

Periphytic Ciliates in Three Shallow Lakes in Eastern Poland: A Comparative Study between a Phytoplankton-Dominated Lake, a Phytoplankton-Macrophyte Lake and a Macrophyte-Dominated Lake

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Tomasz Mieczan (2009) Periphytic ciliates in three shallow lakes in eastern Poland: a comparative study between a phytoplankton-dominated lake, a phytoplankton-macrophyte lake, and a macrophyte-dominated lake. *Zoological Studies* 49(5): 589-600. The aim of this investigation was to determine the abundance and taxonomic composition of periphytic ciliates in relation to selected physical, chemical, and biological factors in 3 shallow lakes in eastern Poland, classified according to the alternate stable state theory as a phytoplankton-dominated lake, a phytoplankton-macrophyte lake, and a macrophyte-dominated lake. Sampling from the reed stems was done on a monthly basis from Apr. to Nov. during 3 yr. Numbers of periphytic ciliates of the reed surface significantly differed among the studied lakes, with the lowest numbers in the macrophyte-dominated lake (37 species), a little higher number in the phytoplankton-macrophyte lake (43 species), and the highest number in the phytoplankton-dominated lake (50 species). The same distribution pattern was observed for ciliate abundances. Generally, the abundance of ciliates was positively correlated with temperature, total organic carbon, nutrients, chlorophyll *a*, and the biomass of periphyton. However, the number of significant correlations between the numbers of ciliates and environmental variables differed in the studied lakes. In the phytoplankton-dominated lake, the density of ciliates was strongly correlated with the periphyton biomass, and concentrations of chlorophyll *a* and total organic carbon; whereas in the phytoplankton-macrophyte and macrophyte-dominated lakes, the density of ciliates was correlated with concentrations of ammonium-nitrogen, nitrate-nitrogen, and total phosphorus. <http://zoolstud.sinica.edu.tw/Journals/49.5/589.pdf>

Key words: Ciliates, Shallow lakes, Alternative stable state concept.

The alternate stable state (ASS) theory typically deals with shallow moderately productive to productive lakes (Scheffer et al. 1993). The 2 major groups of primary producers are macrophytes and phytoplankton. The crux of the ASS theory is that within an intermediate range of nutrient loading, that is characteristic of moderately eutrophic and eutrophic lakes, primary productivity can be determined by either littoral macrophytes or pelagic phytoplankton (Peckham et al. 2006). According to the model of Scheffer et al. (1993), the main controlling factor for the alternative states is the turbidity of the water which regulates the vertical light penetration. Scheffer and Jeppesen

(1998) proposed the existence of intermediate states of lakes: macrophyte-phytoplankton- or phytoplankton-macrophyte-dominated, depending on the superiority of a given community. The phytoplankton-dominated state, is characterized by a higher phytoplankton population and with little submerged vegetation. In phytoplankton-dominated lakes, the development of macrophytes may be inhibited by chemicals released by some toxic algae, as well as retarded by a dense fur of periphyton growing on the surface of the vegetation. The 2nd, macrophyte-dominated state is typical of lakes with transparent water and large bottom areas covered by diverse beds of

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macrophytes, frequently composed of stoneworts, water lilies, and pondweeds. The macrophytes support rich communities of invertebrates, fish, and birds. Macrophytes constitute a vast substrate for the growth of periphytic communities. Periphyton is a biological layer found in various substrata in natural waters and consists of bacteria, algae, fungi, protozoa, and small metazoans (Hameed 2003). Periphytic ciliates as well as other periphyton components were investigated on both natural (stems, leaves, and stones) and artificial substrates. However, still more attention is paid to periphytic ciliates of river and stream ecosystems (e.g., Baldock et al. 1983, Foissner et al. 1992, Kaur and Mehra 1998, Madoni and Zangrossi 2005). Among artificial substrates, the most popular are glass slides due to their easy application and because the results obtained are very similar to those from natural substrates (Kaur and Mehra 1998, Beech and Landers 2002). Periphyton growing on glass slides is quite widely used to determine levels of water pollution (Sládečková 1994). Recent studies showed that protozoa play a very important trophic role in periphytic communities (Mieczan 2005). Among these microorganisms, ciliates are the most striking members and have long been of ecological interest in shallow lakes (Jürgens and Jeppesen 1997, Jürgens et al. 2000, Declerk et al. 2005, Mieczan 2007). During the 1960s and 1970s, few papers appeared that focused on the abundance and taxonomic composition of periphytic ciliata on natural and artificial substrates in fresh water and peatlands (e.g., Wilbert 1969, Nusch 1970, Grolière 1977). In recent years, interest has been renewed in studies of colonization and successional patterns of periphytic communities on artificial substrates in eutrophic waters. Boothroyd and Dickie (1989), Kaur and Mehra (1998), and Mieczan (2002, 2007) reported the presence of similar epiphytic communities on macrophytes and on natural and artificial substrates (i.e., glass slides). In our study, colonization of ciliates followed a similar pattern on both types of substrates where Cytrophorida and Peritrichida dominated. However, little is known about periphytic ciliate communities in shallow, polymictic lakes, classified according to the ASS theory as phytoplankton-dominated, phytoplankton-macrophyte, and macrophyte-dominated lakes. The aims of these investigations were to determine the taxonomic composition and abundance of periphytic ciliates in relation to selected physical, chemical, and biological factors in 3 shallow lakes, classified according to the ASS

theory.

MATERIALS AND METHODS

Study site

The study area comprised 3 shallow, polymictic lakes in the Polesie Lubelskie region of eastern Poland (51°N, 23°E): the phytoplankton-dominated Lake Syczyńskie (with a surface area of 6.0 ha and maximum depth of 4.0 m), phytoplankton-macrophyte Lake Sumin (with a surface area of 91.5 ha and maximum depth of 6.5 m), and the macrophyte-dominated Lake Kleszczów (with a surface area of 53.9 ha and maximum depth of 3.25 m). Lake Syczyńskie is characterized by intensive development of emergent vegetation, dominated by reeds (*Phragmites communis* Trin.) and temporal blooms of *Planktothrix agardhii* (Gomont). In Lake Sumin, the emergent macrophytes are dominated by *Phragmites communis* Trin. and the nymphaeidae (*Nymphaea candida* Presl.). The phytoplankton was dominated by cyanobacteria. In Lake Kleszczów, well-developed belts of emergent (*Phragmites*) and submerged (*Chara fragilis* Desvaux) macrophytes dominate the littoral. The phytoplankton community is predominated by Chlorophyta (Kornijów et al. 2002). In the phytoplankton-dominated lake, the periphyton community is dominated by filamentous chlorophytes (mostly *Cladophora* sp.). Diatoms, small chlorophytes and blue-green algae occurred in the greatest proportion of the total abundance in the phytoplankton-macrophyte and macrophyte-dominated lakes. The physical, chemical, and biological characteristics of water at these lakes are summarized in table 1.

Sampling and enumeration of protozoa

Periphyton was collected from reed stems at a depth of 0.5-1 m. Sampling was done on a monthly basis from Apr. to Nov. 2004-2006. During each sampling occasion, 6 periphyton samples were collected. One sample consisted of 10 cm² of periphyton taken from macrophyte stems using a scalpel. In order to determine the density of ciliates, 4 samples were fixed with Lugol's solution (1% v/v) and allowed to settle for at least 24 h in plankton chambers. The ciliates were counted and identified with an inverted microscope at a magnification of 400-1000x. Ciliates are

highly perishable, and their type of motility is a species-specific feature; for this reason, species determination and measurements were carried out on live material immediately after return to the laboratory and after silver impregnation (Augustin et al. 1984). Taxonomic identification was based primarily on Foissner and Berger (1996) and Foissner et al. (1999). Biomass was estimated by multiplying the numerical abundance by the mean volume calculated from direct volume measurements using appropriate geometric formulas. An obvious shrinkage of stained ciliates was noted with the protargol preparation. Therefore calculated cell volumes were multiplied by a correction factor of 0.4 (Jerome et al. 1993).

Physicochemical parameters

Water samples for chemical analysis were taken simultaneously with the periphyton samples. The following physical and chemical factors were examined: water transparency, temperature, pH, conductivity, total organic carbon (TOC), chlorophyll (Chl.) *a*, ammonium-nitrogen (N-NH₄), nitrate-nitrogen (N-NO₃), and total phosphates (P_{tot}). Water transparency, temperature, conductivity, dissolved oxygen (DO), and pH were recorded in situ using a multiparametric probe (Hanna Instruments, Padova, Italy). TOC was determined using a multiparametric UV analyzer (Secomam, Alès, France), and the remaining factors were analyzed in the laboratory (Hermanowicz et al. 1976). Chl. *a* was determined by a spectrophotometric analysis of the acetone extract of the algae (Golterman 1969). After

drying at 105°C, the wet mass of periphyton was measured.

Statistical analysis

All data collected were statistically analyzed by means of general linear model (GLM) and CORR procedures of the SAS Program (SAS Institute 2001). Species abundances were analyzed by the main effects analysis of variance (ANOVA). The Shannon-Wiener diversity index (*H'*) was calculated using the Multivariate Statistical Package (MVSP) (Kovach Computing Services 2002). In order to estimate the ciliate species richness, different non-parametric extrapolating indices based on incidence data were used. The Beta diversity index, ($\beta - 1$) that quantifies the change in species composition in time or along an environmental gradient (Harrison et al. 1992), was estimated by: $\beta - 1 = \{[(S/\alpha) - 1] / (N - 1)\} \times 100$, where *S* is the total number of ciliate species recorded for each environmental type; α is the mean number of species found in the samples; and *N* is the number of sampling units. A canonical correspondence analysis (CCA) was performed to relate water chemistry variables to ciliate occurrence. The CCA is a direct ordination technique that selects linear combinations of environmental parameters that maximize the dispersion of species scores (Ter Braak 1986, Jongman et al. 1995). All calculations were performed in PC-ORD (McCune and Mefford 1997). A detrended correspondence analysis (DCA), which only uses species data to constrain the ordination, was used to analyze species

Table 1. Physical, chemical, and biological characteristics of the water of the investigated lakes (average values 2004-2006 ± standard deviation)

Lake	Secchi depth (m)	Temperature (°C)	pH	Conductivity (µs/cm)	Dissolved oxygen (mg/L)	N-NO ₃ (mg N/L)
Phytoplankton-dominated lake ^a	0.53 ± 0.10	14.3 ± 8.2	7.9 ± 1.2	496 ± 46	10.3 ± 2.3	0.14 ± 0.02
Phytoplankton-macrophyte lake ^b	1.1 ± 0.20	15.3 ± 7.3	7.4 ± 1.2	376 ± 33	9.3 ± 2.0	0.021 ± 0.01
Macrophyte-dominated lake ^c	2.3 ± 0.25	15.2 ± 8.4	7.4 ± 0.7	260 ± 34	9 ± 2.0	0.002 ± 0.001

Lake	N-NH ₄ (mg N/L)	P _{tot} (mg P/L)	Total organic carbon (mg C/L)	Chlorophyll <i>a</i> (µg/L)	Periphyton biomass (mg/m ²)
Phytoplankton-dominated lake ^a	0.46 ± 0.11	320.1 ± 23.1	7.4 ± 1.1	130.6 ± 42.3	103.2 ± 43.5
Phytoplankton-macrophyte lake ^b	0.21 ± 0.08	98.2 ± 12.4	5.2 ± 0.8	47.6 ± 12.6	84.2 ± 23.6
Macrophyte-dominated lake ^c	0.11 ± 0.02	37.8 ± 8.2	4.2 ± 0.9	26.6 ± 6.8	67.2 ± 20.2

Trophic type: ^ahypertrophic; ^beutrophic; ^cmesotrophic.

assemblage differences between lakes.

RESULTS

Physicochemical parameters, species richness, abundance, and biomass

Statistically significant differences among the studied lakes were found in water transparency, concentrations of P_{tot}, N-NO₃, N-NH₄, Chl. *a*, TOC, and periphyton biomass ($F = 9.30-9.75, p < 0.0001$, ANOVA) (Table 1).

Altogether, 58 species of ciliates were found in the investigated lakes. Differences in the numbers of ciliate taxa among lakes were statistically significant ($F = 165.38; p < 0.0001$, ANOVA). The results from the non-parametric extrapolating index demonstrated that the observed richness represented 80%-93% of the estimated richness (Fig. 1). The greatest

species richness (50 species) was found in the phytoplankton-dominated lake, 43 species were

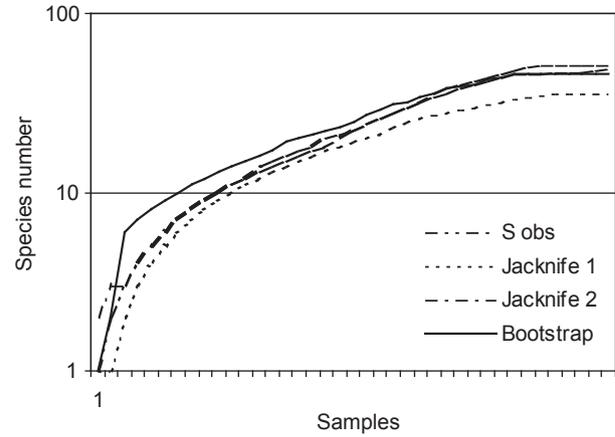


Fig. 1. Results from the non-parametric extrapolating index of the species richness of periphytic ciliates in the investigated lakes.

Table 2. Composition of the major periphytic ciliate taxa found on reed stems in the investigated lakes

Taxon	Phytoplankton-dominated lake	Phytoplankton-macrophyte lake	Macrophyte-dominated lake	Preferred habitat ^a
Cyrtophorida				
<i>Chilodonella uncinata</i> (Ehrenberg, 1838)	+	+	+	P, B
<i>Trochilia minuta</i> (Roux, 1899)	+	+	+	P, B
Haptorida				
<i>Askenasia volvox</i> (Kahl, 1930)			+	PI
<i>Dileptus margaritifer</i> (Ehrenberg, 1838)	+	+		P, B
<i>Enchelys gasterosteus</i> (Kahl, 1926)	+	+		P, B
<i>Enchelys</i> sp.			+	P, B
<i>Lacrymaria olor</i> (Mueller, 1786)	+	+		P, B
<i>Paradileptus elephantinus</i> (Svec, 1897)	+			PI
<i>Plagiopyla nasuta</i> (Stein, 1860)	+			An
<i>Spathidium sensu lato</i>	+	+		P, B, PI
<i>Trachelius ovum</i> (Ehrenberg, 1831)	+		+	P, B, PI
Heterotrichida				
<i>Caenomorpha</i> spp.	+	+		An
<i>Climacostomum virens</i> (Ehrenberg, 1838)	+			B, P
<i>Spirostomum ambiguum</i> (Mueller, 1786)		+		B, P
<i>Stentor</i> sp.	+	+	+	P, B, PI
<i>Stentor multiformis</i> (Mueller, 1786)	+		+	P, B
Hymenostomatida				
<i>Colpidium colpoda</i> (Losana, 1829)	+	+	+	B
<i>Dexiotricha</i> sp. (Kent, 1881)				P, B
<i>Frontonia leucas</i> (Ehrenberg, 1833)	+	+	+	P, B, PI
<i>Lembadion</i> sp.	+		+	B, PI
<i>Ophryoglena</i> spp.	+	+	+	B
<i>Paramecium bursaria</i> (Ehrenberg, 1831)	+	+	+	P, B, PI
<i>Paramecium caudatum</i> (Ehrenberg, 1833)	+			B, PI
<i>Paramecium putrinum</i> (Claparede, Lachmann, 1859)		+		P, B, PI
<i>Philasterides</i> sp.	+			P, B
Scuticociliatida				
<i>Cinetochilum margaritaceum</i> (Ehrenberg, 1831)	+	+	+	P, B, PI

found in phytoplankton-macrophyte lake, and 37 species in the macrophyte-dominated lake (Table 2). It is necessary to point out; however, that the species richness of ciliates was correlated with the total density (Fig. 2). Correlations between the β diversity and the sum of the coefficients of variation of the limnological parameters were not significant and suggested that species changes were not related to limnological variability ($r = -0.37$; $p = 0.126$). The diversity analysis revealed a mean Shannon-Wiener diversity index of 2.32 ± 0.05 . The highest diversity was measured in the phytoplankton-dominated lake

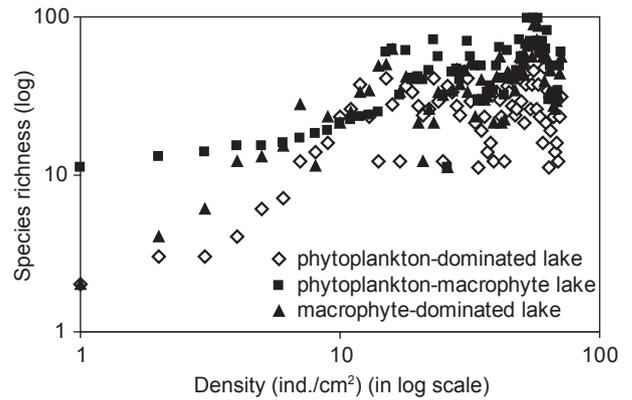


Fig. 2. Relationship between species richness and density.

Table 2. (continued)

Taxon	Phytoplankton-dominated lake	Phytoplankton-macrophyte lake	Macrophyte-dominated lake	Preferred habitat ^a
Hypotrichida				
<i>Aspidisca cicada</i> (Mueller, 1786)	+	+	+	P, B
<i>Euplotes</i> sp.	+	+	+	P, B
<i>Holosticha pullaster</i> (Mueller, 1773)	+	+		B
<i>Stylonychia mytilus</i> -complex	+	+	+	P, B
<i>Urostyla grandis</i> (Ehrenberg, 1830)	+	+		B
Oligotrichida				
<i>Codonella cratera</i> (Leidy, 1877)	+	+	+	PI
<i>Halteria grandinella</i> (Mueller, 1773)	+	+	+	PI, B
<i>Strombidium viride</i> (Stein, 1867)	+	+	+	PI
Peritrichida				
<i>Astylozoon</i> sp.	+			PI
<i>Carchesium</i> sp.		+	+	U
<i>Epistylis</i> sp.		+	+	U
<i>Phascolodon vorticella</i> (Stein, 1859)	+			PI
<i>Pseudovorticella monilata</i> (Tatam, 1870)	+			P, B
<i>Vaginicola crystalina</i> (Ehrenberg, 1830)	+			P
<i>Vorticella convallaria</i> -complex	+	+		P, B, E
<i>Vorticella campanula</i> (Ehrenberg, 1831)	+	+	+	P, B, E
<i>Vorticella microstoma</i> -complex	+	+	+	P, B
<i>Vorticella natans</i> (Faure-Fremiet, 1924)	+	+	+	PI
<i>Vorticella</i> sp.	+	+	+	P, B, PI, E
Pleurostomatida				
<i>Amphileptus claparedii</i> (Stein, 1867)	+	+		P
<i>Amphileptus pleurosigma</i> (Stokes, 1884)	+	+	+	P, B
<i>Amphileptus procerus</i> (Penard, 1922)	+	+	+	B
<i>Litonotus cygnus</i> (Mueller, 1773)	+	+	+	P, B
<i>Litonotus varsaviensis</i> (Wrześniowski, 1866)	+	+		P, B
<i>Litonotus</i> sp.	+	+	+	P, B
<i>Loxophyllum meleagris</i> (Mueller, 1773)		+	+	P, B
Prostomatida				
<i>Bursellopsis</i> sp.	+	+	+	PI
<i>Coleps hirtus</i> (Mueller, 1786)	+	+	+	U
<i>Coleps spetai</i> (Foissner, 1984)	+	+	+	PI
<i>Holophrya</i> sp.	+	+	+	B, PI
<i>Prorodon</i> sp.	+	+	+	P, B
Nassulida				
<i>Chilodontopsis depressa</i> (Perty, 1852)		+		P, B
No. of taxa: 58	50	43	37	

^aAccording to Foissner and Berger (1996): P, periphyton; PI, pelagial; B, benthos; E, epizoic; An, anaerobic; U, ubiquitous (occurring in periphyton, benthos, plankton, and the epizoic zone).

($H' = 2.63$), and the lowest diversity was observed in the macrophyte-dominated lake ($H' = 1.6$). Of all the ciliate species observed, 28 taxa were found in the 3 lakes. Some species were only observed in one of the lakes (a characteristic, exclusive species). In the phytoplankton-dominated lake, the greatest number of 6 taxa exclusive to this lake was noted. These were: *Astylozoon* sp., *Litonotus varsaviensis*, *Paradileptus elephantinus*, *Paramecium caudatum*, *Phascolodon vorticella*, and *Pseudovorticella monilata*. In the macrophyte-dominated lake, *Chilodontopsis depressa*, *Paramecium putrinum*, and *Philasterides* sp. exclusively occurred. *Askenasia volvox* was only found in the phytoplankton-macrophyte lake (Table 2). Numbers of periphytic ciliates on reed surfaces significantly differed among the studied lakes, with the lowest number in the macrophyte-dominated lake (40 individuals (ind./cm^2), a little higher number in the phytoplankton-macrophyte lake (49 ind./cm^2), and the highest number in the phytoplankton-dominated lake (81 ind./cm^2) ($F = 155.33$; $p < 0.0001$, ANOVA). ANOVA indicated that ciliate biomass was significantly higher in the macrophyte-dominated lake (with a mean biomass of $24.6 \mu\text{g/cm}^2$) than in the phytoplankton-dominated and phytoplankton-macrophyte lakes (20.2 and $18 \mu\text{g/cm}^2$, respectively; $F = 111.2$; $p < 0.0001$). The dominance structure in all of the lakes was similar. All of the studied lakes were generally dominated by ciliates belonging to Cyrtophorida (*Chilodonella uncinata*) which constituted $> 28\%$ of the total numbers. Species belonging to the order Cyrtophorida (*Chilodonella uncinata*) constituted 39% to the total number

in the phytoplankton-dominated lake, while species from the orders of Heterotrichida, Oligotrichida, Peritrichida, Pleurostomatida, Prostomatida, and Scuticociliatida constituted 7%-13%. The phytoplankton-macrophyte lake mainly contained species belonging to the order Cyrtophorida (*Chilodonella uncinata*), which constituted 28% of the total number of ciliates. Species belonging to the Heterotrichida, Oligotrichida, Peritrichida, Pleurostomatida, Prostomatida, and Scuticociliatida were also important components (8%-17% of the total numbers). In the macrophyte-dominated lake, species belonging to the Cyrtophorida (*Chilodonella uncinata*), Oligotrichida (*Codonella cratera*), and Heterotrichida (*Stylonychia mytilus*-complex) respectively constituted 28.5%, 23%, and 15% of the total number of ciliates. Ciliates belonging to the other orders reached only 1.6%-6% of the total number (Table 3).

Ciliate abundance and biomass were characterized by spring-autumn maxima in the phytoplankton-macrophyte and macrophyte-dominated lakes, whereas in the phytoplankton-dominated lake, abundance and biomass peaked in spring, summer, and late autumn (Figs. 3A, B). The highest abundances of ciliate communities in the phytoplankton-dominated lake were noted in May, July, and Oct. with dominance by the bacterivorous *Chilodonella uncinata* and *Cinetochilum margaritaceum* and mixotrophic *Coleps hirtus*. In the phytoplankton-macrophyte lake, maxima were noted in May and Oct. with the dominance of *Chilodonella uncinata*, *Cinetochilum margaritaceum*, and *Amphileptus pleurosigma*. In the macrophyte-dominated lake, the highest

Table 3. Dominance structure of periphytic ciliate orders found on reed stems in the investigated lakes (% of total numbers)

Taxon	Phytoplankton-dominated lake	Phytoplankton-macrophyte lake	Macrophyte-dominated lake
Cyrtophorida	39	28	28.5
Hymenostomatida	2	1.6	1.6
Heterotrichida	8	8.6	14.68
Hypotrichida	4	3.7	3.13
Haptorida	2	2.3	1.7
Nassulida	0	0	1.13
Oligotrichida	7.2	13	18
Pleurostomatida	9	8.7	7
Peritrichida	7.2	7.5	6.4
Prostomatida	9	9.5	7
Scuticociliatida	12.73	17	11

cell densities of ciliates occurred in May and Nov. At that time, *Chilodonella uncinata* and the *Stylonychia mytilus*-complex dominated (Fig. 4).

Correlation of environmental variables with periphytic ciliate density

The DCA showed that species compositions of ciliates differed among the investigated lakes (Fig. 5). The ordination also separated the sampling habitats quite well. The phytoplankton-macrophyte lake and macrophyte-dominated lake mostly had high scores on the 1st axis. The phytoplankton-dominated lake was negatively correlated with the 1st axis (Fig. 6). The CCA was based on 10 physical and chemical variables (water transparency, temperature, pH, conductivity, TOC, Chl. *a*, N-NH₄, N-NO₃, and P_{tot}). Chl. *a*, concentrations of TOC, periphyton biomass, and N-NH₄ were the main predictors for ciliate assemblages (*r* = 0.50-0.69). The N-NO₃, P_{tot}, water transparency, and DO played less-

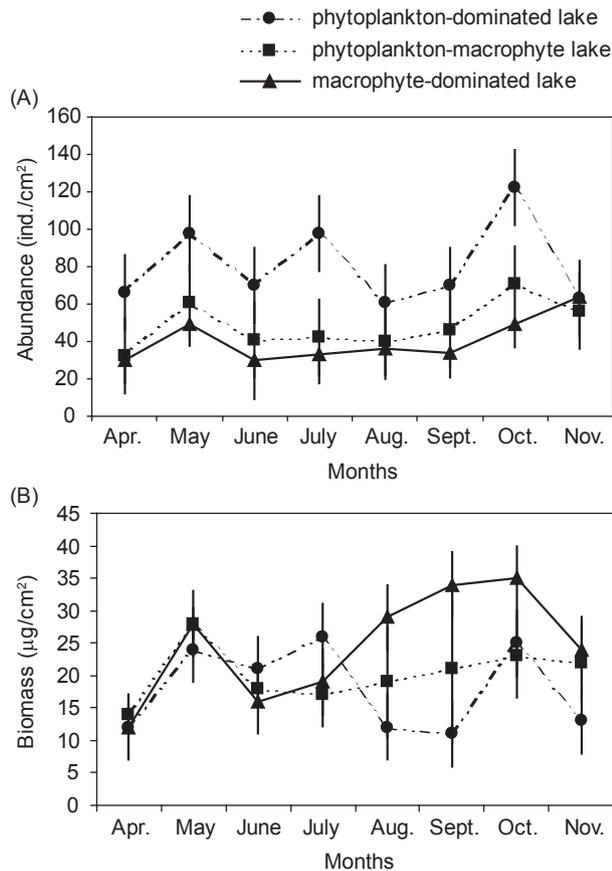


Fig. 3. Seasonal changes in abundance (A) and biomass (B) of ciliates in the investigated lakes (average values for 2004-2006 ± standard deviation).

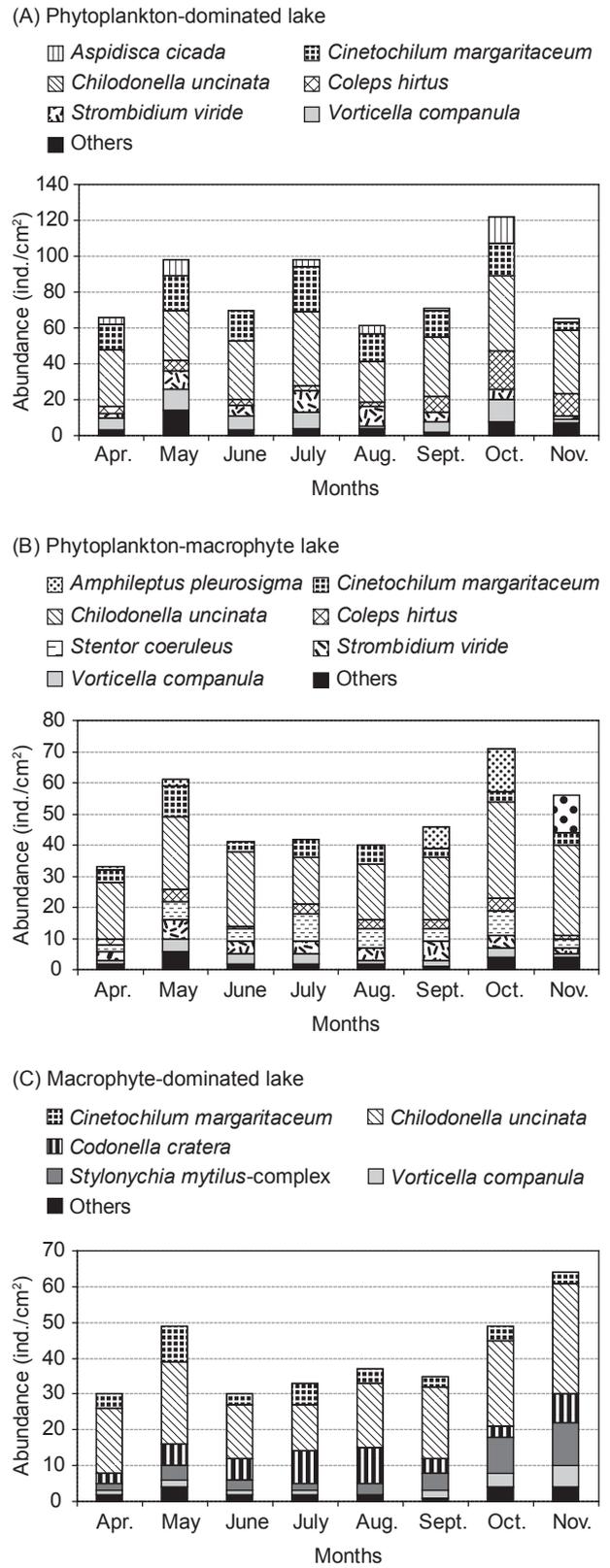


Fig. 4. Changes in the abundances of the dominant protozoan populations in the investigated lakes (average values for 2004-2006).

significant roles ($r = 0.37-0.40$). Classification of environmental changes showed that axis 1 was most closely related to TOC and Chl. *a* and reflects the reaction of ciliates to these factors, while axis 2 was more closely related to the temperature, conductivity, and nutrients. In the CCA diagram, axis 1 accounted for 45% of the total cumulative variance, while axis 2 accounted for 28% of the variance in the ciliate data (Fig. 7). Ciliate communities could be divided into 2 groups. *Aspidisca cicada*, *Chilodonella uncinata*, *Cinetochilum margaritaceum*, *Codonella cratera*, *Halteria grandinella*, *Holosticha pullaster*, *Stentor* sp., the *Stylonychia mytilus*-complex, and *Vorticella* sp. were most frequent and abundant in the phytoplankton-dominated lake where higher concentrations of Chl. *a* and TOC were recorded. On the other hand, *Euplotes* sp., *Paramecium bursaria*, and *Strobilidium viride* were most abundant in the phytoplankton-macrophyte and macrophyte-dominated lakes and were correlated with N-NH₄, N-NO₃, P_{tot}, and temperature (Fig. 7).

DISCUSSION

In the lakes examined, the highest species diversity of ciliates was registered in the phytoplankton-dominated lake, somewhat less

species diversity was found in the phytoplankton-macrophyte lake, while the least was seen in the macrophyte-dominated lake. The total number of species in the phytoplankton-dominated lake (50 taxa) was higher than that observed in other studies (Mieczan 2002). To date; however, there is a lack of data concerning comparisons of periphytic ciliates in other types of lakes. Differences between the observed species number in relation

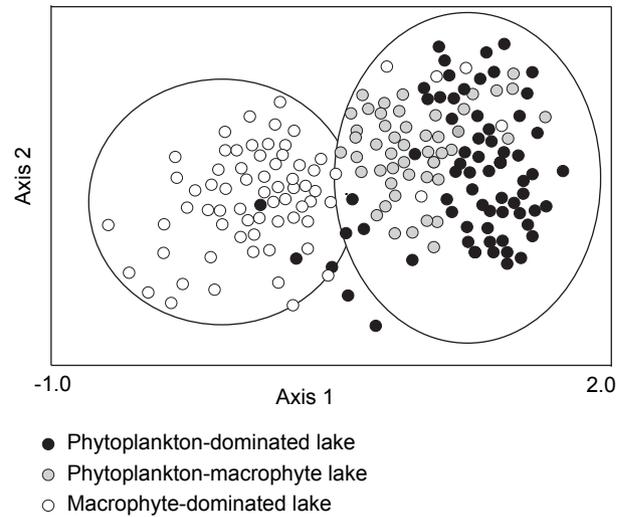


Fig. 5. Sample plot of the detrended correspondence analysis (DCA) of ciliate data.

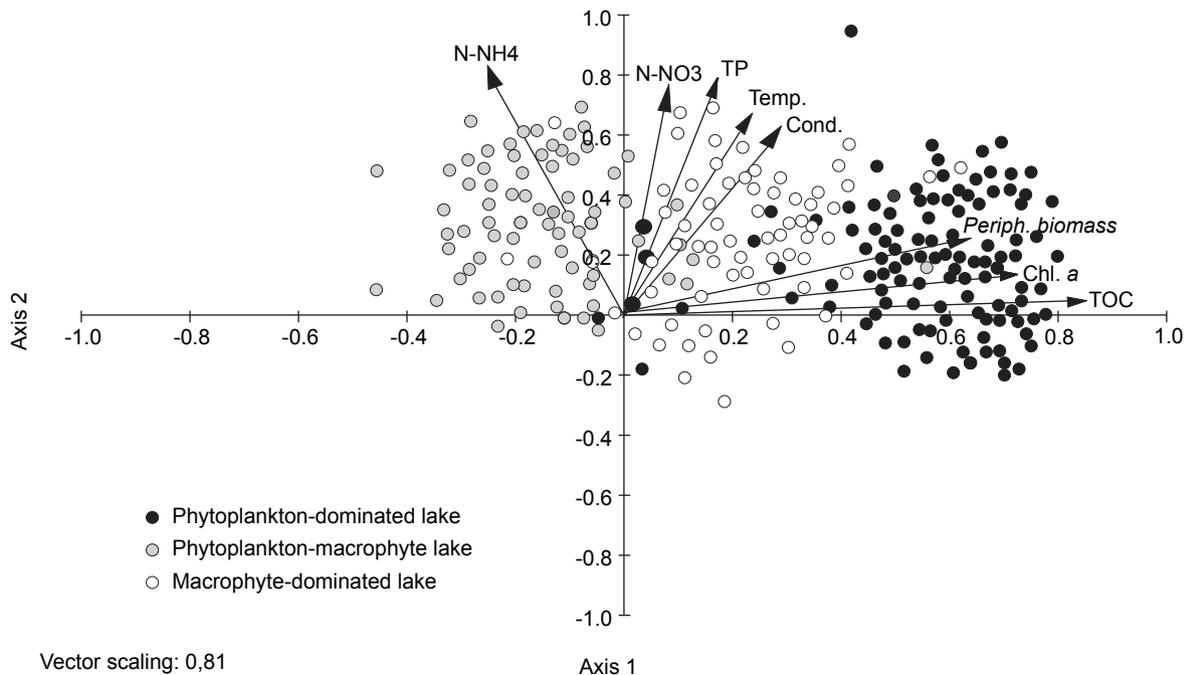


Fig. 6. Canonical correspondence analysis (CCA) ordination diagram: limnological variable coordinates.

to those estimated by non-parametric extrapolating indices can be explained by the higher number of non-periphytic species. According to Harrison et al. (1992), the β diversity is expected to be positively correlated with environmental parameters. This hypothesis was not corroborated by the present study.

Common species that occurred in all of the lakes examined constituted a relatively important group. It may therefore be presumed that the composition of ciliates is not strictly connected with a definite type of lake. Mieczan (2005) investigated periphytic ciliates in 3 lakes of different trophic statuses in Poland, and stated that the Cyrtophorida, Scuticociliatida, and Oligotrichida appeared in lakes from oligo- to eutrophic, whereas Strüdel-Kypke (1999) stated that periphytic Cyrtophorida, Peritrichida, and Prostomatida appeared in dystrophic bog lakes of northern Germany. Domination by the Cyrtophorida (mainly *Chilodonella uncinata*) in all of the studied lakes could have resulted from its wide ecological tolerance (Foissner and Berger 1996, Pérez-Uz et al. 1998, Mieczan 2005 2009).

Groups of characteristic (i.e., exclusive) ciliates, which means that they occurred in only 1

lake, comprising comparatively small numbers of species, very often also have small frequencies and numbers. The least numbers of these species were ascertained in the phytoplankton-macrophyte lake. *Askenasia volvox* was the only species exclusively found in this lake. This species was also observed in planktonic ciliate communities in shallow lakes in an area of France, Germany, and Poland (Sime-Ngando and Grolière 1991, Packroff 1992, Mieczan 2007). The species characteristic of a phytoplankton-dominated lake was *Paradileptus elephantinus*. According to some authors, this species was also seen in eutrophic waters (Laybourn-Parry and Rogerson 1993). In groups of characteristic species of these lakes, *Astylozoon* sp., *Litonotus varsaviensis*, *Paramecium caudatum*, *Phascolodon vorticella*, and *Pseudovorticella monilata* were also found. Research carried out by Foissner et al. (1984) and Belova (1988) confirmed that these species are most often noted in lakes with various eutrophic states. In contrast, in the macrophyte-dominated lake, somewhat less-characteristic species were noted, including: *Chilodontopsis depressa*, *Paramecium putrinum*, and *Philasterides* sp. According to Foissner et al. (1994), these species

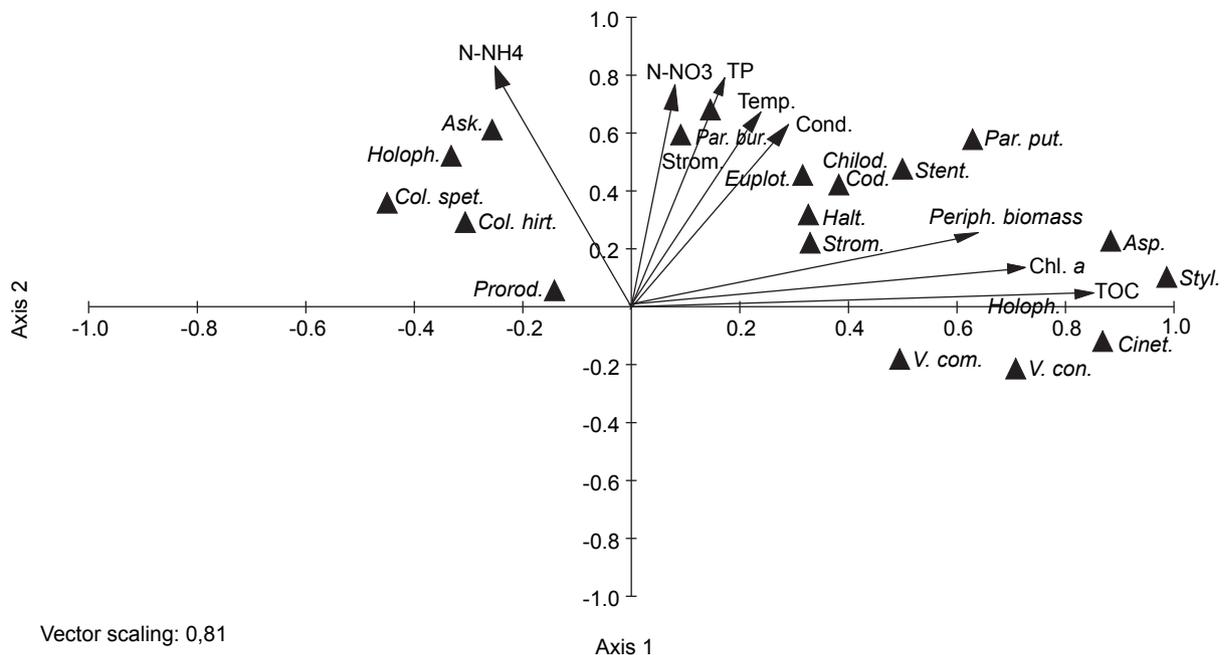


Fig. 7. Canonical correspondence analysis (CCA) ordination diagram showing the relation between environmental variables and common ciliate species. Ask., *Askenasia volvox*; Asp., *Aspidisca cicada*; Chlod., *Chilodonella uncinata*; Cinet., *Cinetochilum margaritaceum*; Col. hirt., *Coleps hirtus*; Col. spet., *Coleps spetai*; Cod., *Codonella cratera*; Euplot., *Euplotes* sp.; Halt., *Halteria grandinella*; Holoph., *Holophrya* sp.; Par. bur., *Paramecium bursaria*; Par. put., *Paramecium putrinum*; Prorod., *Prorodon* sp.; Stent., *Stentor* sp.; Strom., *Strombidium viride*; Styl., *Stylonychia mytilus*-complex; V. com., *Vorticella campanula*; V. con., *Vorticella convallaria*-complex.

occur most often in strongly contaminated water. Some of the exclusive species are typical planktonic and benthic forms. These species probably get at periphyton together with lake water during sample collection. It also seems that planktonic species use the littoral zone (including periphyton mats) as a refuge. The share of typical planktonic species visibly increased in the phytoplankton-macrophyte and macrophyte-dominated lakes. It is probable that macrophytes offer the most attractive environment sufficient for protozooplankton (Mieczan 2007). Some benthic species in the periphyton were probably stirred up by intensive wave action. However, their abundances in the samples remained low, and their ecological impacts on the periphyton community are therefore likely to be small. There are few reports on benthic ciliates being resuspended in the water column in shallow lakes (Nielsen and Kiorboe 1994, Zingel et al. 2006). In the phytoplankton-dominated lake, the density and biomass of ciliates were higher than that found in a phytoplankton-dominated depression reservoir in Poland (Mieczan 2002). According to Velho et al. (2005), the trophic state is essential for determining patterns of variation in spatial and temporal distributions of ciliates. It seems that nutrients have an indirect influence on the prevalence of ciliates through the control of food abundance (mainly bacteria and algae) (Urrutxurt et al. 2003, Mieczan 2009). The higher abundance of protozoan in the phytoplankton-dominated lake was mainly attributed to the abundant algal life, and also the extensive development of bacterial populations stimulated by the decline of *Planktothrix* blooms may have significantly increased the availability of protozoan food resources (Biyu 2000). However, Zingel et al. (2006) demonstrated that the density of ciliates was closely correlated with the biomass of cyanobacteria in lakes in Estonia. The higher density of ciliates in the phytoplankton-dominated lake may also have been the result of the type of periphyton. In this lake, for the complete cycle investigated, *Cladophora* sp. dominated, which created periphyton of a 'filamentous' character. This type of periphyton may create a significant number of microsites for protozoa to use. In the macrophyte-dominated lake, the rapid growth of large macrophytes may absorb a large amount of nutrients of algae, consequently decreasing the growth of ciliates. In general, I observed the highest ciliate biomass in spring and late summer when predation pressure was low, whereas

ciliate populations were strongly reduced in early summer when rotifer and epiphytic Chironomidae abundances were high (Tarkowska-Kukuryk and Mieczan 2008). The strong decline in ciliate populations in early summer was frequently reported in connection with strong predation pressure by *Cricotopus sylvestris* (Tarkowska-Kukuryk and Mieczan 2008). Significantly higher biomass of protozoa in summer and autumn (particular in the macrophyte-dominated lake) could have been additionally related to the great numbers of large-bodied forms, mainly of the *Stylonychia mytilus*-complex. Similar seasonal dynamic variations were observed among periphytic ciliates in lakes with different trophic statuses (Mieczan 2005).

CONCLUSIONS

The physical, chemical, and biological parameters in the water influenced protozoan abundances, and the numbers and strength of this correlation significantly differed in individual lakes. In the phytoplankton-dominated lake, the density of ciliates was strongly correlated with the periphyton biomass and concentrations of chlorophyll *a* and total organic carbon, whereas in the phytoplankton-macrophyte and macrophyte-dominated lakes, the density of ciliates was correlated with concentrations of ammonium-nitrogen, nitrate-nitrogen, and total phosphorus. However, differences in periphytic ciliate community structure among the lakes were mainly driven by the trophic state of the lake rather than by the dominance of primary producers. The results indicate that numbers of ciliates were seasonally variable. Ciliate abundances were characterized by spring-autumn maxima in the phytoplankton-macrophyte and macrophyte-dominated lakes, whereas in the phytoplankton-dominated lake, abundances and biomass peaked in spring, summer, and late autumn.

REFERENCES

- Augustin H, W Foissner, H Adam. 1984. An improved pyridinated silver carbonate method which needs few specimens and yields permanent slides of impregnation ciliates (Protozoa, Ciliophora). *Mikroskopie* **41**: 134-137.
- Baldock B, J Baker, MA Sleight. 1983. Abundance and productivity of protozoa in chalk streams. *Holarctic Ecol.* **6**: 238-246.
- Beech CD, SC Landers. 2002. Ciliated protozoan colonization

- of substrates from Dauphin Island, Alabama. *Eur. J. Protistol.* **1**: 83-89.
- Belova SL. 1988. The species structure of periphytic infusoria associations in the Mezhaik Reservoir. *Biol. Nauki* **88**: 65-67.
- Biyu S. 2000. Planktonic protozooplankton (ciliates, heliozoans and testaceans) in two shallow mesotrophic lake in China - a comparative study between a macrophyte-dominated lake (Biandantang) and an algal lake (Houhu). *Hydrobiologia* **434**: 151-163.
- Boothroyd IKG, BN Dickie. 1989. Macroinvertebrates colonisation of perspex artificial substrates for use in biomonitoring studies. *NZ J. Mar. Freshw. Res.* **23**: 467-478.
- Declerk S, J Vandekerckhove, L Johansson, K Muylaert, JM Conde-Parcuna, K Van Der Gucht et al. 2005. Multi-group biodiversity in shallow lakes along gradients of phosphorus and water plant cover. *Ecology* **86**: 1905-1915.
- Foissner W, H Adam, J Foissner. 1984. Morfologie und Infraciliatur von *Ophrydium eutrophicum* Foissner 1979 und *Ophrydium versatile* O.F. Müller 1786 (Ciliophora, Peritrichida). *Berichte Naturwissenschaftlich-Medizinischen Vereins Innsbruck* **7**: 43-54.
- Foissner W, H Berger. 1996. A user-friendly guide to the ciliates (Protozoa, Ciliophora) commonly used by hydrobiologists as bioindicators in rivers, lakes and waste waters, with notes on their ecology. *Freshwater Biol.* **35**: 375-470.
- Foissner W, H Berger, F Kohmann, eds. 1994. Taxonomische und ökologische Revision der Ciliaten des Saprobien-systems. Hymenostomatida, Prostomatida, Nassulida. Informationsberichte des Bayer. München, Germany: Landesamtes für Wasserwirtschaft.
- Foissner W, H Berger, J Schaumburg, eds. 1999. Identification and ecology of limnetic plankton ciliates. Informationsberichte des Bayer. München, Germany: Landesamtes für Wasserwirtschaft.
- Foissner W, A Unterwiesing, T Henschel. 1992. Comparison of direct stream bed and artificial substrate sampling of ciliates (Protozoa, Ciliophora) in mesosaprobic river. *Limnologica* **22**: 97-104.
- Golterman HL, ed. 1969. Methods for chemical analysis of freshwaters. IBP Handbook no. 8. Oxford: Edinburgh, UK: Blackwell Scientific Publications.
- Grolière CA. 1977. Contribution à l'étude des ciliés des sphaignes: II - Dynamique des populations. *Protistology* **13**: 335-352.
- Hameed HA. 2003. The colonization of periphytic diatom species on artificial substrates in the Ashar Canal, Basrah, Iraq. *Limnologia* **33**: 54-61.
- Harrison S, SJ Ross, JH Lawton. 1992. Beta diversity on geographic gradients in Britain. *J. Anim. Ecol.* **1**: 151-158.
- Hermanowicz W, W Dożańska, J Dolido, B Koziorowski, eds. 1976. Physical and chemical investigation methods of water and sewage. Warsaw, Poland: Arkady.
- Jerome CA, DJS Montagnes, FJR Taylor. 1993. The effect of the quantitative protargol stain and Lugols and Buinos fixatives on cell size: a more accurate estimate ciliate species biomass. *J. Euk. Microbiol.* **40**: 254-259.
- Jongman RHG, CJF Ter Braak, OFR Van Tongeren. 1996. Data analysis in community and landscape ecology. London, UK: Cambridge Univ. Press.
- Jürgens K, E Jeppesen. 1997. Cascading effect on microbial food web structure in a dense macrophyte bed. *Ecol. Stud.* **131**: 262-273.
- Jürgens K, Skibbe O, E Jeppesen. 2000. Impact of metazooplankton on the composition and population dynamics of planktonic ciliates in a shallow, hypertrophic lake. *Aquatic Microbial Ecol.* **17**: 61-75.
- Kaur P, NK Mehra. 1994. An evaluation of a new method for quantitative analysis of epiphytic biota on roots of water hyacinth. *Verhandlungen Int. Assoc. Theor. Appl. Limnol.* **25**: 1137-1141.
- Kaur P, NK Mehra. 1998. Laboratory studies on colonization and succession patterns on periphytic microbiota on artificial and natural substrates. *Verhandlungen Int. Assoc. Theor. Appl. Limnol.* **26**: 1614-1620.
- Kornijów R, W Pęczuła, B Lorens, S Ligęza, J Rechulicz, D Kowalczyk-Pecka. 2002. Shallow Polesie lakes from the view point of the alternative stable states theory. *Acta Agrophys.* **68**: 61-72.
- MVSP. 2002. Multivariate Statistical Package (MVSP). Anglesey, Wales: Kovach Computing Services.
- Laybourn-Parry J, A Rogerson. 1993. Seasonal patterns of protozooplankton in Lake Vindermere, England. *Arch. Hydrobiol.* **129**: 25-43.
- Madoni P, S Zangrossi. 2005. Ciliated protozoa and saprobial evaluation of water quality in the Taro River (northern Italy). *Int. J. Zool.* **72**: 21-25.
- McCune B, MJ Mefford. 1997. Multivariate analysis in ecological data. Version 3.0. Glenden Beach, USA: MjM Software.
- Mieczan T. 2002. Quality and quantity structure of microperiphyton in depression reservoirs (Polesie Lubelskie Region). *Acta Agrophys.* **67**: 181-188.
- Mieczan T. 2005. Periphytic ciliates in littoral zone of three lakes of different trophic status. *Pol. J. Ecol.* **53**: 105-111.
- Mieczan T. 2007. Comparative study of periphytic ciliate communities colonization and succession on natural and artificial substrata in two shallow lakes (eastern Poland). *Ann. Limnol. Int. J. Limnol.* **3**: 179-186.
- Mieczan T. 2009. Ciliates in *Sphagnum* peatlands: vertical micro-distribution, and relationships of species assemblages with environmental parameters. *Zool. Stud.* **48**: 33-48.
- Nielsen TG, T Kiorboe. 1994. Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 2. Ciliates. *Limnol. Oceanogr.* **39**: 508-519.
- Nusch E. 1970. Ökologische und systematische untersuchungen der Peritrichida (Protozoa, Ciliata) im aufwuchs von talsperren und flußstauen mit verchiedenem saprobitätsgrad (mit modellversuchen). *Arch. Hydrobiol.* **37**: 243-386.
- Packroff G. 1992. Faunistic studies on ciliates of three Eifel maar lakes. *Arch. Hydrobiol.* **38**: 209-221.
- Peckham SD, JW Chipman, TM Lillesand, SI Dodson. 2006. Alternate stable states and shape of the lake trophic distribution. *Hydrobiologia* **571**: 401-407.
- Pérez-Uz B, C Franco, M Martin-Cereceda, L Arregui, I Compos, S Serrano et al. 1998. Biofilm characterization of several wastewater treatment plants with rotating biological contactors in Madrid (Spain). *Water Sci. Technol.* **5**: 215-218.
- SAS Institute. 2001. SAS users guide. Vers. 8.2. Cary, NC, SAS Institute.
- Scheffer M, SH Hosper, ML Meijer, B Moss, E Jeppesen. 1993. Alternative equilibriums in shallow lakes. *Trends Ecol.*

- Evol. **8**: 275-279.
- Scheffer M, E Jeppesen. 1998. Alternative stable states. *In* E Jeppesen, M Sondergaard, M Christofersen, eds. The structuring role of submerged macrophytes in lakes. New York: Springer-Verlag, pp. 397-406.
- Sime-Ngando T, CA Groliere. 1991. Effets quantitatifs des fixateurs sur la observation des ciliés planctoniques deau douce. *Arch. Protistenkunde* **140**: 109-120.
- Sládečková A. 1994. The role of periphyton in waste treatment technology. *Verh. Inter. nat. Verein. Limnol.* **25**: 1929-1932.
- Strüdel-Kypke MC, W Schönborn. 1999. Periphyton and sphagnicolous protists of dystrophic bog lakes (Brandenburg, Germany). II. Characteristic species and trophy of the lakes. *Limnologica* **29**: 407-424.
- Tarkowska-Kukuryk M, T Mieczan. 2008. Food preferences of epiphytic Chironomidae in a shallow hypertrophic lake. *Aquat. Insects* **4**: 285-294.
- Ter Braak CJF. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **6**: 1167-1179.
- Urrutxurt I, E Orive, A de la Sota. 2003. Seasonal dynamics of ciliated protozoa and their potential food in an eutrophic estuary (Bay of Biscy). *Estuar. Coastal Shelf Sci.* **57**: 1169-1182.
- Velho LFM, DG Pereira, TA Pagiario, VD Santos, MCZ Perenha, FA Lonsac-Tôha. 2005. Abundance, biomass and size structure of planktonic ciliates in reservoirs with distinct trophic state. *Acta Limnol. Brasil.* **4**: 361-371.
- Wilbert N. 1969. Ökologische untersuchung der aufwuchs- und planktonciliaten eines eutrophen weihers. *Arch. Hydrobiol.* **35**: 411-518.
- Zingel P, H Agasild, T Nöges, V Kisand. 2006. Ciliates are the dominant grazers on pico- and nanoplankton in a shallow, naturally highly eutrophic lake. *Microbial Ecol.* **53**: 134-142.