C	algae, fungi, plants, roots, epid. cells, anim.	SF	4
Monhystera stagnalis Bastian 1865	A, B, C	bac., unic. Euc.	DF	1, 3
Mononchus aquaticus Coetzee 1968	A, B, C	unic. Euc., prot., Rotat., Nemat., Tard.	CH	1, 2
Mononchus sp. Coetzee 1968	C	unic. Euc., prot., Rotat., Nemat., Tard.	CH	1, 2
Paramononchus sp.	A, B, C	unic. Euc., prot., Rotat., Nemat., Tard.	CH	4
Plectus communis Bastian 1865	A	bac., unic. Euc.	DF	1, 2
Plectus sp. 1 Bastian 1865	B, C	bac., unic. Euc.	DF	1, 2
Plectus sp. 2 Bastian 1865	A	bac., unic. Euc.	DF	1, 2
Plectus sp. 3 Bastian 1865	A	bac., unic. Euc.	DF	1, 2
Prodorylaimus sp. 1 Andrássy 1969	A, B, C	algae, fungi, plants, roots, epid. cells, anim.	SF	4
Prodorylaimus sp. 2 Andrássy 1969	A, B, C	algae, fungi, plants, roots, epid. cells, anim.	SF	4
Rhabditis sp. Dujardin 1845	C	bac., unic. Euc.	DF	2
Theristus sp. Bastian 1865	B, C	bac., unic. Euc.	DF	2
Thornia sp. 1 Andrássy 1966	A	algae, fungi, plants, roots, epid. cells, anim.	SF	3
Thornia sp. 2 Andrássy 1966	A, B	algae, fungi, plants, roots, epid. cells, anim.	SF	4
Tobrilus gracilis (Bastian 1865), Andrássy 1959	A, B, C	unic. Euc., prot., Rotat., Nemat., Tard.	CH	3, 4, 5
Tobrilus sp. 1 (Bastian 1865), Andrássy 1959	A	unic. Euc., prot., Rotat., Nemat., Tard.	CH	4
Tobrilus sp. 2 (Bastian 1865), Andrássy 1959	B, C	unic. Euc., prot., Rotat., Nemat., Tard.	CH	4
Tripyla papillata Bastian 1865	A, C	unic. Euc., prot., Rotat., Nemat., Tard.	CH	1, 2
Tylencholaimus sp. de Man 1880	A, B, C	algae, fungi, plants, roots, epid. cells, anim.	SF	4
Discolaimus sp.	A, B	algae, fungi, plants, roots, epid. cells, anim.	SF	4
Laimydorus sp. Andrássy 1969	C	algae, fungi, plants, roots, epid. cells, anim.	SF	4
Trichodorus sp. Andrássy 1969	C	algae, fungi, plants, roots, epid. cells, anim.	SF	4
Indent. 6	B	algae, fungi, plants, roots, epid. cells, anim.	SF	4
Indent. 12	B	algae, fungi, plants, roots, epid. cells, anim.	SF	4

Lake Sakadaš are presented in details by BOGUT (2000), BOGUT & VIDAKOVIĆ (2002) and VIDAKOVIĆ *et al.* (2001).

At site A 256 ind. of nematodes/100 cm^2 on average were recorded, at site B 391 ind./100 cm^2 and at site C 637 ind./100 cm^2. Absolute abundances of all nematode species found at the sites during the period of investigation are presented in Tabs. 3 to 5. PENNAK (1940) found a higher density of nematodes in the sediment of a sandy beach, SCHIEMER *et al.* (1969) recorded a maximum of 6180 ind./100 cm^2 in the sediment of Neusiedlersee, and WASILEWSKA (1973) recorded values ranging from 1170 to 4850 ind./100 cm^2 at the littoral of Mikolajskie Lake. According to PREJS (1977 c), a low density of nematodes is characteristic of areas without macrophytic vegetation. Furthermore, PREJS (1977 c) recorded the highest nematode abundance in the roots area of macrophyta, which closely corresponds to data recorded at site C of the eulittoral of Lake Sakadaš (parts of roots were present in the sediment samples from site C).

During the period of the investigation 45 nematode species were found: 27 species at site A, 32 at site B and 29 at site C (Tab. 2).

The number of nematode species in the sediment of Lake Sakadaš was higher than the number of species found in the sediments of other lakes (WASILEWSKA, 1973; SCHIEMER, 1979). VIDAKOVIĆ & DUPAN (1996) found 23 nematode species in the sediments of a Belje pond in Kopački rit. 21 nematode species were identified in the sediment of the central area of Lake Sakadaš (BOGUT *et al.*, 1999). A total of 39 nematode species were identified in the sediments of lakes and channels of Kopački rit (VIDAKOVIĆ *et al.*, 2000). However, TRAUNSPURGER (1996 a, b) found between 48 and 51 species in the littoral of Lake Königssee and in total about 90 species. Also, PREJS (1977 a) found 52 nematode species in Mikolajskie Lake.

The maximum diversity of nematode species was found in the winter/spring period of investigation at every site (A 17, B 19, C 22) and the minimum diversity (only a few species) was registered in autumn. Such a high number of species in the winter/spring period can be explained by the quality and quantity of the food available in the sediment (bacteria and protozoa) (BOGUT, 2000), because a higher amount of a variety of foods (Fig. 1–3) makes a greater diversity of nematofauna possible (WETZEL, 1975). The minimum diversity of nematodes can be caused by an increase in stressful habitat conditions (BRINKHURST, 1974; WARREN *et al.*, 1995), e.g. an increase in water level can cause a decrease in the number and abundance of nematode species (WASILEWSKA, 1973).

The analysis of nematode feeding-types in the sediment of the eulittoral of Lake Sakadaš showed that 12 nematode species belong to bacteriophages or, according to TRAUNSPURGER (1997), to deposit-feeders: *Alaimus primitivus*, *Alaimus* sp., *Eumonhystera filiformis-vulgaris* group, *Eumonhystera* sp. 1, *Eumonhystera* sp. 2, *Monhystera stagnalis*, *Plectus communis*, *Plectus* sp. 1, *Plectus* sp. 2, *Plectus* sp. 3, *Rhabditis* sp. and *Theristus* sp. (Tab. 3).

Six nematode species were algivorous or epistrate-feeders which feed on algae as their prevailing food: three species of the genera *Chromadorina*, two species of the genera *Ethmolaimus* and an unidentified species of Chromadoridae.

A total of 19 species were identified as belonging to the group of herbivores/omnivorous or suction-feeders. These nematode species possess a stylet in the buccal cavity: five species of the genera *Dorylaimus*, two species of the genera *Mesodorylaimus*, *Prodorylaimus*, *Thornia* and *Eudorylaimus*, one species of *Tylencholaimus*, *Discolaimus*, *Trichodorus*, *Laimydorus*, and two unidentified species.

Fig. 1. Interrelation between absolute nematode densities and amount of organic matter in the sediments at littoral sites.

Eight nematode species were classified into the group of predators/omnivorous or chewers because the morphological characteristics of their buccal cavity indicate predation upon other animal organisms or their remains: *Diplogaster rivalis*, *Mononchus aquaticus*, *Mononchus* sp., *Paramononchus* sp., *Brevitobrilus stefanskii*, *Tobrilus gracilis*, *Raritobrilus steineri* and *Tripyla papillata*.

Fig. 2. Interrelation between absolute nematode densities and total number of bacteria in the sediments at littoral sites.

In the investigation period between February and December 1998 at the eulittoral sites of Lake Sakadaš, the highest percentage recorded was that of chewers, then of suction-feeders, whereas deposit-feeders and epistrate-feeders had low percentage rates (Fig. 4).

Fig. 3. Interrelation between absolute nematode densities and total number of protozoa in the sediments at littoral sites.

Tab. 3. Nematode composition and absolute density (ind./100 cm^2) in the sediment at site A.

Species / 1998	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Aver.	± SD
Brevitobrilus stefanskii	92	159	329	45	8	36	0	37	0	0	0	64.2	96.0
Tobrilus gracilis	5	11	89	55	15	7	0	12	0	0	0	17.6	27.1
Tobrilus sp. 1	0	0	0	0	0	0	0	0	0	0	4	0.4	1.1
Mononchus aquaticus	19	41	1309	0	3	167	0	21	0	0	0	141.8	372.0
Paramononchus sp.	0	0	48	0	0	0	0	0	0	0	3	4.6	13.7
Eumonhystera filiformis-vulgaris group	4	2	3	2	0	3	0	0	1	0	0	1.4	1.4
Monhystera stagnalis	0	0	43	2	0	0	0	0	0	0	0	4.1	12.3
Eumonhystera sp. 1	0	0	2	0	0	0	0	0	0	0	0	0.2	0.6
Eumonhystera sp. 2	0	0	0	0	0	0	0	0	0	0	10	0.9	2.9
Dorylaimus stagnalis	4	4	0	0	0	12	0	0	0	0	3	2.1	3.5
Eudorylaim. obtusicaudatus	0	0	2	0	0	0	0	1	0	0	1	0.4	0.6
Prodorylaimus sp. 1	0	1	1	0	0	0	0	1	0	0	1	0.4	0.5
Prodorylaimus sp. 2	0	0	8	0	0	0	0	0	0	0	0	0.7	2.3
Mesodorylaimus bastiani	0	0	0	0	0	0	0	0	0	1	0	0.1	0.3
Mesodorylaimus sp.	0	0	0	0	0	0	0	0	1	0	1	0.2	0.4
Eudorylaimus sp.	0	1	0	0	0	0	0	0	0	0	0	0.1	0.3
Ethmolaimus pratensis	3	8	7	0	0	0	0	0	0	0	0	1.6	2.9
Diplogaster rivalis	5	1	0	0	0	0	0	0	0	0	0	0.5	1.4
Plectus communis	0	1	0	0	0	0	0	0	0	0	0	0.1	0.3
Plectus sp. 2	0	0	0	0	0	0	0	0	0	1	0	0.1	0.3
Plectus sp. 3	0	0	0	0	0	0	0	0	0	0	1	0.1	0.3
Tripyla pappilata	0	1	4	0	0	0	0	0	0	0	1	0.5	1.2
Chromadorina sp.	0	0	0	0	0	1	0	0	0	0	0	0.1	0.3
Thornia sp. 1	0	0	2	0	0	1	0	1	0	0	0	0.4	0.6
Thornia sp. 2	0	0	0	0	0	0	0	0	4	0	6	0.9	2.0
Tylencholaimus sp.	0	0	0	0	0	0	0	0	0	0	4	0.4	1.1
Discolaimus sp.	0	0	0	0	0	0	0	0	0	0	4	0.4	1.1
TOTAL	**132**	**230**	**1847**	**104**	**26**	**227**	**0**	**73**	**6**	**2**	**29**	**243.3**	**513.5**
S (number of species)	**7**	**11**	**13**	**4**	**3**	**7**	**0**	**6**	**3**	**2**	**12**		

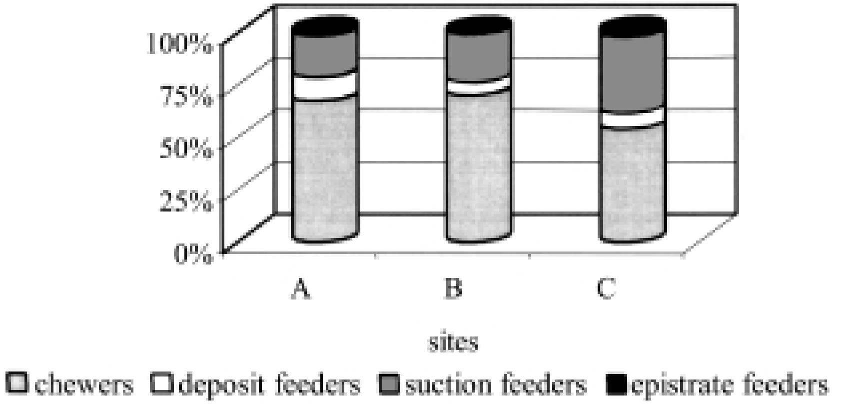

Fig. 4. Percentage rates of nematode feeding-types at the eulittoral sites of Lake Sakadaš.

Chewers were the explicitly dominant group from February to September at site A: in that period the percentage rate of chewers varied from 85.64% to 100%. Suction-feeders assumed dominance (80%) in October and chewers were not found. Suction-feeders and deposit-feeders were represented equally (50% : 50%) in November. In December suction-feeders retained a dominance of 51.73%, the percentage rate of deposit-feeders decreased to 27.58%, whereas chewers were recorded repeatedly, their percentage rate being 20.69% (Fig. 5). Epistrate-feeders were not found at all at site A in the period from July to December 1998.

Seasonal variations in the trophic structure at site B were similar to those at site A (Fig. 5). Chewers were the dominant group until October. Then, they started to be distributed the same as suction-feeders (50% : 50%). Suction-feeders were the dominant group (100%) in November, and they retained their dominance (75%) in December too. Deposit-feeders were not recorded in June, October and November. Otherwise, their rate did not go over 20%. Epistrate-feeders were recorded only in July at site B, with a very low percentage rate of 2.72%.

The variations in the trophic structure of nematodes at site C were different than those at the other two sites (Fig. 5). Moreover, suction-feeders were found at site C in every month of investigation, with a high percentage rate starting as early as July (45.93%). Suction-feeders were the only group recorded in the samples of sediments during the extremely high water levels in October and November.

With regard to the seasonal dynamics of the trophic groups at the three sites, the dominance of chewers was obvious until the autumn period of investigation. A change in the trophic structure of nematofauna was recorded in autumn, when water levels increased. During that period, and as a consequence of the high water level, sediment samples were taken in the area of roots. Results obtained were not unexpected because predators dominate on the soft and sandy sediments without macrophytic vegetation, whereas phytophageous species are mostly abundant in the sediments between macrophyta, also in the root area (PREJS, 1970, 1977 b, c, 1987).

Fig. 5. Seasonal rate variations of chewers and suction-feeders at the littoral sites.

NICHOLAS *et al.* (1992) recorded the highest number of predaceous nematode species (>86%) in the sediments of the shore of Lake Alexandrina, then almost 11% of epistrate- feeders, whereas deposit-feeders and scavengers were represented by a very low percentage rate (<2%). In the shallow littoral (at the depth of 1 m) of oligotrophic Lake Königssee, in the area without macrophyta, TRAUNSPURGER (1997) recorded the highest percentage rate of deposit-feeders (68%), then chewers (19%), and epistrate-feeders (10%), whereas suction-feeders had the lowest rate (<3%).

A statistically significant correlation was recorded between the absolute densities of chewers and total protozoa (ciliata and flagellata) at site B (n = 10, df = 8, p = 0.001, r = **0.971**) and C (n = 10, df = 8, p = 0.005, r = **0.835**), but it was not recorded for the determined variables at site A (n = 10, df = 8, r = – 0.058) during the eleven months of investigation. A statistically significant correlation was found only at site C between the absolute density of suction-feeders and total protozoa (n = 10, df = 8, p = 0.05, r = **0.860**). Seasonal changes in the abundance of bacteria and protozoa during the same timespan are presented in details by BOGUT & VIDAKOVIĆ (2002).

A correlation analysis of data showed that a statistical difference exists between some species from the trophic group of chewers and food resources at the investigated sites of Lake Sakadaš: at site A, a statistically significant correlation was found between the abundance of *B. stefanskii* and the total number of bacteria (df = 9, p = 0.05, r = **0.626**); at site B, between the abundance of *B. stefanskii* and the abundance of total protozoa (df = 8, p = 0.001, r = **0.994**), *T. gracilis* and total protozoa (df = 8, p = 0.001, r = **0.986**) and *M. aquaticus* and total protozoa (df = 8, p = 0.001, r = **0.886**); and, at site C, between the abundance of *B. stefanskii* (df = 8, p = 0.001, r = **0.919**), *T. gracilis* (df = 8, p = 0.001, r = **0.897**) and *Paramononchus* sp. (df = 8, p = 0.001, r = **0.939**), and the abundance of total protozoa (ciliata and flagellata).

Brevitobrilus stefanskii, *Mononchus aquaticus* and *Tobrilus gracilis* had the highest abundance in the sediment of site A, whereas *Thornia* sp. 2 was very abundant during the period of the increased water level. The highest abundances at site B were recorded for the individuals of *M. aquaticus*, *B. stefanskii* and *T. gracilis*, whereas two nematode species with stylets in the buccal cavity (Indent. 6 and *Tylencholaimus* sp.) were high in number, and their presence was connected to the increased water level. *M. aquaticus*, *Paramononchus* sp., *B. stefanskii* and phytoparasitic *Tylencholaimus* sp. were the most abundant in the sediment of site C, whereas *Raritobrilus steineri* was significantly abundant.

According to TRAUNSPURGER (1997a), *B. stefanskii* belongs to chewers (predators) thanks to the morphological characteristics of its buccal cavity. During the investigation presented in this paper, remains of cuticules or other animals' body parts were not found, only particles of organic detritus in the guts. Our opinion is that *B. stefanskii* belongs to the group of detritus-feeders. PREJS (1970) considered *B. stefanskii* to belong to detritus-feeders, too. During the investigation at the eulittoral of Lake Sakadaš, a statistically significant difference was recorded between the absolute density of chewers and the abundance of protozoa at sites B and C, and, since TRAUNSPURGER's (1997a, 2002) classification does not include the detritovorous group of nematodes, individuals of *B. stefanskii* were classified as chewers.

M. aquaticus and *T. gracilis* are cosmopolitan species characteristic of the sediments of eutrophic lakes. *T. gracilis* was recorded in anaerobic conditions of reduced sediments (SCHIEMER *et al.*, 1969; PEHOFER, 1989; OCAÑA & PICAZO, 1991). According to the study by MICOLETZKY (1925) a high abundance of *B. stefanskii* is very closely connected to the sandy structure of sediment. The highest density of *T.*

Tab. 4. Nematode composition and absolute density (ind./100 cm^2) in the sediment at site B.

Species / 1998	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Aver.	± SD
Brevitobrilus stefanskii	1222	106	152	34	4	16	5	3	2	0	1	140.5	345.4
Tobrilus gracilis	257	12	42	20	5	3	8	1	0	0	0	31.6	72.3
Tobrilus sp. 2	0	8	16	9	1	0	0	9	2	0	0	4.1	5.3
Mononchus aquaticus	630	161	302	14	1	125	13	90	0	0	1	121.5	184.8
Paramononchus sp.	17	27	42	3	0	16	0	12	0	0	0	10.6	13.3
Eumonhystera filif.-vulg. gr.	462	14	16	0	0	0	0	0	0	0	0	44.7	132.1
Monhystera stagnalis	5	0	8	0	0	0	0	0	0	0	0	1.2	2.6
Eumonhystera sp. 1	0	0	0	0	0	0	0	0	0	0	3	0.3	0.9
Chromadorina viridis	8	0	0	0	0	0	0	0	0	0	0	0.7	2.3
Dorylaimus stagnalis	64	18	32	3	0	12	0	1	0	0	0	11.8	19.2
Eudorylaim. obtusicaudatus	0	0	0	0	0	0	0	0	0	0	1	0.1	0.3
Dorylaimus sp. 3	0	0	0	0	0	1	0	0	0	0	0	0.1	0.3
Dorylaimus sp. 4	0	0	0	0	0	1	0	0	0	0	0	0.1	0.3
Dorylaimus sp. 6	0	0	0	0	0	0	0	3	0	0	0	0.3	0.9
Prodorylaimus sp. 1	3	1	10	1	0	6	0	1	0	0	0	2.0	3.1
Prodorylaimus sp. 2	8	0	0	0	0	0	0	0	0	0	0	0.7	2.3
Mesodorylaimus bastiani	2	1	1	0	0	0	0	0	0	0	1	0.5	0.7
Eudorylaimus sp.	0	0	0	0	0	0	0	0	0	0	1	0.1	0.3
Theristus sp.	0	1	0	0	0	7	0	0	0	0	0	0.7	2.0
Ethmolaimus pratensis	62	4	40	1	0	0	1	1	0	0	0	9.9	20.0
Diplogaster rivalis	10	0	0	0	0	0	0	0	0	0	0	0.9	2.9
Chromadorina bioculata	0	0	1	0	0	0	0	0	0	0	0	0.1	0.3
Plectus sp. 1	0	0	1	0	0	0	0	0	0	0	0	0.1	0.3
Chromadoridae indent.	0	0	0	0	0	6	0	0	0	0	0	0.5	1.7
Alaimus sp.	0	0	0	0	0	0	0	0	0	0	3	0.3	0.9
Alaimus primitivus	0	0	0	0	0	1	0	0	0	0	0	0.1	0.3
Tripyla pappilata	5	0	4	0	0	4	0	0	0	0	0	1.2	1.9
Thornia sp. 2	0	0	0	0	0	0	0	0	2	0	7	0.8	2.0
Indent. 6	0	0	0	0	0	0	0	0	0	1	0	0.1	0.3
Tylencholaimus sp.	0	0	0	0	0	0	0	0	2	0	12	1.3	3.4
Discolaimus sp.	0	0	0	0	0	0	0	0	0	0	3	0.3	0.9
Indent. 12	3	0	0	0	0	0	0	0	0	0	0	0.3	0.9
Total	**2758**	**353**	**667**	**85**	**11**	**198**	**27**	**121**	**8**	**1**	**33**	**387.5**	**773.9**
S (number of species)	**15**	**11**	**14**	**8**	**4**	**12**	**4**	**9**	**4**	**1**	**10**		

Tab. 5. Nematode composition and absolute density (ind./100 cm^2) in the sediment at site C.

Species / 1998	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Aver.	± SD
Brevitobrilus stefanskii	500	368	2	90	84	2	0	8	0	0	0	95.8	165.0
Tobrilus gracilis	79	63	3	21	29	0	0	0	0	0	0	17.7	27.0
Tobrilus sp. 2	585	162	2	35	76	8	0	1	0	0	0	79.0	167.0
Mononchus sp.	0	0	0	0	0	4	0	0	0	0	0	0.4	1.1
Mononchus aquaticus	153	142	8	68	4	69	4	21	0	0	0	158.7	401.1
Paramononchus sp.	981	419	2	39	0	80	7	23	0	0	0	141.0	290.4
Eumonhystera filif.-vulg. gr.	524	47	14	2	5	0	0	0	0	0	0	53.8	149.3
Monhystera stagnalis	43	4	0	0	0	0	0	0	0	0	0	4.3	12.3
Eumonhystera sp. 1	6	0	0	0	0	0	3	0	0	0	1	0.9	1.8
Dorylaimus stagnalis	165	12	5	3	3	28	0	3	0	0	0	19.9	46.6
Eudorylaim. optusicaudatus	0	0	0	0	0	2	0	0	0	0	6	0.7	1.8
Dorylaimus sp. 3	12	0	0	0	0	2	0	0	0	0	0	1.3	3.4
Dorylaimus sp. 6	6	0	0	0	0	6	0	0	0	0	0	1.1	2.3
Dorylaimus sp. 7	0	0	0	2	0	2	0	0	0	0	0	0.4	0.8
Prodorylaimus sp. 1	98	44	4	0	0	0	1	0	0	0	0	13.4	29.5
Prodorylaimus sp. 2	98	95	0	0	0	88	0	4	0	0	0	25.91	41.6
Mesodorylaimus bastiani	0	4	0	3	0	4	0	0	1	0	0	1.1	1.6
Mesodorylaimus sp.	6	0	0	0	0	6	0	0	0	0	0	1.1	2.3
Eudorylaimus sp.	0	8	0	0	3	0	0	0	1	0	0	1.1	2.4
Ethmolaimus sp.	55	20	0	2	0	0	1	4	0	0	0	7.5	16.1
Diplogaster rivalis	25	0	0	0	0	0	0	0	0	0	0	2.3	7.2
Plectus sp. 1	0	0	0	0	0	2	0	0	0	0	0	0.2	0.6
Chromadorina bioculata	6	0	0	0	0	0	0	0	0	0	0	0.5	1.7
Theristus sp.	0	4	0	0	0	0	0	0	0	0	0	0.4	1.1
Rhabditis sp.	0	0	0	0	0	9	0	0	0	0	0	0.8	2.6
Tripyla pappilata	12	20	1	0	0	0	0	0	0	0	0	3.0	6.4
Tylencholaimus sp.	0	0	0	0	0	8	0	0	0	7	3	4.1	8.7
Laimydorus sp.	0	0	0	0	0	4	0	0	0	3	5	1.1	1.8
Trichodorus sp.	0	0	0	0	0	0	0	0	0	3	2	0.5	1.0
TOTAL	**3354**	**2689**	**41**	**265**	**204**	**324**	**16**	**64**	**2**	**13**	**44**	**637.8**	**1137.4**
S (number of species)	**18**	**15**	**9**	**10**	**7**	**17**	**5**	**7**	**2**	**3**	**5**		

longus and *B. stefanskii*, and somewhat lower of *T. gracilis* and *Dorylaimus helveticus* were recorded by WASILEWSKA (1973) from the eulittoral of Mikolajskie Lake. BOGUT *et al.* (1999) found the highest density of *T. gracilis* in the central area of Lake Sakadaš, and that species was the only one recorded in the summer months during the anoxic conditions in the sediment.

ŠAMOTA *et al.* (1987) investigated the relationship between the abundance of nematodes and the abundance of bacteria in the soils of Kopački rit. They recorded a presence of the phytoparasitic genera *Tylenchorhynchus* and predators/omnivores *Dorylaimus* on the shore of Lake Sakadaš. The investigation of soils of Kopački rit pointed at periodical variations between the abundance of nematodes and bacteria: an increase in the number of bacteria caused an increase in the density of nematodes. TRAUNSPURGER (1997 b) investigated the effect of natural nematode communities on bacterial activity and abundance in a microcosm and concluded that natural communities had an impact on bacterial activity, and that the magnitude of this impact depended on the proportion of activity of feeding bactivores within the community.

Free-living aquatic nematodes are included in the processes of the remineralization of organic matter in the sediment because of their trophic activity, or, in other words, they are a part of the detritus food web (YEATES, 1998). Also, thanks to their trophic activity nematodes play an important role in the transfer of energy to higher trophic levels because they stimulate growth of bacteria and protozoa, the main decomposers of organic detritus (NICHOLAS, 1975; YEATES, 1998).

Because of their activity, nematodes have influence on turbulence and aeration of sediment, which is vitally important for protected areas such as for the flooded area of Kopački rit where detritus accumulates.

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SAŽETAK

Hranidbeni tipovi oblića u eulitoralu Sakadaškog jezera (Park prirode Kopački rit, Hrvatska)

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Trofička struktura faune oblića istraživana je u razdoblju od veljače do prosinca 1998. godine na tri postaje u elitoralnoj zoni Sakadaškog jezera: u pjeskovitom sedimentu 15 cm ispod površine vode (A), na kontaktu vode i obale (B) te na samoj obali (C).

Ukupno je utvrđeno 45 vrsta oblića: 12 »gutača« (bakteriofagnih vrsta), šest »kidača-gutača« (algivornih vrsta), osam »žvakača« (predatora/omnivora) i 19 »isisavača« (fitofaga/omnivora). »Žvakači« su bili osnovna skupina koja je obilježavala faunu oblića u eulitoralu Sakadaškog jezera (67.28% na postaji A, 70.13% na postaji B te 54.16% na postaji C). Najveća relativna gustoća utvrđena je za »žvakače«: *Brevitobrilus stefanskii*, *Mononchus aquaticus* i *Tobrilus gracilis* na postajama A i B, a na postaji C za *B. stefanskii*, *M. aquaticus* i *Paramononchus* sp. Iduća po značajnosti bila je skupina »isisavača«: 19.98% na postaji A, 23.60% na postaji B te 36.97% na postaji C. Manja je bila zastupljenost »gutača« (5.98–11.78%) i najmanja »kidača-gutača« (<2%).

Na promjene u trofičkoj strukturi oblića najveći su utjecaj imali fluktuacije nivoa vode i količina raspoložive hrane u sedimentu. Prateći sezonsku dinamiku pojedinih trofičkih grupa, jasno se uočava dominantnost »žvakača« na svim postajama sve do jesenskog razdoblja istraživanja. U jesen, s porastom vodostaja, došlo je do promjene u trofičkoj strukturi nematofaune – u uzorcima sedimenta prevladavale su vrste iz trofičke grupe »isisavača«, a povećao se i udio »gutača«, dok je istovremeno znatno opao udio »žvakača«, a »kidači-gutači« nisu zabilježeni. Sediment je u jesenskom razdoblju uzorkovan u području makrofitske vegetacije pa dobiveni rezultati nisu neočekivani jer na pjeskovitim sedimentima bez makrofitske vegetacije dominiraju predatorske vrste oblića, dok su u sedimentima između makrofita te u području samog korijenja najbrojnije fitofagne vrste.