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Ciliates in *Sphagnum* Peatlands: Vertical Micro-Distribution, and Relationships of Species Assemblages with Environmental Parameters

Tomasz Mieczan

Department of Hydrobiology, University of Life Sciences, Dobrzańskiego 37, Lublin 20-262, Poland

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Tomasz Mieczan (2009) Ciliates in *Sphagnum* peatlands: vertical micro-distribution, and relationships of species assemblages with environmental parameters. *Zoological Studies* **48**(1): 33-48. The distribution of ciliates living among different species of mosses (*Sphagnum angustifolium*, *S. cuspidatum*, *S. flexuosum*, *S. magellanicum*, *Polytrichum strictum*, and *P. commune*) in eastern Poland *Sphagnum* peatlands is described. The highest species richness (23-35 taxa) occurred in hollows dominated by *S. angustifolium*, *S. flexuosum*, and *S. palustre*. Decidedly lower numbers of taxa (7-10) were observed in hummocks dominated by *S. magellanicum* and *Polytrichum*. The greatest abundance of ciliates was found in micro-sites dominated by *S. flexuosum* (25-30 individuals (ind./g), while the lowest was found in sites dominated by *Polytrichum* (4-6 ind./g). Likewise, independent of the species of mosses, micro-vertical differentiation of these protozoa was found. The number of species and abundance significantly increased at the deepest sampling depth. The upper sampling of mosses (0-5 cm) was dominated by mixotrophic taxa, whereas the deeper sampling level (5-10 cm) showed increases in the proportions of bacterivore species. In peatlands, the factors limiting the occurrence of ciliates are physical and chemical suitability — mainly the total organic carbon content and depth of water table (DWT), but also somewhat lower levels of pH and the species of moss. In turn, an increase in pH also increased the role of nutrients. Such factors have a significant effect on the occurrence of ciliates. The abundances of ciliates in spring and autumn were positively correlated with the concentration of organic matter independent of the species of moss; however, in summer, the influence of pH and DWT increased.
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Key words: Ciliates, Micro-distribution, *Sphagnum*, Peatlands.

Peatlands are generally characterized by rich biodiversity and also play key roles in preserving the stability of ecological relationships in particular regions. At the same time, they belong to the fastest disappearing and most endangered ecosystems in Europe. This is especially disquieting in combination with progressive climate warming (Flessa et al. 1998, Robson et al. 2005). Investigations of the structure and function of various types of peatland ecology have mainly been related to the vegetation. Generally, in the whole of Europe and worldwide, very little is known about the microorganisms and their roles in the functioning of these ecosystems. Peatlands, and especially *Sphagnum*-dominated peatlands, were at 1 time erroneously believed to be devoid of microbial life. In reality, and despite the successful use of *Sphagnum* as surgical dressings, diapers, and menstrual pads, *Sphagnum* mosses and peatlands are home to a high diversity of microorganisms (Gilbert and Mitchell 2006). There are relatively few published studies on the subject, probably because of technical difficulties stemming from the abundance of organic matter particles, that make direct observations challenging, and from the range and variability of water contents of the substrate (Gilbert et al. 2000, Gilbert and Mitchell 2006). In a taxonomical approach to

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*To whom correspondence and reprint requests should be addressed. Tel: 48-81-4610061 ext. 306. Fax: 48-81-4610061.
E-mail:tomasz.mieczan@up.lublin.pl

the ecology of fungi, micro-metazoans and invertebrates are usually studied independently, and the focus is usually on the taxonomy of the species restricted to peatlands (Borcard and Vaucher von Ballmoos 1997). By contrast, little or no attention has been given the abundance and trophic structure of ciliates. These microorganisms are important consumers of pico- and nano-sized producers, as well as nutrient regenerators and important food sources for metazoans (Pierce and Turner 1992). Ciliates were studied quite extensively by Grolière (1975 1977 1978). Among the identified genera, some are ubiquitous (*Cyclidium*, *Paramecium*, *Prorodon*, *Spirostomum*, *Spathidium*, and *Vorticella*), whereas others, such as *Bryometopus* and *Climacostomum*, are specific to peatlands. During the 1990s, 2 papers appeared which focused on the distribution of sphagnophilus ciliates in the area of the eastern Antarctica (Foissner 1996, Petz 1997). In recent years, the structure of microorganisms occurring in peatlands was studied by Mitchell et al. (2003). The distinct domination of heterotrophic organisms (78%-97%) of the total microbial biomass was demonstrated. Until now, investigations of the influence of the physicochemical properties on the occurrence of ciliates in peatlands have solely been conducted on micro-sites dominated by *Sphagnum palustre* (Mieczan 2007a b). They showed that the water table depth (WTD) as well as pH were positively correlated with the density and biomass of ciliates. Such an investigation, however, has never been carried out among other species of mosses. One of the particular aims of the present study was the identification of the taxonomic composition and trophic structure of ciliates occurring among different species of mosses in peatlands. Investigations of testate amoebae showed distinct differences in the vertical micro-distribution (Mitchell and Gilbert 2004, Mazei et al. 2007). It seems that similar differences can also be expected to appear in the case of ciliates. Therefore, one of the aims of this study was to analyze the distribution and micro-vertical structure of ciliates. As shown by Mitchell et al. (2000) and Opavilová and Hájek (2006), peat bog ecosystems are characterized by a distinct micro-topography which, as a consequence, leads to a lengthwise gradation of testate amoebae distribution. What is lacking, however, is research on the occurrence of ciliates in this microenvironment. It was established that the hydrological differentiation of the lower clusters of peat and moss is specifically related to the specific physiochemical environment and has a significant influence on the abundance and structure of ciliates. Especially scarce is information concerning the seasonal taxonomic composition variability and abundance of these microorganisms. Information about that is contained in 2 studies. Gilbert et al. (1998) explicitly wrote about the high numbers of these microorganisms in summer and autumn. On the other hand, Mieczan (2007b) analyzed seasonal variations of ciliates in micro-sites dominated by *S. palustre* and precisely elucidated the spring and autumn peak numbers of these protozoa. Investigations of the seasonal dynamics in ciliate numbers among other species of mosses have not so far been undertaken. Hence, the seasonal dynamics of the composition of taxa, and determining the abundance of these microorganisms is particularly significant for a better understanding of the nutrient and energy flows, as well as recognition of reciprocal species-environment dependence.

To sum up, research was undertaken to verify the following hypotheses: that the physiochemical characteristics of waters significantly influence the species structure of ciliates in peatlands; the hydrological and species variability of mosses have a significant influence on the abundance and structure of these microorganisms; the species richness and abundance show distinct differentiation in vertical micro-distribution; and ciliates are subordinate to strongly delineated seasonal changes in species composition and abundance.

MATERIALS AND METHODS

Study site

This study was performed in peatlands located in the western part of the Polesie Lubelskie, eastern Poland 5 (1°N, 23°E) including a unique territory, which is a miniature tundra at its extreme southwestern European location. Its borders encompass the most precious parts of the Poleski National Park, including lakes and floodplains, as well as swamps and peatlands, which have survived to the present in a relatively unaltered condition. The average monthly air temperatures of Jan. and July are -4.1 and 17.9°C, respectively, and the average annual total rainfall is 551 mm (Kaszewski 2002). The vegetation is dominated by graminoids such as *Eriophorum vaginatum* (L.), *Carex acutiformis* Ehrhart., *Carex gracilis* Curt., *Sphagnum angustifolium* (C.C.O. Jensen ex Russow), *S. cuspidatum* Ehrh. ex Hoffm., *S. flexuosum* Dozy and Molk., *S. magellanicum* Bird., and *Polytrichum* sp. (Table 1).

Field sampling and laboratory analyses

Samples of ciliates were collected from different species of mosses (*S. angustifolium*, *S. cuspidatum*, *S. flexuosum*, *S. magellanicum*, *P. strictum*, and *P. commune*). The micro-sites sampled in this study included hummocks, lawns, and hollows. From Apr. to Nov. 2005-2007, 8 samples were collected from the studied peatlands once a month, for a total of 98 samples. A long knife was used to cut plants out from the vegetation. Each sample was packed into a cylindrical plastic container (10 cm in diameter), which was driven into the moss carpet and cut with the knife. To assess the importance of the vertical distribution of ciliates within the mosses, each sample was cut into 2 parts (subsamples): the living green part (0-5 cm) and the dead brown part (5-10 cm). All samples were stored in a cooler and transported within 1 d to the laboratory. Microorganisms were identified in 4 subsamples, each equal to 5% of the original sample. The abundance of microorganisms was

Table 1. Physical and chemical characteristics of the groundwater

Site	Season[a]	DWT (cm)	pH	Temp. (°C)	Conduct. (μS/cm)	N-NO_3(mg NO_3/dm^3)	PO_4^{3-} (mg PO_4/dm^3)	P_{tot}(mg P/dm^3)	TOC(mg C/dm^3)	Moss species sampled
Blizionki/Lejno 1 (B1)	Spring	13	3.8	8.6	63.9	0.328	0.001	0.039	64.2	*Sphagnum magellanicum, Polytrichum strictum*
	Summer	16	2.52	17.6	53.4	0.599	0.104	0.192	75.5	
	Autumn	13.2	3.6	1.3	85.3	0.170	0.035	0.539	98.2	
Blizionki/Lejno 2 (B2)	Spring	6	3.8	8.5	27.2	0.474	0.027	0.333	66.4	*S. flexuosum*
	Summer	7	3.8	17.4	195.5	0.534	0.050	0.041	77.5	
	Autumn	6	3.4	1.3	85.4	0.376	0.049	0.576	96.5	
Durne Bagno 1 (DB1)	Spring	9	4.7	7.2	117.2	1.654	0.343	0.503	46.2	*S. angustifolium*
	Summer	8	3.64	17.0	157	1.658	0.070	0.286	38.9	
	Autumn	6	3.84	2.4	86.3	1.182	0.333	0.460	53.2	
Durne Bagno 2 (DB2)	Spring	-6	4.43	8.1	99.5	1.079	0.182	0.338	54.3	*S. angustifolium*
	Summer	2	4.64	17.0	94	1.019	0.109	0.147	41.2	
	Autumn	-8	3.94	2.1	75.5	0.663	0.316	1.038	63.2	
Długie (D)	Spring	28	3.2	7.3	39.8	0.600	0.100	0.236	55.2	*S. magellanicum, P. strictum, P. commune*
	Summer	31	3.2	17.3	45.1	0.299	0.288	0.320	66.9	
	Autumn	29	3.4	2.1	45.3	0.662	0.122	0.365	66.2	
Moszne 1 (M1)	Spring	6	3.3	7.9	69	0.762	0.439	0.753	78.2	*S. flexuosum, S. cuspidatum*
	Summer	9	2.4	16.0	73.6	0.449	0.060	0.180	58.8	
	Autumn	9	3.92	2.3	54.5	0.058	0.040	0.358	69.8	
Moszne 2 (M2)	Spring	28	3.2	7.3	34.6	0.622	0.110	0.336	52.3	*S. magellanicum, P. strictum, P. commune*
	Summer	32	2.1	17.3	71.8	0.299	0.288	0.320	66.9	
	Autumn	29	3.3	2.1	45.3	0.662	0.122	0.366	79.2	
Moszne 3 (M3)	Spring	7	4.13	8.1	48.6	0.367	0.091	0.123	43.2	*S. flexuosum, S. palustre*
	Summer	8	3.1	8.2	81.3	1.195	0.081	0.092	96.5	
	Autumn	8	3.90	2.3	54.4	0.058	0.040	0.353	99.8	
Krugłe Bagno/Jelino 1 (J1)	Spring	-6	3.85	8.2	34.7	0.513	0.002	0.149	40.5	*S. angustifolium*
	Summer	-2	4.90	19.1	26.3	0.200	0.075	0.119	33.9	
	Autumn	-8	4.01	1.3	26.0	0.376	0.049	0.576	46.9	
Krugłe Bagno/Jelino 2 (J2)	Spring	12	4.2	8.2	26.0	0.377	0.091	0.120	43.2	*S. magellanicum*
	Summer	14.5	3.9	17.4	53.4	0.238	0.021	0.079	28.9	
	Autumn	11	4.1	1.3	33.2	0.379	0.111	0.229	38.6	

For the period Apr.-Nov. 2005-2007, [a]spring, average values for the period Apr.-June; summer, average values for the period July-Aug.; autumn, average values for the period Sept.-Nov. DWT, depth to water table; Temp., temperature; Conduct., conductivity; P_{tot}, total phosphorus; TOC, total organic carbon.

calculated based on 1 g of plant material. In order to determine ciliates, 4 samples were preserved with Lugol solution. Ciliates were enumerated and identified with an inverted microscope at 400-1000x magnification. Quantitative sampling and counting were performed with classical limnological methods using the Utermölh technique (Utermölh 1958). 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 returning to the laboratory and after silver impregnation (Augustin et al. 1984). The species were determined by means of the following methods: the intravital method which colors vacuoles with indifferent red (that stains macronuclei) and micro- and macro-nuclei with malachite green (Lee et al. 1985); the protargol method which colors cell structures with protein silver (kinetosomes, surface structures, and the citopharynx) (Wilbert 1975); and the Fernandezo-Galiano method which colors cell structures in an ammoniac solution (kinetosomes, and micro- and macronuclei) (Fernandezo-Galiano 1994). The trophic group was identified using the method of Foissner and Berger (1996).

Once a month, physical and chemical factors (depth to the water table (DWT), pH, temperature, conductivity, nitrate-N ($N\text{-}NO_3$), phosphate-P ($P\text{-}PO_4$), total phosphorus (P_{tot}), and total organic carbon (TOC) were examined. The DWT was measured with a ruler in centimeters. The top of the peat moss was taken as 0. The temperature, pH, and conductivity were determined *in situ* using a multiparametric probe (Hanna Instruments), TOC was determined using the multiparametric UV analyzer (Secomam, France), and the remaining factors were analyzed in the laboratory (Hermanowicz et al. 1976).

Statistical analyses

Diversity analysis (Shannon-Wiener diversity index ($\log_{10}$-based)) was performed using the Multivariate Statistical Package (MVSP) (Kovach Computering Services, 2002). The Gini evenness measure was calculated because of the independence of the number of taxa per sample which therefore allowed better comparisons between samples (Nijssen et al. 1998). Additionally, rarefaction was used to compare species richness among micro-sites, using EcoSim vers. 5.0 (Gotelli and Graves 1996). All statistical analyses were carried out using the SAS Program (2001). All abiotic and biotic data were log-transformed to approximate a normal distribution and to linearize bivariate relationships. Full-factorial analysis of variance (ANOVA) was used to test for significant effects of the independent factors (type of micro-site, vertical micro-distribution, and time) on ciliate species richness and abundance. Relationships between microbial communities and environmental variables were analyzed using a redundancy analysis (RDA) (Ter Braak 1988-1992). Species data were transformed prior to the analysis using the Hellinger distance (Rao 1995). This transformation allowed the use of Euclidian-based methods such as RDA rather than Chi-squared distance-based methods such as canonical correspondence analysis (CCA) to analyze species data. This option was recently suggested as a way to overcome a problem associated with the Chi-squared metric: rare species may have a much larger influence on the analysis than common species (Legendre and Gallagher 2001). Monte Carlo permutation tests were used to determine the significance of the variables. Non-significant variables were included as passive variables as in a redundancy analysis. Correlations between abundance of ciliates and environmental factors (seasonal aspect) were assessed using Spearman correlation coefficients.

RESULTS

Environmental variables

The DWT significantly fluctuated during the sampling periods. The water table was highest in spring and the sampling sites were the wettest, whereas the water table was lowest and the sites were driest during summer. In the samples, the DWT gradient ranged from -8 (i.e., submerged) to 32 cm, with a pH range of 2.1-4.90, a conductivity range of 26-195 μS/cm, and a TOC range of 28.9-99.8 mg C/dm^3. Conductivity and nutrients reached the highest values at high-pH micro-sites. The TOC content reached the highest values in low-pH micro-sites. Descriptions of the sampling sites with coordinates, parameters measured, and moss species found are given in table 1.

Ciliate species richness

Species richness significantly varied with depth, season, and habitat type. There was also a significant interaction between micro-distribution and time (Table 2). The highest species richness (27-35 taxa) occurred in hollows dominated by *S. angustifolium*, *S. cuspidatum*, *S. flexuosum* and *S. palustre*. Decidedly lower numbers of taxa (7-10) were observed in hummocks dominated by *S. magellanicum* and *Polytrichum*. The diversity analysis revealed a mean Shannon-Wiener diversity index of 0.92 ± 0.05 and a Gini-evenness measure of 0.39 ± 0.01. The highest diversity was measured in hollows (H' = 1.23), and the lowest diversity was observed in hummocks (H' = 0.03). The mean number of taxa/sample was 11 ± 1, with a maximum of 35 taxa in samples in hollows and a minimum of 2 taxa in hummocks. Considering hummocks, lawns, and hollows as a single habitat across the entire sampling region, levels of species richness in lawns and hollows were greater than those in hummocks (by rarefaction analysis) (Fig. 1). The greatest species richness occurred in the spring and autumn periods. The species richness increased with depth and was higher for the deeper level (brown part, 5-10 cm), compared to the living green part (0-5 cm) (Table 3). The Shannon-Wiener diversity index ranged from 1.33 for the deepest part to 0.33 for the green, living part; Gini evenness values were 0.31 and 0.23, and numbers of taxa/sample were 34 and 4, respectively. Jaccard's index of similarity ranged 50%-65%. The group of characteristic (i.e., exclusive) taxa, which means those occurring with only 1 species of moss, was composed of a comparatively small number of taxa. The species occurring exclusively in *S. magellanicum* was *Platyophyra vorax*. The species typical of mosses occurring in low-pH environments and with appreciable levels of water (*S. angustifolium*) was *Leptopharynx costatus*. In turn, in a microenvironment with considerable dampness as well as pH > 4 dominated by *S. flexuosum*, 2 characteristic species occurred: *Aspidisca costata* and *Chilodontopsis depressa*. The 2 most frequent species, i.e., which occurred in all studied mosses (*Paramecium bursaria* and *Par. putrinum*) are eurytopic forms particularly common in all freshwater ecosystems (Table 3).

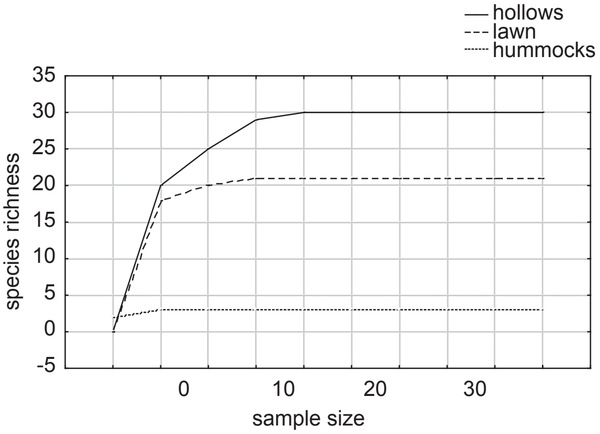


Fig. 1. Rarefaction plot of species richness in hummocks vs. lawn and hollows.

Abundance

From the full-factorial ANOVA, the vertical micro-distribution, site, and time of year in which the material was collected all had statistically significant influences on the number of ciliates. It follows from the statistical analysis that the type of environment (hummocks, lawns, and hollows) had the greatest influence along with time. Additionally, interactions between vertical micro-distribution and site and between site and time were significant (Table 2). The highest abundances of ciliates were noted in micro-sites dominated by *S. flexuosum* (25-30 ind./g), while the lowest were

Table 2. Effect of micro-distribution (1), micro-sites (2), and time (3) and their interactions on ciliates species richness and abundance

	Number of species				Abundance			
	d.f. [a]	*d.f.* [b]	*F*	*p*	*d.f.* [a]	*d.f.* [b]	*F*	*p*
Micro-distribution (1)	1	8	7.6	0.0220	1	8	6.20	0.0432
Micro-sites (2)	1	8	20.04	0.0001	11	88	3.94	0.0001
Time (3)	11	88	1.90	0.0423	11	88	2.16	0.0123
1 x 2	11	8	3.12	0.0270	11	8	3.12	0.0270
1 x 3	11	88	1.23	0.3974	11	88	1.03	0.2275
2 x 3	11	88	1.10	0.3977	11	88	2.14	0.0241
1 x 2 x 3	11	88	0.50	0.7714	11	88	0.48	0.8814

[a] Main effects degree of freedom; [b] error degrees of freedom.

Table 3. Composition and frequency (% of samples) of ciliate taxa found in Sphagnum-dominated peatlands

Taxon	Size (μm)	Main food[a]	Moss species													
			S. ang.		*S. cusp.*		*S. flex.*		*S. mag.*		*S. pal.*		*P. str.*		*P. comm.*	
			U	L	U	L	U	L	U	L	U	L	U	L	U	L
Amphileptus claparedii (Stein, 1867)	> 50	P		10		10		10								
Amphileptus pleurosigma (Stokes, 1884)	> 200	P		20		19		10		10		10				
Askenasia volvox (Kahl, 1930)	< 50	A, M		40		35		21				23				
Aspidisca costata (Mueller, 1786)	< 50	B						20								
Chilodonella uncinata (Ehrenberg, 1838)	> 50	B		15		15		70				85		10		
Chilodontopsis depressa (Perty, 1852)	> 50	B, A						20								
Cinetochilum margaritaceum (Ehrenberg, 1831)	< 50	B, A		65		66	21	57				75				
Chlamydonella spp.	< 50	B										20		10		
Codonella cratera (Leidy, 1877)	> 50	A		65		70		21				25				
Coleps hirtus (Mueller, 1786)	> 50	O		20		20		10				10				
Coleps spetai (Foissner, 1984)	> 50	A, M						15				10				
Colpoda steinii (Maupas, 1883)	< 50	B						69				80		21		23
Colpoda cucullus (Muller, 1773)	> 50	O		10		10		20				45				28
Colpidium colpoda (Losana, 1829)	> 50	O	23	85	25	90	24	25				65		55		
Cyclidium glaucoma (Muller, 1773)	< 50	B		10		11		10								
Cyrtohymena muscorum (Kahl, 1932)	> 50	O		5		5		5		20						
Didinium sp.	> 50	P						5				10				
Disematostoma tetraedricum (Faure-Fremiet, 1924)	> 50	A, M		21		22		30								
Euplotes sp.	> 50	O		10		10		10		20						
Gastronauta spp.	< 50	A										10		10		
Holosticha pullaster (Mueller, 1773)	> 50	B, A		60		55		20								21
Kahlilembus attenuotus (Smith, 1897)	< 50	B		29		33						30				
Lacrymaria olor (Mueller, 1786)	> 200	P		10		8		10								
Leptopharynx costatus (Mermod, 1914)	< 50	B, A		20												
Litonotus sp.	> 200	P						10								20
*Loxophyllum meleagri*s (Mueller, 1773)	> 200	P						10		15						
Oxytricha sp.	> 50	O								30		21				
Paradileptus elephantinus (Svec, 1897)	> 200	O		10		10		20								
Paramecium bursaria (Ehrenberg, 1831)	> 50	B, A,M	90	30	80	46	89	70	90	80	90	70	90	75	80	70
Paramecium putrinum (Claparade, Lachmann, 1859)	> 50	O	93	30	63	40	70	65	82	75	80	80	65	65	90	62
Platyophrya vorax (Kahl, 1926)	< 50	O								20	20					
Podophrya sp.	> 50	P		10		12		10		25						
Prorodon sp.	> 200	P						10				20				
Spathidium sensu lato	> 50	P		10		10		10								
Spirostomum ambigum (Mueller, 1786)	> 200	O		3		3		10								
Stentor amethystinus (Leydy, 1880)	> 200	B, A, M						10				15				
Stentor coeruleus (Ehrenberg, 1830)	> 200	O		5		6		8								
Stokesia sp.	> 50	B, A, M						5		10						
Strombidium viride (Stein, 1867)	> 50	B, A, M		25		24		35				55				
Stylonychia mytilus-complex	> 200	O		30		28		45								23
Tokophrya sp.	> 50	P						5				10				
Trachelius ovum (Ehrenberg, 1831)	> 200	P		10				18								
Vorticella companula (Ehrenberg, 1831)	> 50	B, A						5				21				
Urostylla grandis (Ehrenberg, 1830)	> 200	O								20		10				
Total species number			3	27	3	25	4	35	2	10	3	23	2	7	2	7

[a] Trophic groups: A, algivores; B, bacterivores; M, mixotrophs; O, omnivores; P, predators (Foissner and Berger 1996). *S. ang.*, *Sphagnum angustifolium*; *S. cusp.*, *S. cuspidatum*; *S. flex.*, *S. flexuosum*; *S. mag.*, *S. magellanicum*; *S. pal.*, *S. palustre*; *P. str.*, *Polytrichum strictum*; *P. comm.*, *P. commune*; U, upper assemblage 0-5 cm; L, lower assemblage 5-10 cm.

in micro-sites dominated by *Polytrichum* (4-6 ind./g). The abundance of ciliates was decidedly higher in hollows compared to hummocks (Fig. 2). The most abundant species among mosses occurring in an environment with a very low pH (*S. angustifolium*, *S. cuspidatum*, and *S. palustre*) and appreciable concentrations of TOC were *Colpidium colpoda* and *Chilodonella uncinata*, while *Holosticha pullaster* was dominant in micro-sites at pH > 4. In all species of mosses examined, there were appreciable vertical differences in the abundances of protozoa. In the uppermost sampling of mosses, the abundance of ciliates was the lowest, and in general only the mixotrophic *Paramecium* dominated, whereas in the deepest sampling abundances were appreciably higher with domination by *Colpidium colpoda*, *Chilodonella uncinata*, and *Cinetochilum margaritaceum* (Figs. 3, 4A, B). Generally, however, independent of the moss species in environments at pH < 4, 2 abundance peaks were observed in spring and autumn (maximum); whereas in micro-sites at pH

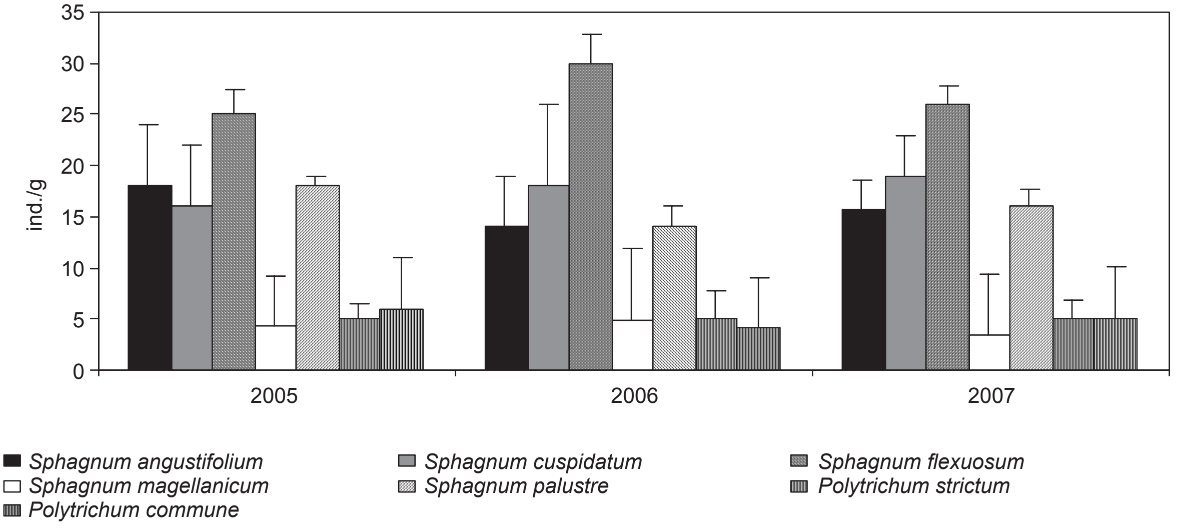


Fig. 2. Average (Apr.-Nov.) density of ciliates associated with the investigated species of mosses.

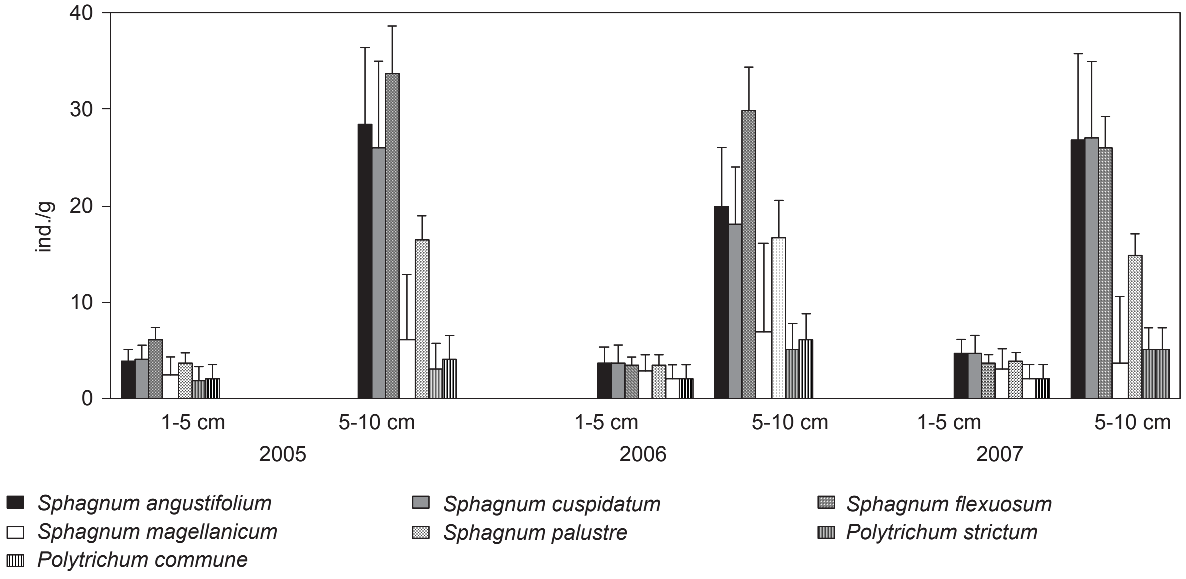


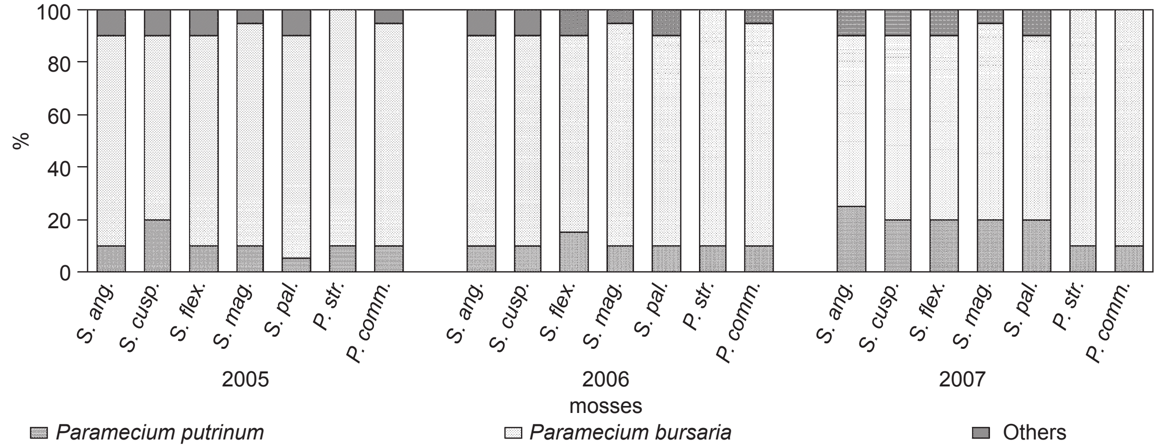
Fig. 3. Average (Apr.-Nov.) density of ciliates associated with the investigated species of mosses along a vertical gradient (0-5 and 5-10 cm).

> 4, a summer peak was also observed (Figs. 5A, B). In spring and autumn, *Chilodonella uncinata* and *Colpidium* sp. dominated. In summer, besides *Chilodonella*, numerous *Cinetochilum margaritaceum*, *Paramecium burasria*, and *Strombidium viride* also occurred.

Size classes and feeding groups

Ciliates combined from all sampling dates and sites were dominated by medium-sized ciliates (50-200 μm) comprising of up to 50%-90% of the total. Small species (15-50 μm) represented 10%-45% and large ciliates (> 200 μm) 10%-23% of the samples. Size classes of ciliates clearly differed between individual species of mosses. *Sphagnum magellanicum* and *Polytrichum* were dominated by large forms; however, the remaining moss species were dominated by small and medium ciliates. In the upper sampling of mosses, medium-sized species dominated, whereas in the deeper sampling, the proportion of small species clearly increased (Figs. 6A, B). Ciliate feeding groups consisted of bacterivores, algae-diatom feeders, mixotrophic ones, predators, and omnivores (Table 3). Bacterivore taxa clearly dominated among *S. angustifolium*, *S. cuspidatum*, *S. flexuosum*, and *S. palustre* (30%-45%). In turn, *S. magellanicum* and *Polytrichum* were dominated by omnivorous and mixotrophic ciliates, at

(A) Upper assemblages (1-5 cm)



(B) Lower assemblages (5-10 cm)

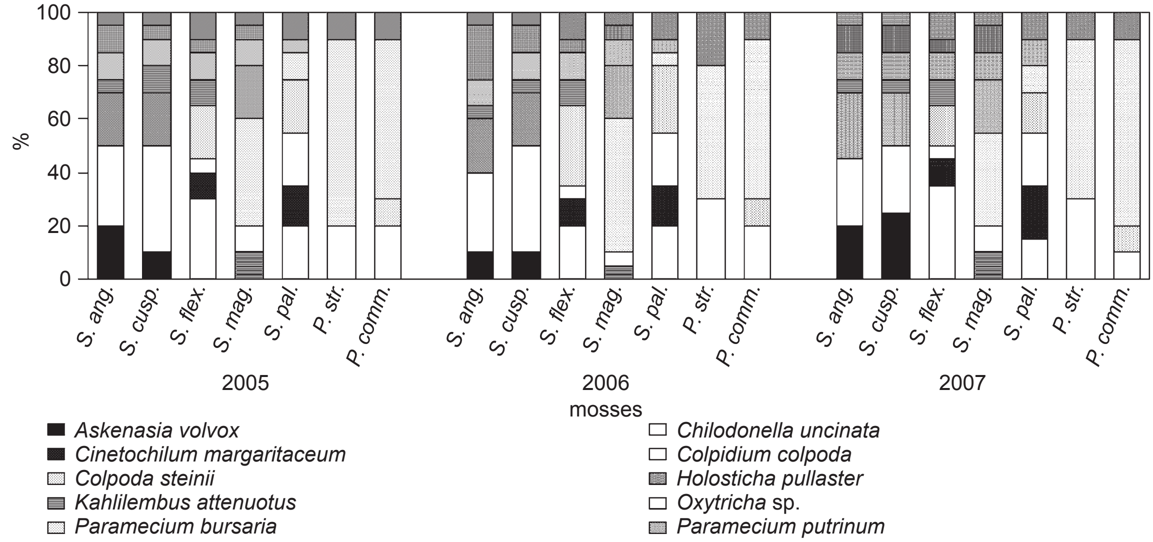


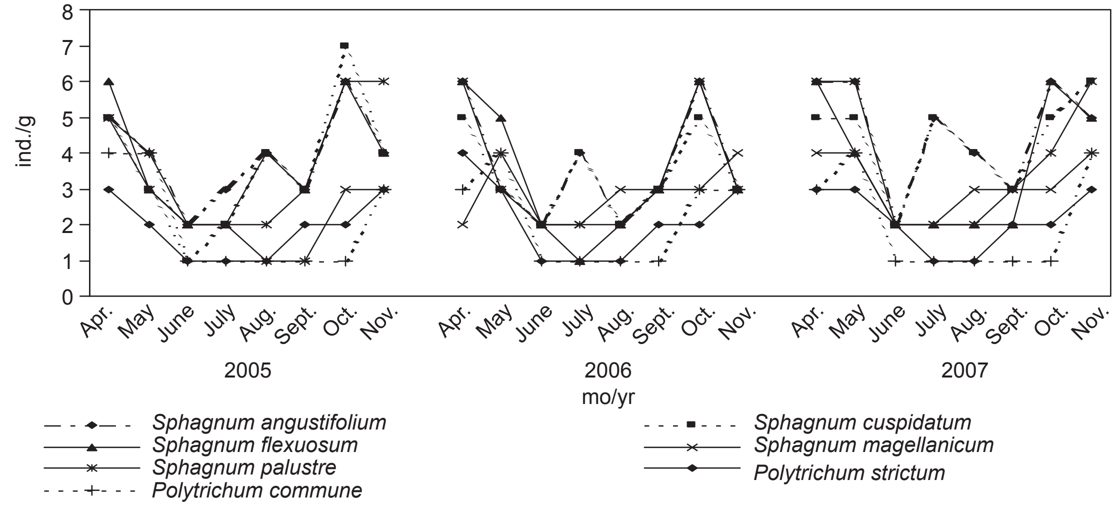
Fig. 4. Domination structure of ciliates associated with the investigated species of mosses along a vertical gradient (% of total numbers).

25%-30% of the total number. The upper sampling of the mosses was dominated by mixotrophic taxa, whereas the deeper sampling level showed increased proportions of bacterivore species (Figs. 7A, B).

Correlations of ciliates with environmental variables

The ordination also separated the sampled habitats and moss species quite well. Hummock sites dominated by *S. magellanicum*, *P. commune*, and *P. strictum* mostly had high scores on the 1st axis. Hollows and lawn sites colonized by *S. angustifolium*, *S. cuspidatum*, *S. flexuosum*, and *S. palustre* were negatively correlated with the 1st axis (Fig. 8A). In the RDA of ciliate data, 4 environmental variables were significant: DWT, pH, TOC, and P_{tot}. Together, these variables explained 54% of the variation in the species data. WTD and TOC were positively correlated with the 1st axis, while pH and P_{tot} were positively correlated with the 2nd axis. Monte Carlo permutation tests (Ter Braak 1988) on these variables showed that DWT and concentrations of TOC were significant at $p <$ 0.001. The pH gradient and P_{tot} gradient (vectors) were shorter and played less significant roles than the other two. The RDA ordination showed that species could be separated into 3 groups. The 1st group included species associated with

(A) Upper assemblages (1-5 cm)



(B) Lower assemblages (5-10 cm)

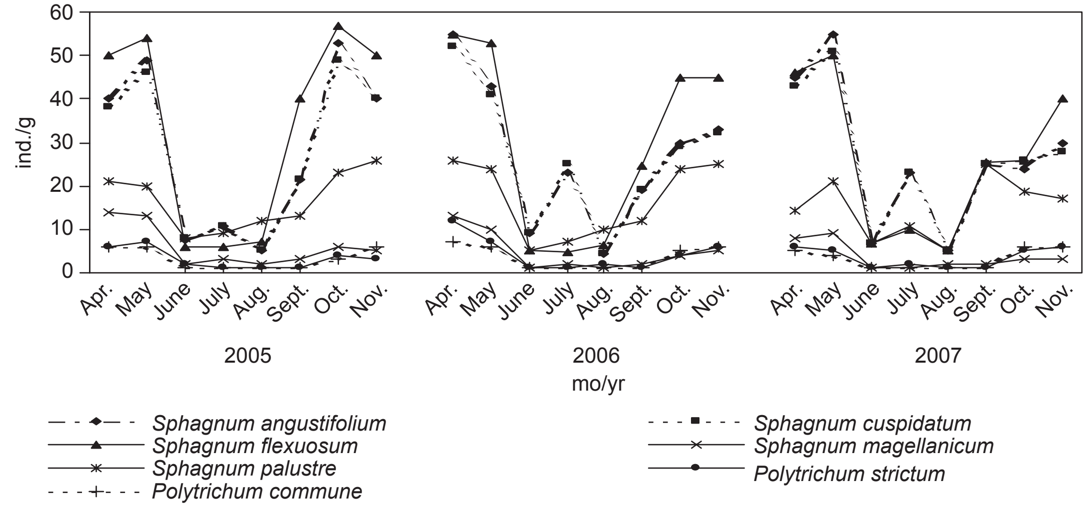


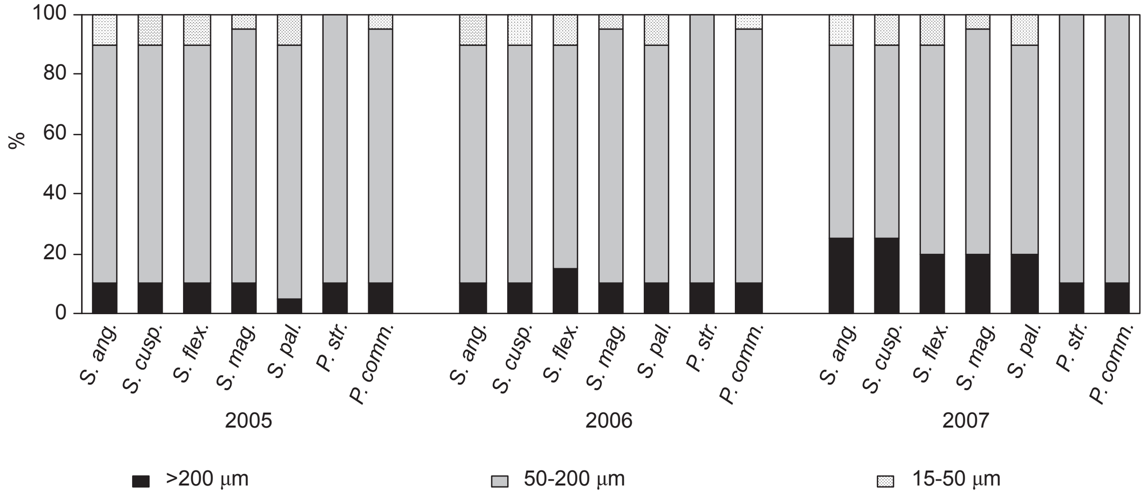
Fig. 5. Seasonal patterns of the density of ciliates associated with the investigated species of mosses along a vertical gradient.

high DWT values (i.e., dry conditions) and low pH (*Paramecium bursaria* and *Par. putrinum*). The 2nd group included species that were associated with low DWT values (wet conditions), low pH, and high TOC contents (*Chilodonella uncinata*, *Cinetochilum margaritaceum*, *Colpidium colpoda*, *Colpoda steinii*, *Codonella cratera*, *Disematostoma tetraedricum*, *Holosticha pullaster*, *Kahlilembus attenuotus*, *Strombidium viride*, and the *Stylonychia mytilus*-complex). The 3rd group included species associated with high-pH conditions, mid-range DWT, and lower concentrations of TOC (*Askenasia volvox*, *Oxytricha* sp., and *Vorticella companula*) (Fig. 8B). Results showed that ciliate abundances were more dependent on pH in summer (Spearman coefficient of correlation $r = 0.63$, $p \leq 0.01$). In spring and autumn, contents of TOC and nutrients were probably the major regulators of the abundance of ciliates ($r = 0.32$-0.64 and $r = 0.41$-0.51, $p \leq 0.05$, respectively) (Table 4).

DISCUSSION

In the investigated mosses, 7-35 ciliate taxa were found. In the peatlands of the Poleski National Park (Łęczna-Włodawa Lakeland, E. Poland) in micro-sites dominated by *S. palustre*, 15-23 species of ciliates occurred (Mieczan 2007a). The number of species of ciliates

(A) Upper assemblages (1-5 cm)



(B) Lower assemblages (5-10 cm)

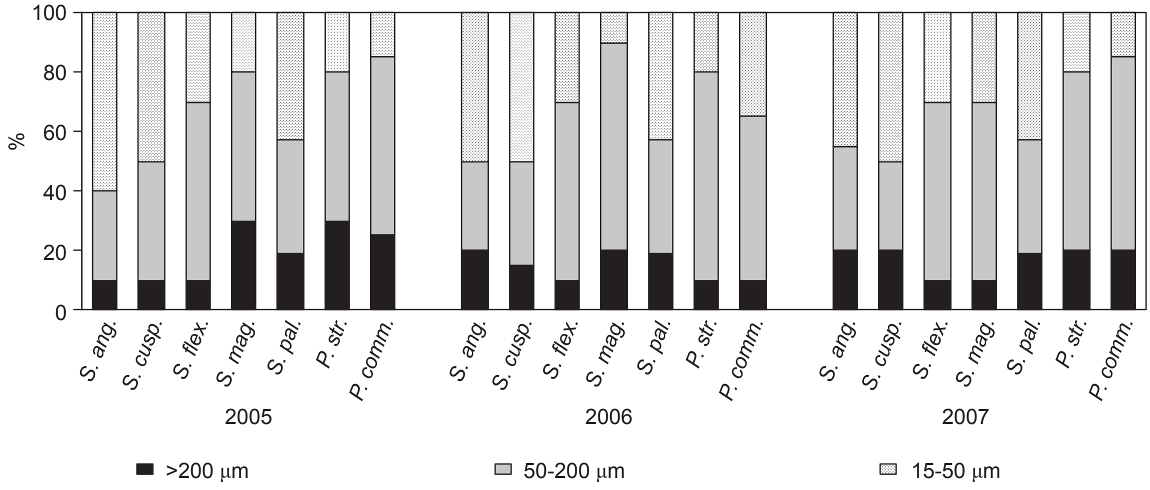
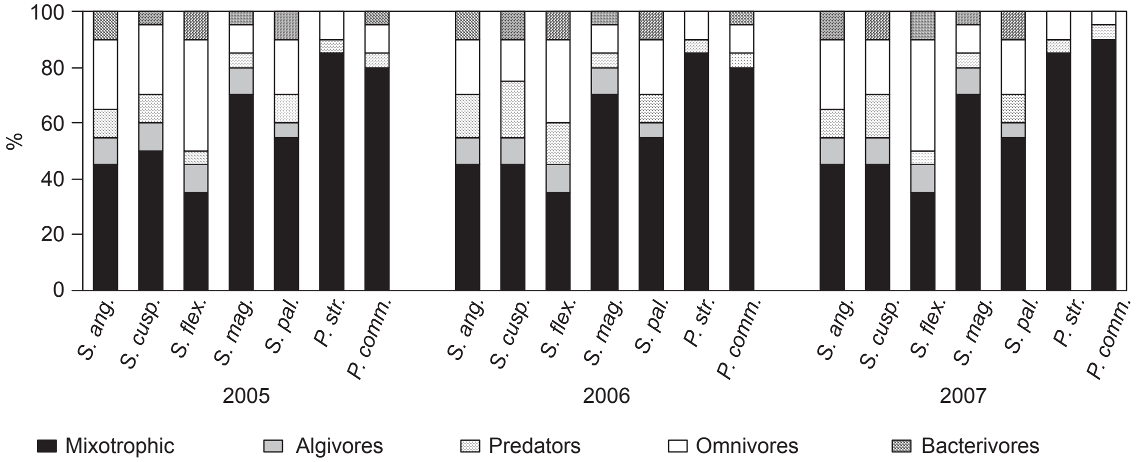


Fig. 6. Percentages of the dominant size classes for ciliates associated with the investigated species of mosses.

increased with a decrease in pH, and increases in TOC concentrations and moisture conditions. The opposite tendency, however, was observed in a lake ecosystem where low pH values clearly limited the number of ciliate taxa (Crisman and Brezonik 1980, Mieczan 2007c). It seems that in peatlands, the factors influencing to the highest degree of ciliate species richness are the organic carbon content and moisture. The present study shows the significant relationship between ciliate species richness and type of microenvironment. Therefore, in hollows dominated by *S. angustifolium*, *S. cuspidatum*, *S. flexuosum*, and *S. palustre*, significantly higher numbers of species were noted in comparison to hummocks dominated by *S. magellanicum* and *Polytrichum*. Bobrov et al. (2007) observed a clear increase in the variety of species of testate amoebae in hollows. In comparatively large groups of ciliates, as much as 48% of the total number of taxa was composed of common taxa, i.e., occurring in all moss species studied. It may be that the species composition of ciliates is not strictly connected to definite moss species, but to a significantly high degree is dependent on the physical and chemical suitability of the microenvironment. Groups of characteristic (i.e., exclusive) ciliates, which means that they occur with only 1 species of moss comprising comparatively small numbers of taxa, very often also have small frequencies and numbers. The genus occurring exclusively in *S. magellanicum* was *Platyophyra*. This genus

(A) Upper assemblages (1-5 cm)



(B) Lower assemblages (5-10 cm)

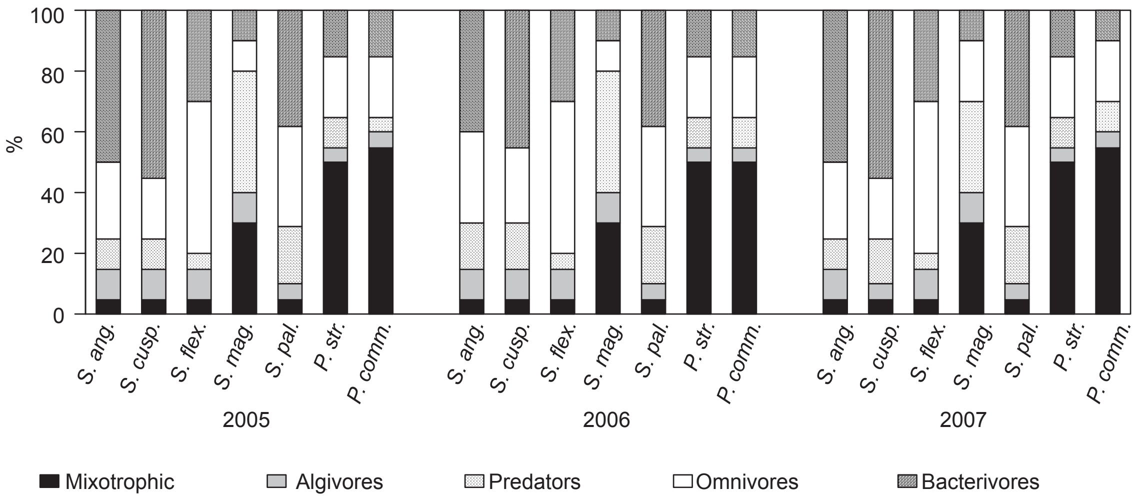


Fig. 7. Percentages of dominant feeding groups for ciliates associated with the investigated species of mosses.

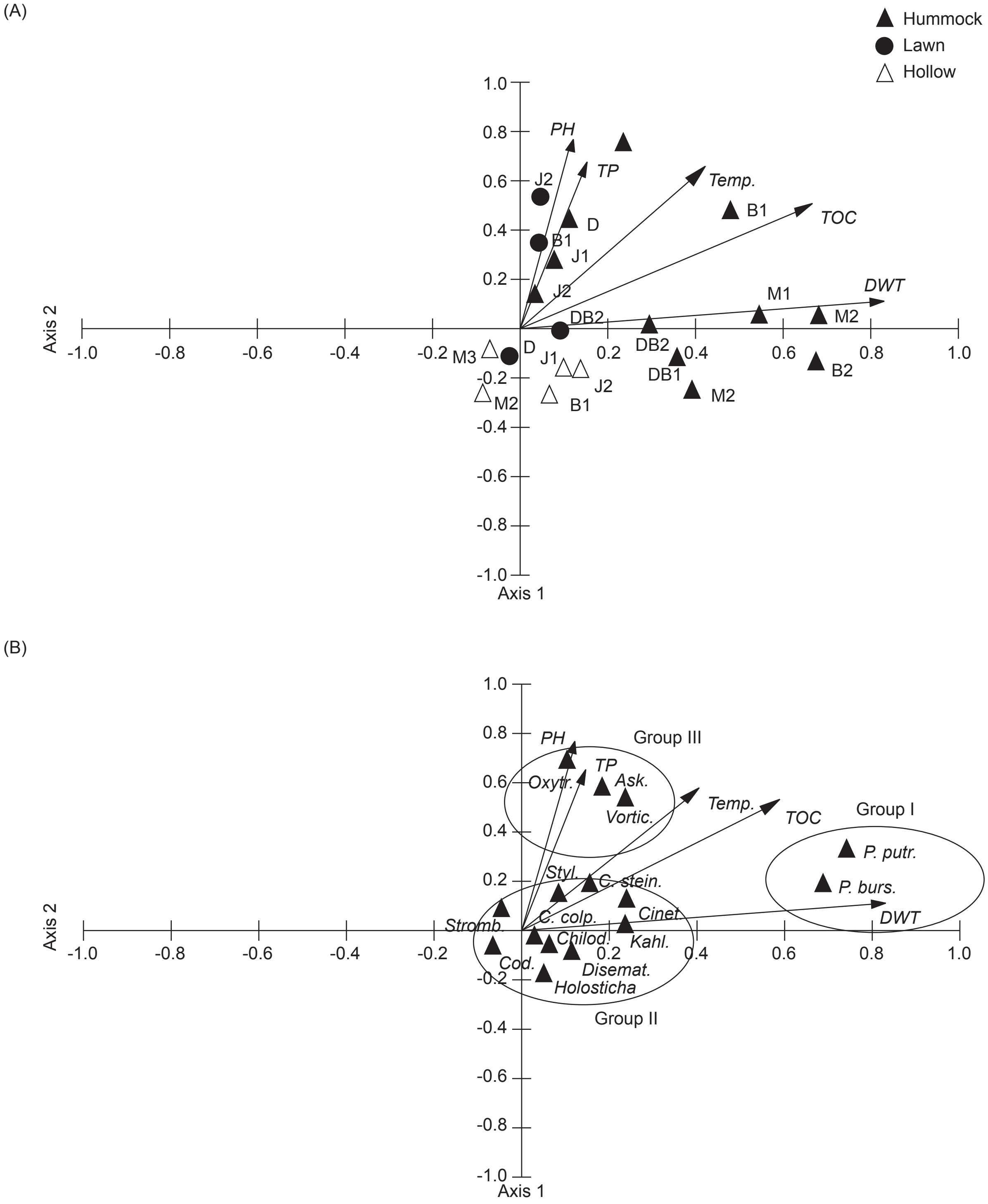


Fig. 8. Biplots of the RDA analysis of ciliate data from *Sphagnum*-dominated peatlands with representation of samples (symbols, in A), species (lines, in B) and environmental variables (arrows, in both biplots). Species data were log-transformed, and rare species were down-weighted (*Ask., Askenasia volvox*; *Chilod*., *Chilodonella uncinata*; *Cinet*., *Cinetochilum margaritaceum*; *Cod*., *Codonella cratera*; *C. colp*., *Colpidium colpoda*; *C. stein*., *Colpoda steinii*; *Disemat*., *Disematostoma tetraedricum*; *Kahl*., *Kahlilembus attenuotus*; *Holosticha*, *Holosticha pullaster*; *Oxytr*., *Oxytricha* sp.; *P. burs*., *Paramecium bursaria*; *P. putr*., *Paramecium putrinum*; *Stromb*., *Strombidium viride*; *Styl*., *Stylonychia mytilus*-complex; *Vortic*., *Vorticella companula*).

was also seen in mosses in the upper soil layer (Foissner and Berger 1996, Bamforth et al. 2001). The characteristic species in mosses occurring in environments with low pH and DWT values (i.e., wet conditions) was *Leptopharynx costatus*. According to 1 study (Foissner et al. 1994), this species occurs most often in oligo- and beta-mesosaprobic environments. Grolière (1977) stated that this species did not occur in *Sphagnum*-dominated peatlands in an area of France, whereas Strüdel-Kypke and Schönborn (1999) reported its occurrence on glass slides exposed in dystrophic lakes in Germany. In turn, in micro-sites with an appreciable water level and pH > 4, 2 characteristic taxa occurred: *Aspidisca costata* and *Chilodontopsis depressa*. These species were also observed in periphytic ciliate communities in mezotrophic, eutrophic, and dystrophic lakes (Mieczan 2005). Similar to species richness, the number of ciliates was also significantly higher in hollows compared to hummocks. Moreover, the number of ciliates observed in particular species of mosses which dominated the hollows were differentiated into 2 separate groups. Differentiation was probably the result of pH, the TOC content, and fertility of the micro-sites. The 1st group, with the highest number, was comprised of mosses (*S. cuspidatum* and *S. flexuosum*) which occur in environments with a very low pH value and a higher concentration of TOC. The 2nd group, with a distinctly lower number of ciliates, occurred in micro-sites at pH > 4, but with a lower concentration of TOC (*S. angustifolium*). The abundance of ciliates observed was close

Table 4. Spearman correlation coefficients between ciliate density and physical and chemical factors of the investigated peatlands (average values for period Apr.-Nov. 2005-2007)

Site name	Season	DWT	pH	Temp.	Conduct.	N-NO_3	PO_4^{3-}	P_{tot}	TOC
Blizionki/Lejno 1 (B1)	Spring	0.33*	0.35*	-	-	-	-	-	0.56**
	Summer	0.40*	0.40*	0.41*	-	-	-	-	0.40*
	Autumn	0.31*	0.31*	-	-	-	-	-	0.64**
Blizionki/Lejno 2 (B2)	Spring	0.40*	0.40*	-	-	-	-	-	0.60**
	Summer	0.46*	0.44*	0.40*	-	-	-	-	0.48*
	Autumn	0.38*	0.40*	-	-	-	-	-	0.73**
Durne Bagno 1 (DB1)	Spring	0.43*	0.44*	-	-	-	0.43*	0.51*	0.41*
	Summer	0.54**	0.48*	-	-	-	-	-	0.40*
	Autumn	0.33*	0.36*	-	-	-	-	0.48*	0.43*
Durne Bagno 2 (DB2)	Spring	0.43*	0.43*	-	-	-	0.41*	0.43*	0.40*
	Summer	0.48*	0.45*	0.42*	-	-	-	-	0.36*
	Autumn	0.45*	0.42*	-	-	-	0.44*	0.51*	0.42*
Długie (D)	Spring	0.33*	0.40*	-	-	-	-	-	0.48*
	Summer	0.41*	0.43*	0.45*	-	-	-	-	0.37*
	Autumn	0.38*	0.38*	0.39*	-	-	-	-	0.56**
Moszne 1 (M1)	Spring	0.40*	0.38*	-	-	-	-	-	0.48*
	Summer	0.42*	0.42*	0.42*	-	-	-	-	0.42*
	Autumn	0.40*	0.40*	-	-	-	-	-	0.55*
Moszne 2 (M2)	Spring	0.35*	0.38*	0.39*	-	-	-	-	0.47*
	Summer	0.38*	0.48*	0.40*	-	-	-	-	0.32*
	Autumn	0.33*	0.36*	-	-	-	-	-	0.51**
Moszne 3 (M3)	Spring	0.51**	0.51**	-	-	-	-	-	0.51**
	Summer	0.55**	0.54**	0.48*	-	-	-	-	0.48*
	Autumn	0.50**	0.48*	-	-	-	-	-	0.58**
Krugłe Bagno/Jelino 1 (J1)	Spring	0.47*	0.46*	-	-	-	-	-	0.36*
	Summer	0.47*	0.49*	0.48*	-	-	-	-	0.33*
	Autumn	0.46*	0.46*	-	-	-	-	0.43*	0.41*
Krugłe Bagno/Jelino 2 (J2)	Spring	0.35*	0.35*	-	-	-	-	-	0.45*
	Summer	0.41*	0.41*	0.52*	-	-	-	-	0.41*
	Autumn	0.33*	0.38*	-	-	-	-	-	0.48*

$^*p \le 0.05$; $^{**}\ p \le 0.01$, -, not significant. DWT, depth of the water table; Temp., temperature; Conduct., conductivity; P_{tot}, total phosphorus; TOC, total organic carbon.

to that found in *S. palustre* (Mieczan 2007a). In the upper layer of mosses, the number of ciliates was lower and the total number was dominated by *Paramecium*, whereas in the lower layer the number was distinctly higher. Groups of bacterivore species increased but mixotrophic species decreased with depth. Significant groups of mixotrophic taxa in the upper, living part of the mosses were observed as were incidental testate amoebae (Strüdel-Kypke 1999). Such a significant difference in the vertical distribution was probably a result of the degree of dampness and fertility of the micro-sites. A clear paucity of mixotrophic taxa in the lower part of the mosses could also be a consequence of unutilized light conditions. A similar regularity was observed in *Sphagnum* mats in dystrophic peat bog lakes in Germany (Strüdel-Kypke 1999). In habitats with very low pH values, Colpodea, Cyrtophorida, and Heterotrichida occurred as the most numerous taxa, and were determined to be permanent components throughout the entire period of the study. Oligotrichida (*Strombidium viride*) also had a significant contribution. They occurred in large numbers in a microenvironment with an appreciable level of water where *S. angustifolium*, *S. cuspidatum*, and *Sphagnum S. palustre* were dominant. However, the contribution of the Scuticociliatada (*Cinetochilum margaritaceum*) increased with a rise in the pH level. Colpodea (*Colpidium colpoda*) and Cyrtophorida (*Chilodonella uncinata*) occur in great numbers as well in oligotrophic environments, such as eutrophic areas. In turn, the Scuticociliada as a rule occurs in great numbers in eutrophic waters and is also observed in humic lakes, as well as in peat bog ecosystems (Järvinen 1993, Mieczan 2007a). Beaver and Crisman (1981) showed that the Oligotrichida clearly dominates in waters at pH < 5. In turn, research conducted in recent years has shown that the Heterotrichida dominates in ecosystems with very low pH values (Packroff 2000). Furthermore, Beaver and Crisman (1981) observed the occurrence of small ciliates, with dimensions of 20-30 μm, increasing to dimensions of 40-50 μm, with the greater acidity of lake water. Similar situations occurred in the present study. As demonstrated by research conducted by Finlay (1980), water temperature likewise has a significant, favorable influence on the occurrence of ciliates in reservoirs with considerable fertility. The present study also showed that in an ombrotrophic environment, the temperature had a significant influence on the number of ciliates. Many ciliates occur in waters with a broad temperature range, or are eurythermic, and higher temperatures usually cause an abundant growth of ciliates (Mieczan 2007b). Similarly, in peatlands, the strongest correlation between temperature and abundance of microorganisms was observed in summer. It seems that in peatlands, the factor with the greatest influence on the occurrence of ciliates is the TOC content. In every habitat, the TOC content in the water was positively correlated with the abundance of ciliates, although the strength of this connection was significantly higher in micro-sites at pH < 4. A clear correlation between the organic matter and total numbers of ciliates was also observed in European humic lakes (Amblard et al. 1995). According to Fischer et al. (1998), the abundance and production of bacteria in peatlands also significantly increase together with an increase in the organic matter content in the water, and with a drop in the pH. In microenvironments at pH < 4, the strongest favorable correlation occurred between ciliate abundances and nutrient contents in the water. Independent of the species of mosses in a habitat at pH < 4, 2 peaks occurred in abundance in spring and autumn, although in habitats at pH > 4, a summer peak in ciliate numbers was also found. The greatest abundance of ciliates in micro-sites at pH < 4 conforms to regular significant levels of water and maximum concentrations of TOC in the water; whereas in micro-sites at pH > 4, this conformed to a higher concentration of total phosphorus. Similar seasonal dynamics were also observed in micro-sites dominated by *S. palustre*, with pH values from strongly acidic to neutral (Mieczan 2007a).

CONCLUSIONS

It therefore seems that in peatlands, relationships between ciliates and species of mosses do not necessarily imply a direct ecological link between the 2 types of organisms, but is explained by the fact that the moisture conditions of micro-sites primarily define the niches of moss species. In accordance with the 1st and 2nd hypotheses, in peatlands, factors limiting the occurrence of ciliates are physical and chemical parameters: mainly the total organic carbon content and water table depth, but also somewhat lower levels of pH. In turn, the increase in pH also increases the role of nutrients. Such factors significantly determine the occurrence of ciliates. This study showed clear seasonal patterns in densities of assemblage of ciliates. The abundances of ciliates in spring and autumn were positively correlated with the concentration of total organic carbon; however in summer, the influences of pH and water table depth increase. Likewise, independent of the species of mosses, micro-vertical differentiation of these protozoa was found. A similar number of species, like the abundance, significantly increased at the deeper sampling depth. The upper level of the mosses was dominated by mixotrophic taxa, whereas the deeper sampling level showed an increase in the proportion of bacterivore species.

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