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INFLUENCE OF TYPE OF SUBSTRATE AND WATER CHEMISTRY ON THE STRUCTURE AND SUCCESSION OF PERIPHYTIC CILIATE COMMUNITIES IN HYPERTROPHIC LAKE

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Abstract: The aims of the study was to establish whether differences exist between periphytic ciliate communities on different substrates; to determine whether colonization time would yield an abundance and taxonomic composition of ciliates; to assess the effect of physical and chemical factors on the distribution of ciliates in a shallow hypertrophic lake. Generally the species richness as well as the abundance of periphytic ciliates are determined mostly by the habitats and chemical properties of the waters (especially the content of total organic carbon and nitrate nitrogen), and, to a lesser extent, by the type of the colonized substrate. Moreover, exposition time of the substrates affected both an increase in the richness of periphytic ciliates and the changes in their trophic structure. At the beginning of the experiment the substrates were intensively colonized by typically bacterivorous species, yet prolonged exposition time resulted in an increasing proportion of omnivorous species.

INTRODUCTION

In recent years, there has been renewed interest in studies of colonization and successional patterns of periphytic communities on artificial and natural substrates [13, 16]. A few investigators have noted that artificial substrates are biased with respect to characterizing natural communities, while others argue that natural substrates pose problems with sampling design and quantification [13]. The periphyton forms on the surface of artificial and natural substrata of freshwater lakes and rivers and it consists of mucilage of slime, bacteria, algae, fungi, protozoa and small metazoans [10]. Periphyton plays a very important role in carbon fixation and nutrient cycling in aquatic ecosystems. Natural substrata that maintain periphyton are different in origin and size; this variability in the nature of substrata, and the corresponding variation of microbial communities, has always made quantitive studies difficult. To facilitate such studies, artificial substrata have been used for several years. Their usage simplifies the natural complexity and reduces the disruption of the habitat because there is no need to remove large amounts of natural substrata. Furthermore, since the total surface area is known, problems with the measurement of irregular natural substrata are eliminated. Because of their uniform size and inert surface, glass slides are among the most frequently used artificial substrata [13, 16]. Many recent studies have shown that ciliates play a very important trophic role in periphytic communities [19, 20, 24]. Protozoa are known to be an important food source for metazoa and effectively transfer picoplanktonic production to higher trophic levels. They can feed on bacteria, auto- and heterotrophic pico- and nanoplankton and provide dissolved organic matter as nutrients to bacteria. Rapid growth, high turnover rates and short generation times allow protozoan communities to respond immediately to changing environmental conditions. Hence many species can be highly valuable bioindicators in water quality analyses [22, 24]. However, still more attention is paid to planktonic ciliates of marine and river ecosystems [1, 2, 22]. In Polish limnological studies only a few publications have reported abundance and taxonomic composition of periphytic ciliata on natural substrates in eutrophic lakes [19, 20, 21]. Another publication dealing with periphytic ciliates presented mainly the data on ciliate numbers belonging to the order Peritrichida on *Phragmites australis* in oligo-, mezo- and eutrophic Hungarian lakes [17]. Spatial distribution of periphytic ciliates on natural substrates in a eutrophic lake has been also studied by Primc-Habdija *et al.* [24]. Boothroyd and Dickie [5] have reported the presence of similar epiphytic communities on macrophytes as well as on natural and artificial substrates. To date, no research has been carried out on periphytic ciliates on natural and artificial substrates in the hypertrophic lakes.

The aim of the present study, therefore, was to establish differences between periphytic ciliate communities on different substrates; to determine whether colonization time would yield an abundance and taxonomic composition of ciliates; to assess the effect of physical and chemical factors on the distribution of ciliates in shallow hypertrophic lake.

STUDY AREA, MATERIALS AND METHODS

Samples were collected in a hypertrophic Lake Syczyńskie (surface area 6.0 ha, max depth 4.0 m). Lake Syczyńskie is situated on Pagóry Chełmskie. Its southern shore borders with carbonate peat-bogs, while the rest of the lake is surrounded by village Syczyn [14, 15]. Lake Syczyńskie is characterized by intensive development of emergent vegetation, dominated by reed (*Phragmites australis* (Cav.) Trin. ex Steud.) and temporal blooms of *Planktotrix agardhii* (Gomont).

The periphyton was collected from the reed stems and glass slides in littoral zone at a depth of 0.1–0.5 m. Three perspex frames with 6 microscopic glass-slides (2 x 5 cm each) were placed near the *Phragmites* bed. The frames were placed horizontally and the slides vertically. Sampling was done monthly from April to November 2007. On each sampling occasion 6 periphyton samples were collected from each type of substrate. New substrata were then placed for colonization in the next month. One sample consisted of 10 cm^{-2} of periphyton taken from the macrophyte stems and glass-slides by means of a scalpel. In order to determine the density of ciliates, 4 samples were fixed with Lugol's solution (1% v/v) and settled for at least 24 h in plankton chambers. The laboratory experiment was performed in order to trace the colonization and succession patterns of periphytic ciliate communities on particular types of substrates. In laboratory conditions natural (stems of *Phragmites australis*) and artificial substrates (glass slides) were placed in three aquariums (depth of 0.1–0.5 m) filled with water collected from the studied lake. Three aquariums, contained sediment of about 4–5 cm depth to serve as a benthic substrate. The microcosms were maintained at 20 ± 2°C. The course of substrates colonization processes was observed during the period of one month, in 4-day intervals. The ciliates were counted and identified with an inverted microscope at magnification x 400–1000. Taxonomic determination was based primarily on Foissner and Berger [8], Foissner *et al.* [9].

The water samples for chemical analyses were taken simultaneously with the periphyton samples. Direct water measurements comprised transparency, by means of a Secchi disc, pH and conductivity using an electrode. Concentrations of $N\text{-}NO_3$ and P_{tot} were done according to Hermanowicz *et al.* [11]. Total organic carbon (TOC) was determined by using the PASTEL UV.

One-way ANOVAs were run on the number of species per square centimeter and total number of cells on the reed stems and glass slides. Correlation between physical and chemical parameters and ciliate density were analyzed by calculating Pearson's correlation.

RESULTS

Physicochemical properties of water

Physicochemical properties of water were different in particular months. The transparency of water (SD) was the lowest in summer (August – 0.23 m) and the highest in early spring (0.54 m). Water pH did not reveal any significant differences and in all months it amounted to the values adequate for neutral or alkaline water (pH = 7.3–8.42). Conductivity was the highest in October, reaching 496 $\mu S \cdot cm^{-1}$. In the remaining months its values were from 339 $\mu S \cdot cm^{-1}$ to 495 $\mu S \cdot cm^{-1}$. The mean concentration of oxygen varied from 10.3 mg $O_2 \cdot dm^{-3}$ in April to 12.4 mg $O_2 \cdot dm^{-3}$ in August. Total organic carbon content fluctuated between 6.4 mg $C \cdot dm^{-3}$ in summer and > 7.7 mg $C \cdot dm^{-3}$ in spring and autumn. The mean content of nitrate nitrogen was 0.07 mg $N \cdot dm^{-3}$, reaching its highest values in autumn. Total phosphorus concentrations were highest in spring and autumn (0.303 $mg \cdot dm^{-3}$ and 0.283 $mg \cdot dm^{-3}$, respectively), and lowest in summer, when they did not exceed 0.194 $mg \cdot dm^{-3}$ (Tab. 1). Physicochemical properties of water used in the experiment were very different on particular days of exposition. The differences were highest in the case of conductivity, total organic carbon (TOC) and nitrate nitrogen ($N\text{-}NO_3$), and lowest as regards temperature, pH, dissolved oxygen and concentration of total phosphorus (Tab. 1).

Species richness and abundance of ciliates in the field

The number of species of periphytic ciliates was not significantly different in the studied types of substrates. Thirty nine ciliate taxa were identified on natural substrates (reed steams), and slightly less (37) on artificial substrates (glass slides). Thirty-seven taxa (94.8%) were common for the studied substrates. Mean abundance of peryphytic ciliates on the studied substrates revealed slight differences ($P > 0.05$). Their higher density was observed on reed stems and it amounted to 77 $ind. \cdot cm^{-2}$. A slightly lower abundance was noted on glass slides – 71 $ind. \cdot cm^{-2}$. Irrespective of the type of the substrate, ciliate abundance was the highest in autumn (November) and the lowest in summer (June or July) (Fig. 1). The domination structure of periphytic ciliates was similar on natural and artificial substrates. Both types were dominated by Hymenostomatida, Pleurostomatida and Oligotrichida (Fig. 2 A, B). Also, the percentage share of individual trophic groups

Table 1. Physical and chemical characteristics of the water of investigated lake and in laboratory experiment

	SD [m]	pH	Conductivity [μS·cm^{-1}]	Dissolved oxygen [mg·dm^{-3}]	P_{tot} [mg·dm^{-3}]	N-NO$_3$ [mg·dm^{-3}]	TOC [mg C·dm^{-3}]
Months	lake						
IV	0.54	7.6	495	10.3	0.203	0.04	7.7
VI	0.5	8.42	451	11.9	0.303	0.07	6.3
VIII	0.23	7.7	339	12.4	0.194	0.11	7.1
X	0.32	7.3	496	10.8	0.283	0.03	7.9
Days	laboratory experiment						
3	–	8	500	7.9	0.221	0.21	8
7	–	8.2	490	6.2	0.222	0.21	9
11	–	8.2	484	6.8	0.222	0.2	8
15	–	7	521	6.8	0.221	0.2	11
19	–	7.2	522	6.8	0.231	0.2	10
23	–	6.9	540	8.1	0.235	1.11	11
27	–	8	551	6.3	0.238	1.21	12
31	–	7.1	565	6.1	0.236	0.8	11.8
35	–	6.9	550	4.8	0.238	1.11	14
39	–	7.1	547	5.2	0.235	0.91	13.3

was similar on both types of the examined substrates. Both substrates were dominated by omnivorous species which constituted 28% and 29% of ciliate density, respectively. Bacterivorous ciliates occurred in high numbers (25%) as well (Fig. 3 A, B).

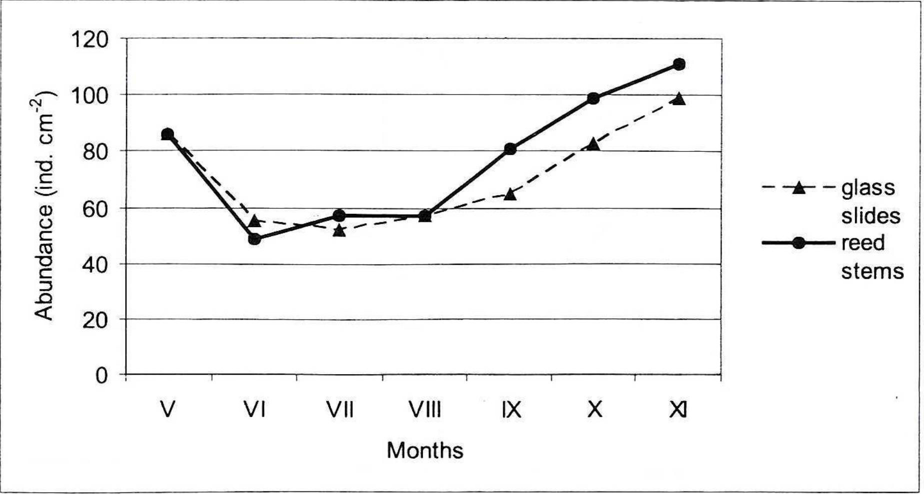

Fig. 1. Seasonal patterns of the density of periphytic ciliates community on natural and artificial substrata in littoral of investigated lake

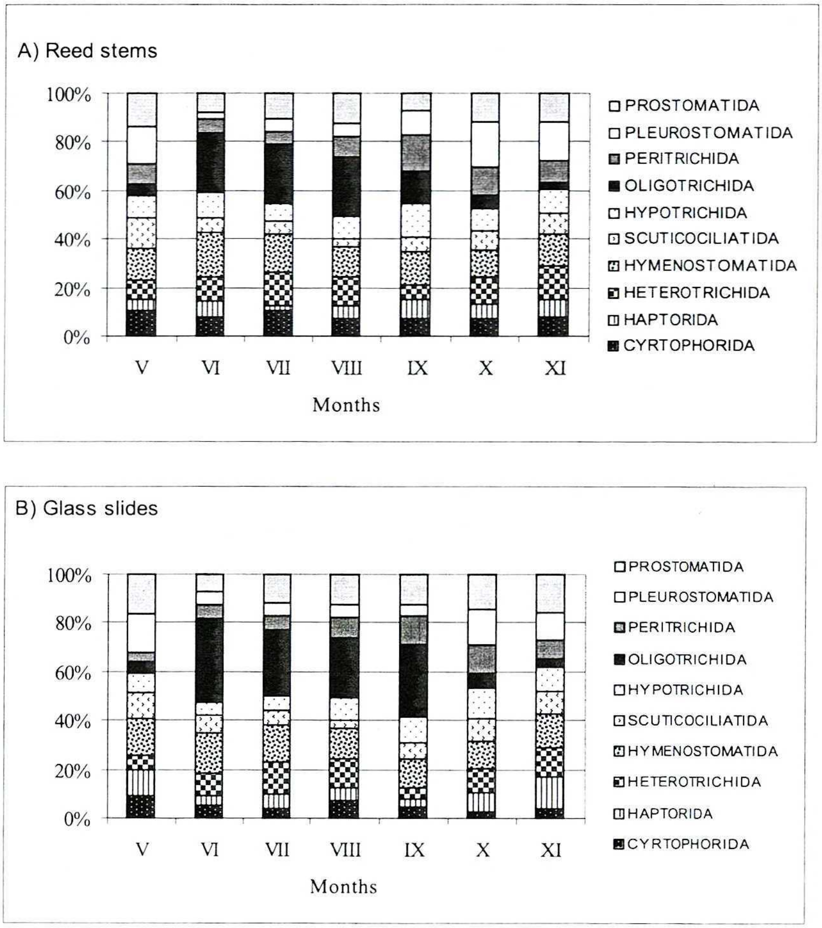

Fig. 2 A, B. Seasonal patterns of abundance of the common Ciliata on natural and artificial substrata in littoral of investigated lake (% of total numbers)

Species richness and abundance of ciliates in laboratory experiment

Nineteen taxa of periphytic ciliates were observed in the course of experiment. Species diversity of periphytic ciliates revealed some slight differences between the studied substrates ($P > 0.05$). Fourteen taxa (74%) were common for the substrates examined. The most significant differences were observed at the end of the experiment (day 31, 35 and 39), as well as on the 15th, 19th and 23rd day of substrates' exposition (ANOVA $F(4.2) = 21$, $P = 0.018$). The mean density of ciliates on glass slides reached 38 ind. cm^{-2}. A lower abundance was noted on reed stems, amounting to 30 ind.$\cdot cm^{-2}$. The lowest number of ciliates was observed on the third day of exposition, whereas the highest increase in the density of these micro organisms occurred on the 31st day of the substrates' exposition (Fig. 4). On the 3rd day ciliates representing merely two orders: Cyrtophorida and Hypotrichida. Reed stems were definitely dominated by Hypotrichida, constituting 75% of the total

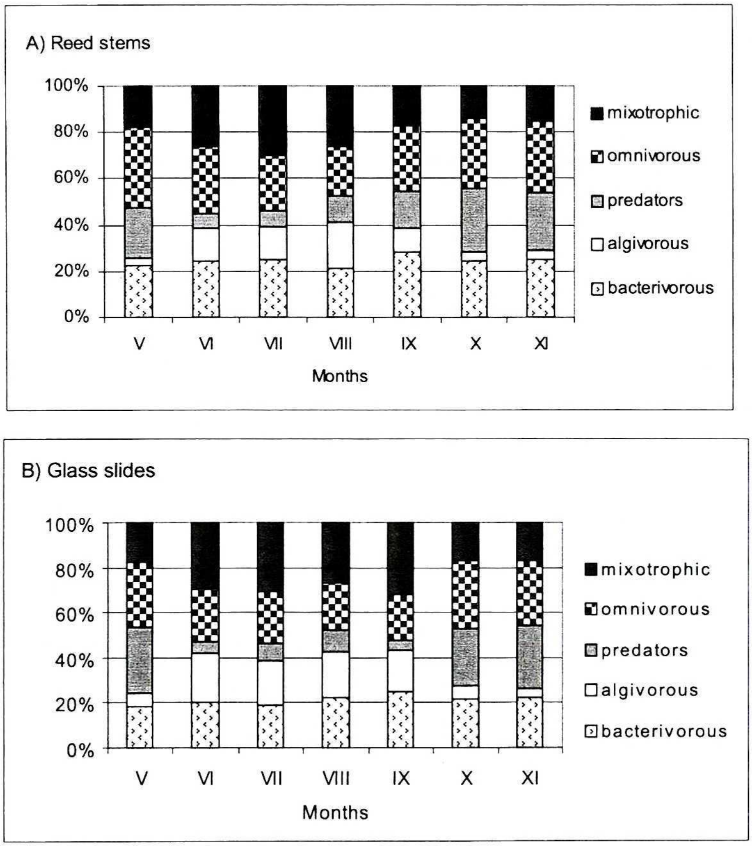

Fig. 3 A, B. Seasonal patterns of trophic groups of periphytic ciliates found on natural and artificial substrata in littoral of investigated lake

number. Glass slides, on the other hand, were dominated by Cyrtophorida which made 54% of the total density. On the 7th day of exposition both natural and artificial substrates were dominated by the species representing Hypotrichida, constituting, respectively, 57% and 47% of the total numbers. During the successive days of the exposition the proportion of Pleurostomatida and Peritrichida clearly increased (Fig. 5 A, B). The percentage share of particular trophic groups revealed only insignificant differences between the studied substrates. Bacterivorous ciliates were prevalent on both reed stems and glass slides. Their proportion on the natural substrates reached 53%, whereas it was as much as 63% on the artificial ones. Omnivorous ciliates constituted 20% of the total number on reed stems and 16% on glass slides. Predatory and mixotrophic species constituted 13% each of all trophic groups on natural substrates. In the course of exposition, bacterivorous and omnivorous ciliates were more abundant (Fig. 6 A, B).

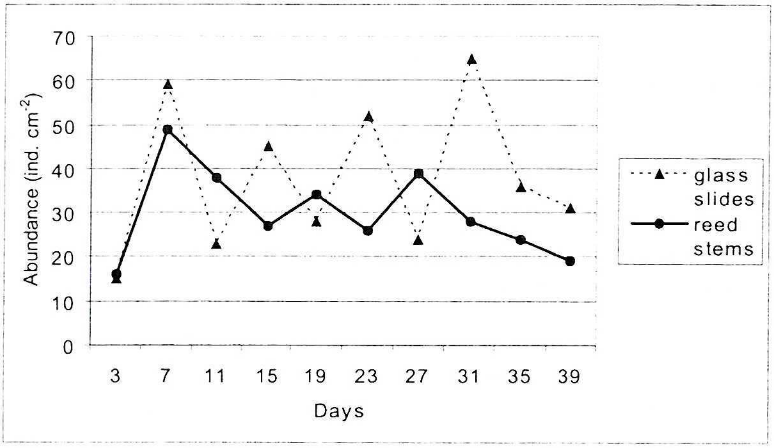

Fig. 4. The relative density of ciliates on artificial and natural substrata in laboratory experiment from day 3 to 39 day period

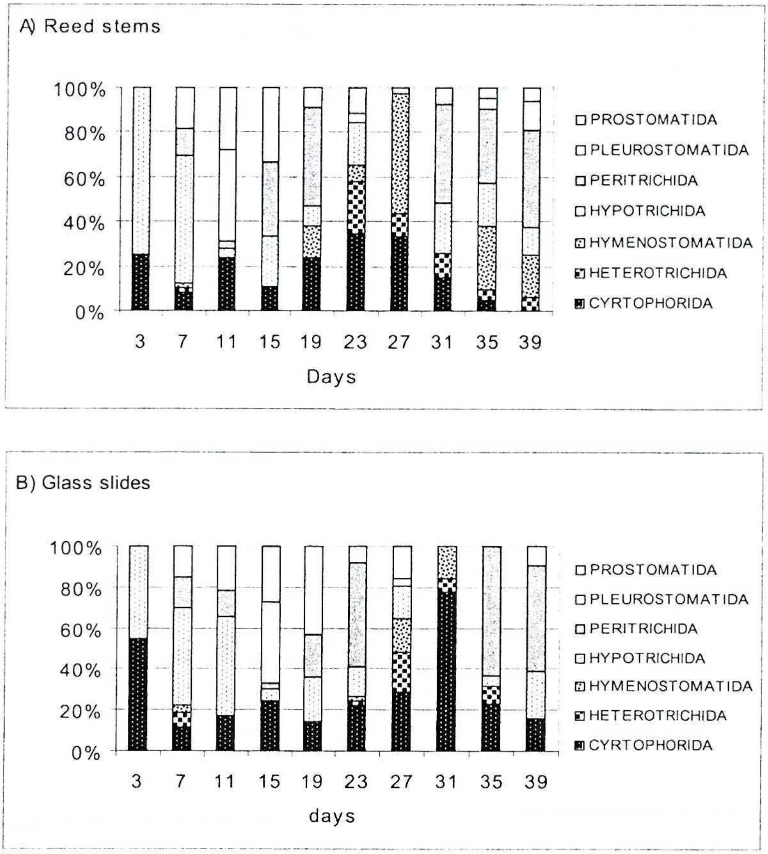

Fig. 5 A, B. Domination structure of Ciliata on artificial and natural substrata in laboratory experiment from day 3 to 39 day period (% of total numbers)

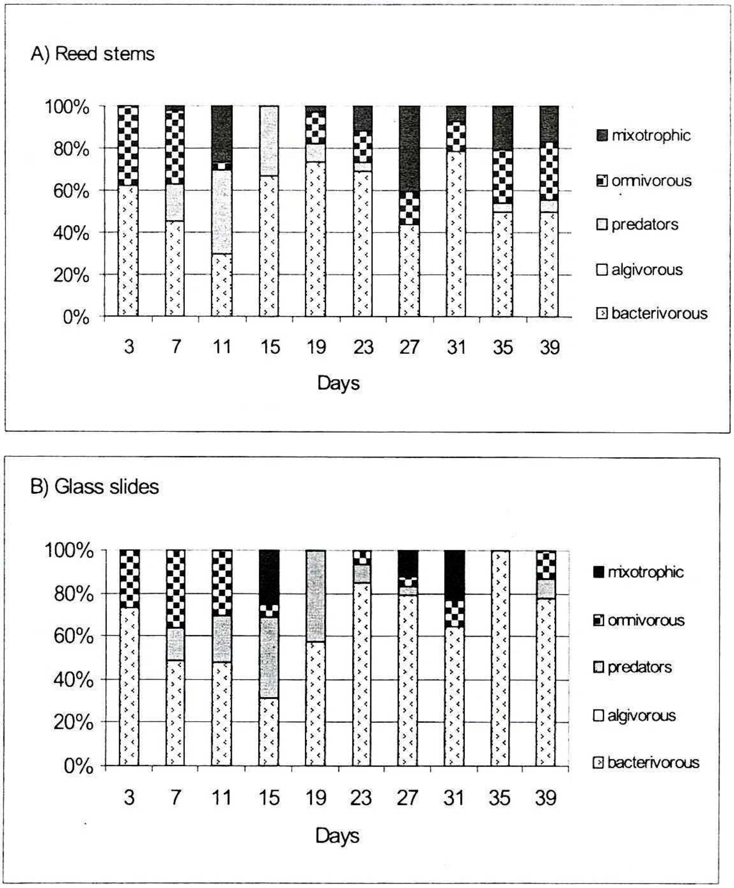

Fig. 6 A, B. Trophic groups of periphytic ciliates found on natural and artificial substrata in laboratory experiment from day 3 to 39 day period

The effect of chemical properties of water on the abundance of periphytic ciliates

Both in the lake and in the laboratory environment, irrespective of the type of the substrate, the abundance of ciliates correlated positively with conductivity. Correlation coefficient on reed stems reached the value of 0.53, $p \leq 0.05$, whereas its value on glass slides was $r = 0.43–0.54$, $p \leq 0.05$. On natural substrates the abundance of periphytic ciliates correlated positively with the content of TOC in water ($r = 0.53$, $p \leq 0.05$). On artificial substrates the correlations between ciliate numbers and concentrations of total organic carbon were slightly stronger ($r = 0.64–0.66$, $p \leq 0.01$). Irrespective of the type of substrate, the abundance of ciliates correlated positively with total phosphorus and concentrations of nitrate nitrogen ($r = 0.43–0.45$, $p \leq 0.05$ and $r = 0.40$ $p \leq 0.05$, $r = 0.63$, $p \leq 0.01$, respectively) (Tab. 2).

Table 2. Linear correlation coefficients between ciliate density and physical and chemical factors in investigated lake and in laboratory microcosms ($n = 16$, $P \leq 0.01$)

Sites/parameters	pH	Conductivity [$\mu S \cdot cm^{-1}$]	Dissolved oxygen [$mg \cdot dm^{-3}$]	P_{tot} [$mg \cdot dm^{-3}$]	$N\text{-}NO_3$ [$mg \cdot dm^{-3}$]	TOC [$mg\ C \cdot dm^{-3}$]
Lake – reed stems	–	0.53	–	0.43	0.63	0.53
Lake – glass slides	–	0.54	–	0.44	0.60	0.64
Laboratory experiment – reed stems	–	0.47	–	0.45	0.40	0.39
Laboratory experiment – glass slides	–	0.43	–	0.44	0.60	0.66

DISCUSSION

On the basis of the conducted studies it was concluded that the number of species of periphytic ciliates on natural and artificial substrates is almost identical. Such a situation occurred both in the case of samples collected from the lake and in laboratory conditions. An extremely high similarity in the taxonomic composition of ciliates inhabiting natural and artificial substrates was also observed by Chadwick and Canton [7], Boothroyd and Dickie [5], and Mieczan [21]. In late summer and in autumn *Cladophora sp.* was developing intensively on the stems of *Phragmites australis* in Lake Syczyńskie, forming a periphyton of "thread-like" character. This type of periphyton seems to create larger numbers of micro-niches and, consequently, it is willingly inhabited by periphytic ciliates. On the other hand, glass slides were dominated by the periphyton of "shell-like" character with a clear prevalence of diatoms. Characteristic (exclusive) species constituted a small group on both the stems and on glass slides. In Lake Syczyńskie reed stems were inhabited by only two species of the group, *Litonotus varsaviensis* and *Holophrya sp.* *Litonotus varsaviensis* was also found as a characteristic species in a eutrophic lake situated in Łęczna-Włodawa Lakeland [19]. Ciliates representing *Holophyra* on the stems of *Phragmites australis* were also noted in eutrophic and dystrophic lakes [21]. In laboratory conditions two characteristic taxa, *Chlamydonella sp.* and *Litonotus cygnus*, occurred. *Chlamydonella sp.* genus comprises species of wide ecological tolerance and it was observed in different types of trophic lakes, as well as in peat ecosystems [21]. *Litonotus cygnus* occurred quite abundantly on the stems of *Phragmites australis* in the eutrophic lake [21]. Glass slides revealed 3 characteristic taxa, namely *Vorticella microstoma* – complex, *Carchesium sp. and Litonotus sp.*

The density of periphytic ciliates in Lake Syczyńskie showed slight differences between natural and artificial substrates. Their higher numbers (77 ind.·cm^{-2}) were found on reed stems and slightly lower ones on glass slides (71 ind.·cm^{-2}). The abundance of periphytic ciliates revealed similar tendencies in eutrophic lakes [20]. On the other hand, studies focused on the density of periphytic ciliates on glass substrates in a eutrophic lake in Croatia showed that the abundance of the communities fluctuated between 40 and up to 2.400 ind.·cm^{-2} [23], whereas in dystrophic lakes in Germany their numbers on glass slides did not exceed 30 ind.·cm^{-2} [27]. In laboratory conditions a higher density was noted on artificial substrates. A lower abundance of ciliates on reed stems may result from the fact that throughout the whole period of the studies in the experimental laboratory conditions the substrate was intensively colonized by rotifers and nematodes which can control to a high extent the abundance of protozoan. In laboratory conditions the abundance of ciliates did not increase after a long period of exposition (day 35 and 39). The occurrence of protozoa species on new substrate is in accordance with the Mac Arthur and Wilson [18] model for the colonization of islands. At the early stage of colonization, the immigration rate of species to the substrate is high. As the colonization proceeds, the immigration rate declines.

In field conditions the densities of periphytic ciliates remained on a similar level in particular months. The highest richness was noted on both reed stems and glass slides in autumn (November). The lowest density for both types of substrates was observed in summer (June – July). The increase in the number of ciliates in autumn could have resulted from feeding conditions profitable for that group of micro organisms. In autumn the littoral zone was characterized by a significant content of organic matter. High densities of such organisms at that period may also have been a consequence of a distinct increase in their abundance in the pelagial zone. The studies performed by Sanders and Wickham [25] point at a periodical occurrence of planktonic species in the periphyton complex. On the other hand, low abundance of periphytic ciliates in summer may have resulted from their being consumed by the organisms representing higher trophic levels. In the studied lake, especially in June, extremely high numbers of planktonic crustacean fauna were observed, particularly the ones representing Daphnia genus. Indeed, as proved by the studies performed by Carrias *et al.* [6], these organisms do control the abundance of protozoans. The natural substrates of Lake Syczyńskie were dominated by ciliates representing the genera of Hymenostomatida and Pleurostomatida. Another numerous group was Prostomatida. The prevalence of this order was also noted in eutrophic lakes [19]. The most numerous groups on artificial substrates were Oligotrichida and Hymenostomatida. In the laboratory reed stems were dominated by ciliates belonging to the orders of Hypotrichida, Peritrichida and Cytophorida. The species representing these orders include mainly typically periphytic forms and are especially abundant in eutrophic and hypertrophic waters [8]. In Lake Syczyńskie, irrespective of the type of the substrate, omnivorous and bacterivorous species prevailed. High numbers of omnivorous ciliates in freshwater reservoirs were also observed by other authors [2]. The examinations of periphytic ciliates carried out in eutrophic lakes revealed that at the early stages of colonization natural and artificial substrates were dominated by bacterivorous species, whereas after approximately two weeks of exposition the proportion of algivorous and mixotrophic species increased as well. The studies performed by Beaker [1] prove that bacteria appear already 4 hours after the exposition of the substrates. Most probably, such an early and numerous occurrences of bacterivorous organisms is the effect of beneficial feeding conditions. Natural substrates also revealed large numbers of mixotrophic ciliates. Mixotrophs occur copiously in reservoirs of different trophic status [4]. Physiological flexibility of mixotrophes provides them with an advantage in changeable and unpredictable conditions which characterize shallow hypertrophic lakes [12]. Observed in this study low numbers of algivorous ciliates in the periphyton may have resulted from difficulty in finding appropriate food since periphyton was dominated by large-cell algae, filamentous and colony-forming organisms which were inaccessible or hardly accessible for the ciliates. The results of the laboratory studies were similar. The trophic structure of periphytic ciliates in field conditions showed relatively low seasonal variability. In spring natural substrates were dominated by omnivorous species, whereas artificial substrates were abundantly inhabited, apart from omnivorous, by predatory species. In summer the prevalence of mixotrophic species was noted on both types of substrates. An increase in the number of mixotrophic species was also recorded in a eutrophic lake, and their occurrence may be related to an increase in the density of fine phytoplankton [21]. In autumn the proportion of bacterivorous ciliates increased on both reed stems and glass slides. Natural substrates revealed also very numerous omnivorous species in that period, whereas artificial substrates were abundant in mixotrophic species. The increase in the share of bacterivorous species was probably related to advantageous feeding conditions resulting from a high content of total organic carbon in the water. Both in the lake and in the laboratory conditions the densities of ciliates on the two studied substrates were closely correlated with conductivity and the content of TOC in the water. An increase in the numbers of ciliates on natural and artificial substrates accompanying an increase of the two agents was observed by other authors [20]. Clearly positive correlations between the content of TOC in the water and the abundance of ciliates on the stems of *Phragmites australis* and on glass slides were also noted in the eutrophic reservoir [21]. The abundance of ciliates on the studied substrates was also strongly related with the content of nitrate nitrogen and total phosphorus in the water. Similar correlations were observed in shallow eutrophic lakes [3, 20, 21].

CONCLUSIONS

Species richness as well as the abundance of periphytic ciliates are determined to the highest degree by the habitats and chemical properties of the waters (especially the content of TOC and nitrate nitrogen), and, to a lower degree, by the type of the colonized substrate. Moreover, exposition time of the substrates affected both an increase in the richness of periphytic ciliates and the changes in their trophic structure. At the beginning of the experiment the substrates were intensively colonized by typically bacterivorous species, yet prolonged exposition time resulted in an increasing proportion of omnivorous species.

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WPŁYW RODZAJU PODŁOŻA ORAZ WŁAŚCIWOŚCI CHEMICZNYCH WODY NA STRUKTURĘ I SUKCESJĘ ZESPOŁU ORZĘSKÓW PERYFITONOWYCH W JEZIORZE HYPERTROFICZNYM

Celem pracy było porównanie składu taksonomicznego i liczebności zespołu orzęsków peryfitonowych zasiedlających różne podłoża; określenie, w jaki sposób czas ekspozycji podłoży wpływa na obfitość tych mikroorganizmów oraz analiza zależności pomiędzy wybranymi właściwościami fizyczno-chemicznymi wód a orzęskami w jeziorze hypertroficznym. Wykazano, że zarówno bogactwo gatunkowe jak i obfitość orzęsków peryfitonowych w największym stopniu determinują zasoby pokarmowe siedliska oraz właściwości chemiczne wód (głównie zawartość całkowitego węgla organicznego oraz azotu azotanowego), w mniejszym zaś stopniu rodzaj kolonizowanego podłoża. Czas ekspozycji podłoży wpływał zarówno na wzrost obfitości peryfitonowych orzęsków jak i zmianę ich struktury troficznej. Na początku eksperymentu podłoża były intensywnie kolonizowane przez gatunki typowo bakteriożerne, wraz ze wzrostem czasu ekspozycji podłoży wzrastał udział gatunków wszystkożernych.