

Annual and spatial distribution of the ciliates in lakes of the Bohemian Forest

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Abstract

We studied the annual and spatial distribution of ciliates in three lakes in the Bohemian Forest (=Šumava Mts., Böhmerwald) Čertovo Lake (CT), Plešné Lake (PL) and Prášílské Lake (PR), using the quantitative protargol staining method. In addition, we also sampled other five Bohemian Forest lakes: Černé Lake (CN), Laka (LA), Grosser Arbersee (GA), Kleiner Arbersee (KA), and Rachelsee (RA). CT, PR, CN and LA were dominated by algivorous prostomatids (particularly *Urotricha furcata* and *U. pseudofurcata*). Mixotrophic oligotrichs (*Pelagostrombidium fallax*, *P. mirabile* and *Limnostrombidium pelagicum*), biomass-dominated only the epilimnetic assemblage in PL. The omnivorous oligotrichs (*Halteria grandinella*, *H. sp.*) were important in deeper layers of PR, CT and PL, large hymenostomatids in CT, PL and LA. The sampling covering all eight lakes showed that CN and RA had the poorest ciliate fauna but GA and particularly KA showed rich communities dominated with *Halteria grandinella* and prostomatids and with very important influence of particle-related species (including *Stentor* sp.). In all the lakes, the maximum ciliate biomass was located below the thermocline (if found), particularly in the near-bottom layer. Surprisingly, in the oxygen depletion, urotrichas and/or *Coleps* spp. were found in high numbers accompanying the typical (rhodo- and cryptomonad) phytoplankton species. The ciliate assemblages were comparable with low-alkalinity mountain lakes above the timberline.

Key words: ciliates, acid lakes, stratification

INTRODUCTION

The temporal and spatial changes in the distribution of ciliates within freshwater plankton communities have been well documented (BEAVER & CRISMAN 1982, MÜLLER et al. 1991, WEISSE & MÜLLER 1998). In a water body with a seasonal stratification, their development in the spring is apparently controlled more by nutrients than by zooplankton predation, i.e. “bottom-up” controlled (via exhaustion of limiting nutrients for primary production; WEISSE et al. 1990); but occasionally zooplankton predation upon protozoa (reviewed in GIFFORD 1991) increasingly dominates, thus limiting their development due to “top-down” effects (e.g., ŠIMEK et al. 1990). Mountain lakes were supposed to be poor in microorganisms and even the presence of ciliates was considered unlikely due to the lack of nutrients (oligotrophy), low temperature and/or low pH (frequently naturally acidic including, e.g., dystrophic lakes, or acidified). Protozoan presence is controlled in such environment, by the complex of mechanisms particularly relating to pH (BELL & TRANVIK 1993, CALLIERI & HEINIMAA 1997, MACEK et al., in press). On the other hand, there may be a lack of higher trophic levels such as large zooplankton and fish (VRBA et al. 1996 and references therein). Recently, MOLAR project

("Mountain Lakes Research") supported more detailed studies of microbial food webs in the above timberline-lakes as a fundamental contribution to the classical limnological studies (CALLIERI & BERTONI 1999, FELIP et al. 1999, WILLE et al. 1999, MACEK et al. 2000).

Among the dominant ciliates, mixotrophic ciliates (particularly oligotrichs of genera *Pelagostrombidium* and *Limnostrombidium*) were reported to be important in oligotrophic environments (reviewed in BEAVER & CRISMAN 1989) and also in oligo to mesotrophic European lakes (MÜLLER 1989, MÜLLER et al. 1991; MACEK et al. 1996, 2001; CALLIERI & HEINIMAA 1997; FELIP et al. 1999). On the other hand, they were not almost observed dominating in artificially acidified lakes: There were found prevailing algivorous prostomatids, particularly genus *Urotricha* or *Balanion planctonicum*. Also gymnostomatids, particularly *Mesodinium* spp., might be important (CALLIERI & BERTONI 1999, FELIP et al. 1999, WILLE et al. 1999, MACEK et al. 2000, MACEK et al. in press). It is possible to speculate on the importance of a watershed soil cover and even a possible introduction of ciliates from surrounding areas (FELIP et al. 1999, STRAŠKRABOVÁ et al. 2000, Macek et al. in press).

The aim of the study was to analyse the annual and spatial distribution of ciliates in the Bohemian Forest lakes and to compare the distribution of taxa and that of ecological types of ciliates (e.g., filtering bacterivores, algivorous hunters, mixotrophic photosynthesising and anaerobic ciliates). The study forms part of the long-term investigation in the area centred particularly to the oligotrophic or slightly dystrophic lakes Čertovo and Prášílské.

MATERIAL AND METHODS

Sampling

Eight lakes in the Bohemian Forest (Böhmerwald, Šumava Mts.) are surrounded by the Norway spruce forest: they are characterised by low alkalinity due to atmospheric acidification that has resulted in the absence or low abundance of large zooplankton; the trophic status of the lakes varied from oligotrophy in Čertovo and Prášílské Lakes to meso-eutrophy in Plešné Lake (Table 1; for more details see Vrba et al. 1996, 2000).

Samples were taken from the boat, above the maximum lake depth using a transparent Friedinger sampler during ice-free period at mostly five layers (surface, 2 m, thermocline, bottom and one additional level, frequently 8 m) as mentioned in Table 1. Temperature and oxygen were *in situ* measured using the DataSonde 4 (Hydrolab, USA).

Sample treatment and ciliate identification

Samples were fixed with Lugol's iodine and allowed to sediment in the volumetric columns for a week, concentrated (10%) samples were postfixed with Bouin's fluid (for more details see STRAŠKRABOVÁ et al. 1999) and the quantitative protargol staining (QPS) was applied (MONTAGNES & LYNN 1987, modified by SKIBBE 1994). Samples were filtered (20 to 100 ml of the original sample, i.e. 2 to 10 ml of the concentrated one) and agar-mounted onto membrane filters (1.2 µm, Millipore, Ireland). Formalin (10%) fixed membranes were stained (60°C), dehydrated in ethanol, phenol-xylol and xylol series and neutral Canada balsam-mounted. The whole filter area was inspected at 500× to 1250× with two microscopes, both equipped with Nomarski (DIC) contrast (Olympus, Japan; Nikon, Japan). For identification, FOISSNER (1994), FOISSNER et al. (1999) and literature cited therein was used. When the number of specimens was low and/or the quality of the preparation was not sufficient, the identification finished on the genus level. For all observed specimens, individual cell volume was calculated (using simple shape models) from dimensions measured in the protargol stained samples. To estimate organic carbon content, the conversion factors of 0.368 pg C.µm⁻³ (JEROME et al. 1993) was used.

Table 1. Topographic, morphometric and chemical (late summer surface) characteristics of the Bohemian Forest lakes (for more details see VRBA et al. 2000).

Czech name	lake code	latitude	altitude	surface	pH	ANC ^a	TP ^b	DOC ^c	Number of samplings	Bottom	trophy status
German name		longitude	(m)	(ha)		$\mu\text{mol.l}^{-1}$	$\mu\text{g.l}^{-1}$	mg.l^{-1}		(m)	
Čertovo jezero	CT	49°10'N 13°12'E	1028	10.3	4.50	-49	5.4	2.83	6	32	oligotrophic; bottom anoxia strongly acidified
Prášilské jezero	PR	49°05'N 13°24'E	1079	4.2	5.08	-11	5.5	4.29	6	14.5	oligotrophic; bottom anoxia moderately acidified
Stubenbacher See	PL	48°47'N 13°52'E	1090	7.5	5.17	-2	8.9	2.77	6	17	mesotrophic; bottom anoxia strongly acidified
Plešné jezero	CN	49°11'N 13°11'E	1008	18.4	4.78	-23	4.1	2.25	1	37	oligotrophic strongly acidified
Schwarzer See	RA	48°58'N 13°24'E	1071	5.7	4.97	-20	2.7	0.91	1	12.5	oligotrophic strongly acidified
Roklanské jezero	GA	49°06'N 13°07'E	935	7.7	5.91	14	7.2	2.43	1	15.5	oligotrophic; oxygen depletion; acidic
Velké Javorské jezero	KA	49°08'N 13°09'E	918	9.4	5.51	-1	6.2	2.95	1	8	oligotrophic; oxygen depletion; moderately acidified
Großer Arbersee	LA	49°07'N 13°20'E	1096	2.8	5.81	16	6.4	4.10	1	2.5	oligotrophic, unstratified acidic
Malé Javorské jezero											
Kleiner Arbersee											
Jezero Laka											
Lakka See											

^aANC – acid neutralising capacity (alkalinity); ^bTP – total phosphorus; ^cDOC – dissolved organic carbon

Table 3. Ciliate numbers in the water column (C) and above the bottom (B) in the Bohemian Forest lakes (nd – non detected, see Table 1 for the key of the lakes).

ciliates (cells.l ⁻¹)		CT ^a	PR ^a	PL ^a	CN ^b	LA ^b	GA ^b	KA ^b	RA ^b
minute oligotrichs	C	10	20	38	nd	520	80	380	nd
	B	12	160	140	nd	260	nd	120	nd
peritrichs	C	nd	nd	nd	nd	40	nd	nd	nd
	B	nd	nd	nd	nd	nd	nd	nd	nd
minute scuticociliates	C	24	nd	66	nd	40	15	nd	nd
	B	110	80	130	nd	nd	160	680	nd
large hymenostomatids	C	3	nd	nd	nd	nd	3	nd	nd
	B	3	nd	62	nd	nd	140	40	nd
mixotrophic oligotrichs	C	1	nd	62	nd	nd	nd	nd	nd
	B	nd	nd	7	nd	nd	nd	nd	nd
gymnostomatids ^c	C	nd	nd	3	nd	70	3	nd	nd
	B	12	4	nd	nd	260	nd	20	nd
algivorous prostomatids	C	120	420	660	190	270	42	510	74
	B	670	2000	2400	40	230	nd	4300	10
others ^d	C	nd	1	nd	nd	60	nd	2	nd
	B	nd	4	nd	nd	20	nd	40	nd
total	C	160	450	830	190	1000	140	900	74
	B	810	2300	2700	40	770	300	5200	10

^a seasonal averages (CT, PR, PL); ^b one-sampling data; ^c without *Trachelius ovum*; ^d with *T. ovum* and *Stentor* sp.

RESULTS

Distributions of ciliate numbers within the water column are shown in Figs. 1–4, the most important taxa with respective feeding pattern are summarised in Table 2. Water column mean numbers and biomasses are pooled in the Tables 3 and 4, respectively. There was observed an accumulated organic sediment come mostly from the surrounding forest area in the bottom that caused apparent differences between the water column and the above-bottom samples.

Ciliate abundance, biomass and composition

Among the intensively studied lakes, PL (Fig. 1) showed both the highest annual mean of water column and bottom ciliate numbers (0.83 and 2.74 cell.ml⁻¹; Table 3). Also in LA and KA, the water column mean of 1.0 and 0.9 cell.ml⁻¹, respectively, were observed. In the bottom samples, PR showed high mean value of 2.3 cell.ml⁻¹ as well; KA (one sampling only) showed the absolute maximum (5.2 cell.ml⁻¹). From the point of biomasses, however, the position of PL as the most rich in ciliates was surpassed only in KA due to the presence of huge *Trachelius ovum* and *Stentor* sp. (*S. muelleri* or *coeruleus*; uncertain identification due to the fixation; Table 4).

According to the contributions of different feeding patterns found among ciliates, the studied lakes were mostly typical by dominance of prostomatids (Figs. 1–4). Algivorous hunting prostomatids (genera *Urotricha*, *Holophrya* and *Prorodon*) were found in all lakes, mostly dominating in both numbers and biomass. Note worthy that in CN, urotrichas were the only identified ciliates (Fig. 4).

- minute oligotrichs
- ▨ scuticociliates
- ▤ large hymenostomatids
- ▧ large oligotrichs

- ▩ gymnostomatids
- algivorous prostomatids
- others
- ⊗ oxycline

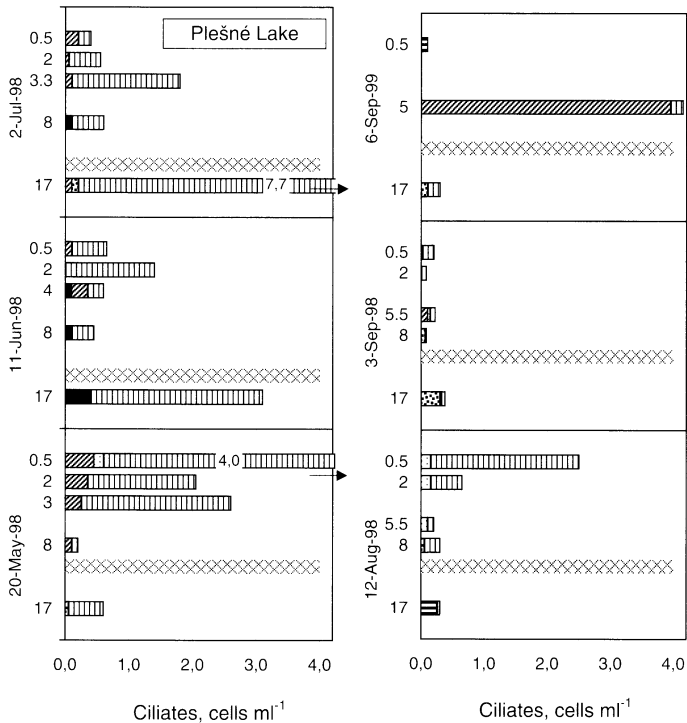


Fig. 1. Distribution of the ciliates (numbers, cell.ml⁻¹) within the water column of Plešné Lake.

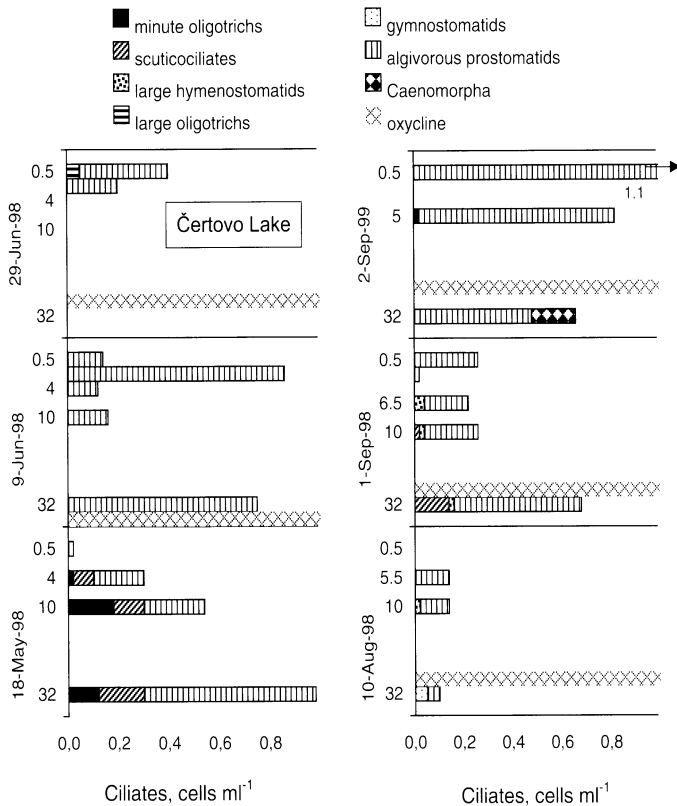


Fig. 2. Distribution of the ciliates (numbers, cell.ml⁻¹) within the water column of Čertovo Lake.

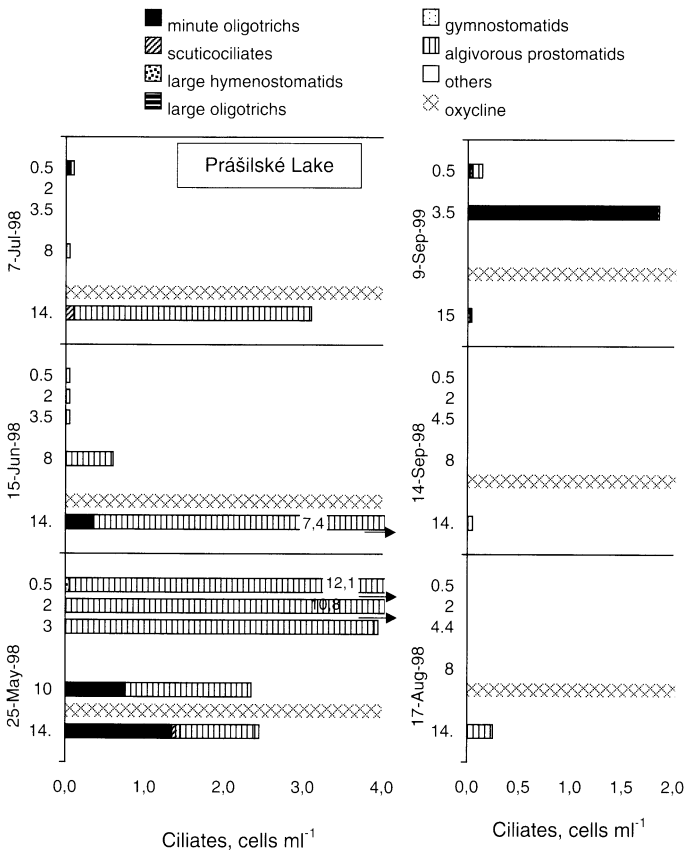


Fig. 3. Distribution of the ciliates (numbers, cell.ml⁻¹) within the water column of Prášílské Lake.

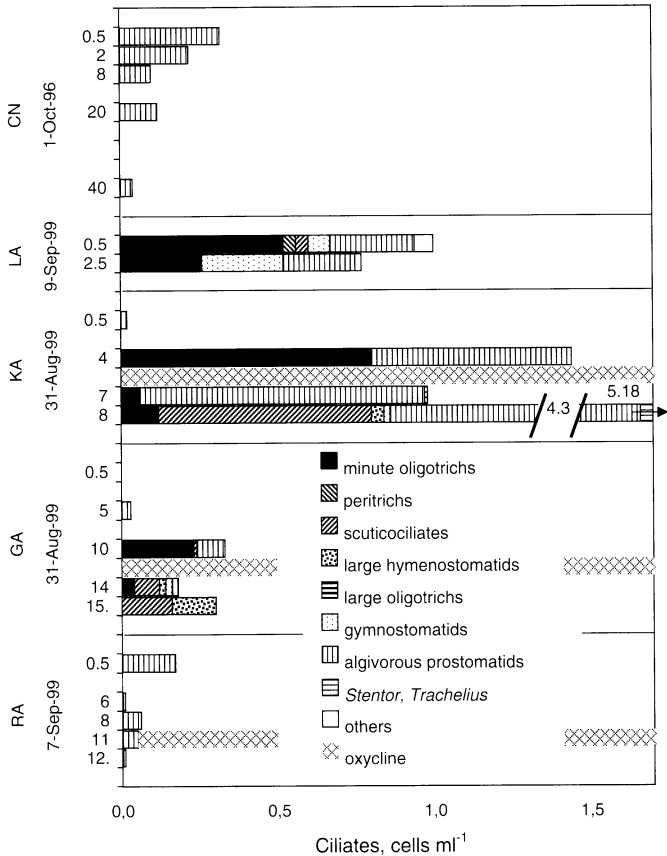


Fig. 4. Distribution of the ciliates (numbers, cell.m⁻¹) within the water column of Černé Lake (CN), Laka (LA), Rachelsee (RA), Kleiner Arbersee (KA), and Grosser Arbersee (GA).

Though the presence of picoplanktivorous or omnivorous ciliates was not scarce, they dominated the assemblages only occasionally: e.g., the late summer peak of minute oligotrichs ($\sim 20 \mu\text{m}$) *Halteria* spp. in PR and PL or the spring peaks of oligotrichs (both mixotrophic and minute bacterivorous) and/or scuticociliates ($\sim 20 \mu\text{m}$) in PR, PL, LA and KA. Although the mixotrophic coarse filter-feeding oligotrichs (*Pelagostrombidium fallax*, *P. mirabile* or *Limnostrombidium pelagicum*) were scarce, they sometimes significantly contributed to the ciliate biomass in PL and CT due to their size (see Table 2). In the bottom parts, an organic detritus content produced a lack of oxygen that resulted in a higher contribution of hymenostomatids to the ciliate assemblage. In addition, very large anaerobic *Caenomorpha* sp. was observed twice in CT (autumn sampling).

Distribution of ciliate numbers and biomass within the water column

The highest mean annual ciliate numbers were found in the deeper part of all lakes (Table 3, 4), however, the surface layers showed higher numbers during the phytoplankton peaks (Figs. 1–4). Typically, prostomatids, such as minute ($\sim 25 \mu\text{m}$) *Urotricha* spp., peaked at the very bottom or at the layer sampled above (around 13 m). Also minute oligotrichs (*Halteria* cf. *grandinella* and another *Halteria* sp.) occurred rather at the layer above the bottom than at the very bottom where microaerobic conditions were common. These samples additionally contained, along with bacterivorous scuticociliates, large hymenostomatids (*Dexiotricha* sp. in PL and *Lembadion* sp. in PR) and even the anaerobic *Caenomorpha* sp.

Table 4. Mean ciliate biomass (organic carbon) in the water column (C) and above the bottom (B) in the Bohemian Forest lakes (see Table 1 for the key).

ciliates ($\mu\text{g}\cdot\text{L}^{-1}$)		CT ^a	PR ^a	PL ^a	CN ^b	LA ^b	GA ^b	KA ^b	RA ^b
minute oligotrichs	C	0.013	0.008	0.041	nd	1.7	0.14	0.64	nd
	B	0.019	0.086	0.16	nd	0.41	nd	0.19	nd
peritrichs	C	nd	nd	nd	nd	0.083	nd	nd	nd
	B	nd	nd	nd	nd	nd	nd	nd	nd
minute scuticociliates	C	0.024	nd	0.027	nd	0.031	0.04	nd	nd
	B	0.110	0.035	0.10	nd	nd	0.16	0.73	nd
large hymenostomatids	C	0.059	0.002	nd	nd	nd	0.007	nd	nd
	B	0.140	nd	0.70	nd	nd	0.67	0.37	nd
mixotrophic oligotrichs	C	0.007	nd	0.48	nd	nd	nd	nd	nd
	B	nd	nd	0.052	nd	nd	nd	nd	nd
gymnostomatids ^c	C	nd	nd	0.010	nd	0.134	0.011	nd	nd
	B	0.032	0.012	nd	nd	0.569	nd	0.063	nd
algi vorous prostomatids	C	0.16	0.12	0.59	0.075	0.32	0.059	0.42	0.32
	B	0.51	0.74	2.75	0.008	0.36	nd	11.8	0.019
others ^d	C	nd	0.001	nd	nd	0.044	nd	1.6	nd
	B	nd	0.011	nd	nd	0.067	nd	16.3	nd
total	C	0.24	0.13	1.15	0.075	1.69	0.23	2.65	0.32
	B	0.85	0.89	3.77	0.008	1.41	0.83	29.5	0.019

^a seasonal averages (CT, PR, PL); ^b one-sampling data; ^c without *Trachelius ovum*; ^d with *T. ovum* and *Stentor* sp.

DISCUSSION

Protargol staining on the membrane filters used in the study has been criticised for underestimating abundance of some ciliate groups, however, other methods were not sufficient to identify ciliates effectively in the lakes with their low abundance (JEROME et al. 1993, SKIBBE 1994, PFISTER et al. 1999). The results observed in the study (both ciliate composition and numbers) are comparable with published information from alpine and sub alpine lakes (e.g., SALBRECHTER & ARNDT 1994, JAMES et al. 1995, WEISSE & MÜLLER 1998, CALLIERI & BERTONI 1999, FELIP et al. 1999).

It is suggested that an acidification pronounced in the less ion concentration and low pH waters leads to changes in the plankton communities (e.g., BELL & TRANVIK 1993). The Bohemian Forest lakes are all acidified and large zooplankton is represented mostly by rotifers; the ciliate communities tend towards the absolute domination of mixotrophic species and then algivorous ones (MACEK et al. in press). On the other hand, eutrophication and/or increasing alkalinity return (stabilisation of carbonate-buffered balance) might lead towards the diversification within the plankton (e.g., STRASKRABOVÁ et al. 2000). Such shifts reflected in the species diversity as well in the diversity of feeding strategies could be seen also on the ciliate communities, comparing, e.g., acidified-oligotrophic CT with eutrophic PL or even positive alkalinity KA. Generally, complex ciliate assemblages containing all feeding behaviour should replace absolute dominance of algivorous prostomatids. However, such changes could be related also to the changes in bacterioplankton composition that surpassed the article content.

Predominance of mixotrophic ciliate (mostly oligotrichous) species was found in oligotrophic lakes (BEAVER & CRISMAN 1982). Ingestion of bacteria and small algae could overpass, apart from proven phosphorus limitation (STRASKRABOVÁ et al. 2000), also a limitation by organic carbon assumed for acid waters (BELL & TRANVIK 1993, VRBA et al. 1996, ŠIMEK et al. 1998, MACEK et al. 2001). Generally, acidified water bodies might behave similarly to naturally oligotrophic ones (STRASKRABOVÁ et al. 2000 and literature cited therein). However, among the studied lakes, the mixotrophic fine- to coarse filter feeders ciliates were not so important being temporarily dominant only in the epilimnetic biomass in PL and CT (cf. ŠIMEK et al. 1996, MACEK et al. in press). Among them, the strombidiids *Pelagostrombidium fallax* and *P. mirabile*, and/or *Limnostrombidium pelagicum* were the most important. The large mixotrophic *Stichotricha secunda*, repeatedly found in PR seems to be the typical ciliate inhabiting the pelagic zone of shallow lakes, probably living also outside its shell, described from benthic samples (observed also in an oligo-mesotrophic lake, Piburger See, Tyrol, Austria, MACEK et al. 1996; and in a bog lake, Große Fuchskuhle, Neubrandenburg, Germany, MACEK et al. 2001). Surprisingly, mixotrophic gymnostomatids (such as *Askenasia chlorelligella*) were not recorded.

Among dominant ciliates, specialised algivorous genus *Urotricha* was found in all lakes being typically represented by *Urotricha furcata* and *U. pseudofurcata* (~25 µm). They dominated in number as well as in biomass, namely in acidified CT and PL (more eutrophic). In comparison with the reported data, typical *Urotricha pelagica* was scarce (e.g., MÜLLER 1989, MACEK et al. 1996) as well as genera *Holophrya* and *Prorodon* (however, significantly contributed to the ciliate biomass in some lakes). Also *Balanion planctonicum* was found only in small numbers that was in contrast with its published dominance in many oligo- to mesotrophic lakes (MÜLLER 1989, SOMMARUGA & PSENNER 1993, SALBRECHTER & ARNDT 1994, WILLE et al. 1999). Large algivorous scuticociliates, *Histiobalantium* spp. (WEISSE & MÜLLER 1998) were not observed. Heterotrophic *Coleps* spp. were observed rarely, but when present, in high concentration in the decaying phytoplankton in the bottom (e.g. SALBRECHTER & ARNDT 1994, JAMES et al. 1995).

Except for some seasonal peaks, bacterivorous and/or omnivorous fine filter feeding ciliates (such as oligotrichs, peritrichs and scuticociliates) were quite scarce in the epilimnion (cf. MÜLLER 1989, FOISSNER 1994, SALBRECHTER & ARNDT 1994, JAMES et al. 1995, MACEK et al. 1996, STABELL 1996, WEISSE & MÜLLER 1998). It seems that the oligotrophic-dystrophic pelagic environment is too poor in feeding particles to meet the food requirements of the genus *Halteria* (cf. ŠIMEK et al. 1996, 2000). Nevertheless, the peaks of *Halteria* spp. (late summer in PR and PL, spring in CT, PR and PL) were found, frequently being located below the thermocline and/or at the above bottom-layers (cf. FENCHEL 1986, CALLIERI & HEINIMAA 1997, WEISSE & MÜLLER 1998). Among halterias, only the most abundant *Halteria grandinella* was identified although another *Halteria* sp. could be distinguished (very minute forms with well pronounced adoral zone of membranelles extended to one half of the ciliate body), however, the number of specimens and the preparation quality was not sufficient to unambiguously identify them.

The peaks of minute scuticociliates were frequently linked to the phytoplankton decay producing bacterial development (MÜLLER et al. 1991, ŠIMEK et al. 1996, MACEK et al. 1996) but that was not the case in the studied lakes. Minute scuticociliate (particularly *Cyclidium*-like and *Cinetochilum margaritaceum*) were found quite abundant just after melting of the ice (spring in CT, PR and PL).

The composition of microaerobic ciliates at the very bottom of some lakes was very distinct from the water column samples, including typically large hymenostomatids such as *Dextrotricha* sp. in PL or *Lembadion* sp. in PR. Unsymbiotic *Stentor* sp. (*S. muelleri* or *coeruleus*) was found along with *Trachelius ovum* in KA; although the genus *Stentor* could be found typically in a pelagic zone of some lakes (e.g., JAMES et al. 1995; MACEK et al. 2001), *T. ovum* was observed probably being related to re-suspended particles from the deeper part (cf. FOISSNER et al. 1999).

Even above the organically rich sediment of the lakes, large oxycline-related (microaerobic) ciliates (such as genera *Loxodes* or *Spirostomum*), known from such environments, were not found (cf. GUHL & FINLAY 1993, MACEK et al. 2000). On the other hand, the anaerobic *Caenomorpha* sp. very well known from an anaerobic lake environment (e.g., GUHL & FINLAY 1993) was observed twice in CT. Actually, it was rather surprising that the anaerobic ciliates were not recorded earlier in other Bohemian Forest lakes with anoxic hypolimnion. On the other hand, it is in concordance with the opinion of FOISSNER et al. (1999) that anaerobic ciliates are not planktonic.

Unsymbiotic gymnostomatids (particularly genera *Mesodinium* and *Lagynophrya*) are reported from the oligo- to mesotrophic environment (MÜLLER et al. 1991, MACEK et al. 1996, WEISSE & MÜLLER, 1998): They were scarce but repeatedly found (Table 2) confirming thus the previous literature reports (cf. MÜLLER et al. 1991, MACEK et al. 1996).

CONCLUSIONS

The dominance of algalivorous prostomatids within the ciliate assemblage was typical for all lakes. On the other hand, an appearance of the mixotrophic oligotrichs was scarcer than supposed taking into account the ability of such ciliates to compete more efficiently for nutrients with phytoplankton. It was observed that in the lakes with increasing alkalinity, the ciliate community was more diversified from the point of view of the number of species as well from the point of view of feeding strategies, however, such changes are slow and the data set was not sufficient to prove the significance.

Generally, the ciliate taxa found in the investigated lakes do not markedly differ from those

reported from other mountain (above timberline) water bodies. Some of the investigated lakes showed higher richness connected with an accumulated organic substrate in the bottom and quite rich microaerobic to anaerobic ciliate communities. It has not been the aim of the study to define the source of this matter (autochthonous or contamination?) but, comparing with oligotrophic water bodies under similar conditions, the ciliate community composition was not surprising.

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