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PELAGIC CILIATED PROTOZOA IN LAKE PEIPSI: COMMUNITY COMPOSITION AND SEASONAL DYNAMICS

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Abstract. Seasonal population dynamics and community composition of planktonic ciliates of Lake Peipsi was studied in 1997–98. Ciliate abundance and biomass peaked in spring (May) and in summer (July, August) reaching values up to 18 640 cells L^{-1} and 587.4 µg L^{-1} . The community of ciliates was dominated by oligotrichs, haptorids, scuticociliates, prostomatids, and peritrichs. Larger herbivorous species dominated in spring. In summer these were replaced by smaller bacterivores. The abundance and biomass of ciliates in Lake Peipsi were in the same range as reported from many temperate lakes, with values typical of mesotrophic waters. Altogether 23 identifiable taxa were found.

Key words: pelagic ciliates, community composition, seasonal dynamics, trophic links.

INTRODUCTION

Ciliates are unicellular eukaryotes, which can be found in almost every aquatic environment. They have an important role both in freshwater and marine food webs, although their significance in pelagic food chains has been fully recognized only during the last decade. Clear evidence exists that planktonic ciliates are an important food resource for large metazooplankton (Porter et al., 1979; Dolan & Coats, 1991; Gifford, 1991). While ciliates can consume sizeable proportions of bacterio- and phytoplankton production, metazooplankton predation on ciliates could be an important trophic link between pico- and nanoplankton and metazoans. In addition to their role in energy transfer to higher trophic levels, ciliated protozoa act in bio-geochemical cycling of phosphorus and nitrogen and can increase the availability of nutrients for phytoplankton growth (Johannes, 1965; Buechler & Dillon, 1974; Berman et al., 1987). The number of papers based on freshwater protozooplankton investigations has increased recently (Hecky & Kling, 1981; Pace & Orcutt, 1981; Taylor & Heynen, 1987; Beaver et al., 1988; Carrick & Fahnenstiel, 1990; Laybourn-Parry et al., 1990; Carrias et al., 1994; James et al., 1995). However, the role of ciliated protozoa in lake ecosystems is far from clear. Studies describing seasonal succession of ciliates in freshwater ecosystems are still lacking.

The aim of this study was to describe the community structure, abundance, and seasonality of planktonic ciliated protozoa in Lake Peipsi, the fifth largest lake in Europe.

MATERIAL AND METHODS

The data set used in the present paper consists of protozooplankton analyses made on Lake Peipsi in 1997-98. The sampling period lasted from May to November in both years. Ciliate samples were collected monthly from sampling stations 4 and 11 in 1997 and 4, 11, 16, and 38 in 1998. The entire water column was sampled with a Ruttner water sampler. Samples were integrated and then 250 mL subsamples were preserved and fixed with acidified Lugol's iodine. Ciliate biomass and community composition were determined using the Utermöhl (1958) technique. Samples were stored at 4°C in the dark. Volumes of 50 mL were settled for at least 24 h in plankton chambers. Ciliates were enumerated and identified with an inverted microscope (Olympus IX50) at ×400-1000 magnification. The entire content of each Utermöhl chamber was surveyed. Ciliates were usually identified to genus level by consulting several works (Kahl, 1930, 1931, 1932, 1935; Kutikova & Starobogatov, 1977; Patterson & Hedley, 1992; Foissner & Berger, 1996). The taxonomy followed mainly the scheme of Corliss (1979). The first 20 measurable specimens encountered for each taxon were measured. Biovolumes of each taxa were estimated by assuming geometric shapes. Specific gravity was assumed to be 1.0 g mL⁻¹ (Finlay, 1982). so the biomass was expressed as wet weight.

RESULTS AND DISCUSSION

During the investigation period 1997–98 the population of ciliated protozoans was mainly dominated by oligotrichs. The most common oligotrichs were *Strobilidium* spp., *Strombidium* sp., *Codonella cratera*, and *Tintinnidium fluviatile*. On some occasions also haptorids (*Askenasia volvox, Mesodinium* sp., *Dileptus* sp.), prostomatids (*Urotricha* spp., *Balanion* sp., *Coleps* sp.), peritrichs

(Vorticella spp., Epistylis procumbens), and scuticociliates (Uronema sp., Cyclidium sp.) were quite important (Fig. 1). All these groups are reported as relatively common components of lacustrine protozooplankton (Shcherbakov, 1969; Mamaeva, 1976; Pace & Orcutt, 1981; Hecky & Kling, 1981; Beaver & Crisman, 1982; Carrick & Fahnenstiel, 1990; Laybourn-Parry et al., 1990; Müller et al., 1991; James et al., 1995). The ciliate genera found in this study are typical of temperate lakes. The greatest species diversity in both years was observed in July. A list of species is given in Table 1. Altogether 23 identifiable taxa were found.

The abundance and biomass of ciliates occurring in L. Peipsi were in the same range as reported from many temperate lakes and typical of mesotrophic waters. The maximum abundance was observed in sampling station 38 (23 July 1998, 18 640 cells L^{-1}) and the maximum biomass in sampling station 16 (13 August 1998, 587.4 µg L^{-1}).

In spring larger herbivorous oligotrichs (*Strombidium* sp., *Strobilidium* sp., *Codonella cratera*, *Tintinnidium fluviatile*) dominated in all sampling stations. In summer the abundance and biomass of large oligotrichs decreased, staying low also during autumn. In sampling stations 11, 16, and 38 also a second peak in ciliate abundance appeared in summer (Figs. 2 and 3). This peak was due to small bacterivorous species (*Uronema* sp., *Cyclidium* sp., *Strobilidium* sp. with $\emptyset < 40 \,\mu$ m). The second peak was always higher than the spring peak of herbivores. In sampling station 4, bacterivorous species were almost absent and so the maximum abundance and biomass occurred in spring. Beaver & Crisman (1982), who investigated 20 freshwater lakes along the trophic gradient, found that the large algivorous species were progressively replaced by small bacterivorous ciliates in more eutrophic conditions. While the occurrence of small bacterivores is more typical of eutrophic waters, the results indicate that in



Fig. 1. Relative importance of different groups of ciliates in L. Peipsi in 1997–98 as a percentage of total abundance.

sampling stations 11, 16, and 38 more eutrophic conditions occur. During summer also haptorids and prostomatids were common in sampling stations 16 and 38. The appearance of large carnivorous ciliates usually coincides with the summer peaks of smaller bacterio- and bacterio-herbivorous ciliates, which are very likely the major food source for carnivores.

Table 1. Species list of Ciliophora found in L. Peipsi in 1997–98 (x = present, - = not present)

Taxon	1997	1998
Haptorida		és.
Dilentus en	x	x
Mesodinium puler Claparéde & Lachmann 1858	_	x
Askenasia volvox Claparéde & Lachmann, 1859		x
Didinium sp.		x
Lacrymaria sp.	- 74	x
Heterotrichida		
Stentor amethystinus Leidy, 1880	x	-
Scuticociliatida		
Scuticociliatida sp.		x
Cyclidium sp.	x	x
Uronema sp.	(Philo cilliate nun	x
with the data on the seasonality of chilates		
Oligotrichida		
Strobilidium sp. 1	x	x
Strobilidium sp. 2	x	x
Strombidium sp.	x	х
Halteria grandinella O. F. Müller, 1773	quor ta mi dave	х
Tintinnidium fluviatile Stein, 1833	х	X
Codonella cratera Leidy, 1877	x	x need x
Tintinnopsis tubulosa Levander, 1894	(19972)_There an	Laybox x Party
Peritrichida		
Vertically and an English 1024		
Vorticella natans Faure-Fremiet, 1924	Several oligotroj	Anner Deales In
Enistylis procumbers Zacharias 1807	X	x econd arrest lai
Epistyus procumbens Zachanas, 1697	X	ate summer (Zin
Prostomatida		
Coleps spetai Foissner, 1984	development M	x
Urotricha farcta Claparéde & Lachmann, 1859	x	x
Urotricha sp.	- (0101	X
Balanion sp.	x	x



Fig. 2. Ciliate abundance and biomass in L. Peipsi in 1997.

Peaks in planktonic ciliate numbers, described in L. Peipsi in spring and late summer, are in good accordance with the data on the seasonality of ciliates (Beaver & Crisman, 1989). It has been found that the spring peak of ciliates is dominated by larger herbivorous ciliates and the second peak in summer is formed mostly by smaller bacterivores (e.g. Carrick & Fahnenstiel, 1990, Šimek & Staškrabová, 1992). In L. Peipsi, the maximum cell density and biomass were found mostly in summer. However, in most temperate lakes across the trophic spectrum the maximum abundance of ciliates is achieved in late spring (Laybourn-Parry, 1992). There are exceptions to this trend, however. In shallow Ruster Poschen, the maximum abundance of ciliates was recorded in late summer, not in spring (Schönberger, 1994). Gates & Lewg (1984) described late summer peaks in several oligotrophic lakes in Ontario. Also in L. Võrtsjärv, the second largest lake in Estonia, the highest ciliate numbers are usually recorded in late summer (Zingel, 1999).

Ciliate collapse in early summer coincides usually with the start of metazooplankton development. Metazooplankton is known to prey intensively on ciliates (Sorokin & Paveljeva, 1972; Maly, 1975; Berk et al., 1977; Heinbokel & Beers, 1979; Porter et al., 1979) and can so affect their numbers. Various studies conducted in enclosures have demonstrated the limiting effects of copepods on



Fig. 3. Ciliate abundance and biomass in L. Peipsi in 1998.

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ciliates (Carrick et al., 1991; Taylor & Johansson, 1991). Wickham & Gilbert (1991, 1993) showed that both large and small cladocerans can suppress ciliates through predation and interference, rather than exploitative competition. According to Laybourn-Parry (1992), also competition for food resources may be one of the main factors controlling the temporal patterns of ciliates.

The patterns of ciliate abundance and species composition found in this study are unlikely to be controlled by any single factor. Further studies on the distribution and feeding modes of ciliated protozoans in L. Peipsi are needed to get more detailed information on their role in the food web and factors controlling their seasonality.

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PEIPSI JÄRVE PLANKTILISED TSILIAADID: KOOSLUSE STRUKTUUR JA SESOONNE DÜNAAMIKA

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Aastatel 1997–1998 uuriti Peipsi järve planktiliste tsiliaatide populatsiooni dünaamikat ja koosluse struktuuri. Arvukus ja biomass olid kõrged kevadel (mais) ja suvel (juulis, augustis), tõustes väärtusteni 18 640 rakku I^{-1} ja 587,4 µg I^{-1} ning langesid vahemikku, mis on tüüpiline mesotroofsetele parasvöötme järvedele. Tsiliaatide koosluses olid domineerivad oligotrihhid, haptoriidid, skutikotsiliaadid, prostomatiidid ja peritrihhid. Kevadel olid arvukaimad suured herbivoorsed liigid, mis asendusid suvel väiksemate bakterivooridega. Kokku leiti Peipsi järvest 23 planktiliste tsiliaatide taksonit.