The influence of emergent and submerged macrophyte beds on ciliate communities in a shallow lake

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Key words: shallow lake, macrophytes, plankton, ciliates

Abstract

Relationships between ciliates and the presence of emergent and submerged vegetation were studied in a shallow lake in eastern Poland. Samples were collected in zones of Phragmites, Typha, Batrachium, Elodea, Stratiotes and from the open water zone. The abundance and biomass of ciliates were significantly higher at sites with structurally most complex plants than in the open water or sparsely vegetated sites. The redundancy analysis indicated that bacterial abundance and total organic carbon were the most influential variables that determine the distribution of ciliates. However, chlorophyll 𝑎 and 𝑃₄₀ have a lesser influence on the distribution of these microorganisms. Based on differences in macrophyte structure, two groups of habitats with similar patterns of size-related ciliate distribution were distinguished. The first group consisted of three vegetation zones of sparse stem structure and the open water zone, the second group comprised submerged macrophyte species, which were more complex.

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INTRODUCTION

The contribution of aquatic macrophytes in the structure and function of freshwater habitats has long been recognized, and numerous studies support the argument that shifts in the species composition of littoral macrophyte communities will likely have a significant effect on the abundance and distribution of phytophilous macroinvertebrates (Basu et al. 2000, Colon-Gaud et al. 2004). Investigations that have attempted to quantify the structural complexity of plant species and relate it to invertebrate assemblage composition, as well as the body-size distribution, have so far been concerned with a single plant taxa, and limited mainly to terrestrial and marine environments (Shorrocks et al. 1991, Davenport et al. 1999). Macrophyte beds are favorable to the development of zooplankton, as they provide refuge from fish predation. Many studies have reported that in the presence of planktivorous fish, the zooplankton abundance is much higher within dense plant beds than in the open water (Jeppesen et al. 1997, Basu et al. 2000). The division of zooplankton communities within the vegetation of lakes is well known for some invertebrate species and fish (Nurminen & Horppila 2002). Rotifers, cladocerans and copepods are the major secondary producers of both pelagic and vegetation areas on a worldwide scale. Some species are commonly found in both areas, whereas others are found within, or in the near vicinity of vegetation stands (Ali et al. 2007, Kuczyńska-Kippen 2007). And thus, it seems probable that differentiation may also concern the habitat distinctiveness on a smaller scale, e.g. the transitional and central zones of a single macrophyte bed.

Protozoa play a significant role in freshwater lakes. Among these microorganisms, ciliates are the most conspicuous members and have long been of ecological interest in shallow lakes. Most of the ecological researches have focused on open-water habitats, rather than on the littoral zone of lakes, and little has been known about the microorganisms in various types of macrophyte communities. In the worldwide ecological studies, there were only a few publications regarding the abundance of ciliates living among macrophytes (Jürgens & Jeppesen 1997; Mieczan 2007, 2008). This paper aims at comparing the planktonic ciliate communities between different zones of macrophytes (central and outer parts) with those in the open water in a shallow lake for a better understanding of the influence exerted by emergent and submerged macrophytes on the diversity of ciliates and at determining the effects of various water variables on the abundance and distribution of these microorganisms.
MATERIALS AND METHODS

Ciliates were investigated in Lake Piskory (the area of 154 ha, the average depth ca. 1 m, eastern Poland) with well-developed zones of macrophytes. Samples were collected in spring, summer and autumn 2006 in zones of *Phragmites australis* (Car.) Trin. ex Stend., *Typha latifolia* L., *Batrachium aquatile* Dum., *Elodea canadensis* L. and *Stratiotes aloides* L. Additionally, ciliates were collected from the open water zone surrounding the vegetation zones. The sites had ca. 5–6 m² of macrophytes’ zones. Samples of ciliates were collected from the central and peripheral parts of the macrophytes’ zones, as well as from the open-water zone, 2–3 m away. At each type of habitat, four samples were collected from the central and peripheral part. 10 l volumes were collected in the open-water zone by means of a 5-l Bernatowicz sampler. In zones of macrophytes, protozooplankton was sampled with a plexiglass core (length 1.5 m, ø50 mm); twenty subsamples, about 0.5 l each, were poured into a calibrated vessel to form a composite sample (10 l), which was concentrated using a 10 µm plankton net and fixed with Lugol’s solution. Three subsamples of 10 ml were settled for at least 24 h in plankton chambers. Ciliates were counted and identified with an inverted microscope. Ciliate biomass was estimated by multiplying the numerical abundance by the mean cell volume calculated from direct volume measurements, using appropriate geometric formulas (Finlay 1982). Taxonomic identifications were based mostly on Foissner&Berger (1996). The abundance of bacteria was determined with the use of DAPI, according to Porter&Feig (1980). 10 ml of water were preserved in formaldehyde up to the final concentration of 2% and kept in darkness at a temperature of 4°C. Subsamples of 2 ml were condensed on polycarbon filters coloured with irgalan (pore diameter of 0.2 µm). The content of total organic carbon (TOC) was determined using the PASTEL UV, and the remaining factors (chlorophyll *a* and *P*₉₀) were analyzed in the laboratory (Golterman 1969). Analysis of variance (ANOVA and the Tukey multiple comparison test) was used to test for significant effect of the three independent factors (macrophyte beds, zones: central vs. peripheral and time) on ciliate abundance. The relationships between microbial communities and environmental variables (bacterial abundance, concentrations of chlorophyll *a* and *P*₉₀) were analyzed using the redundancy analysis (RDA) (Ter Braak 1988–1992).

RESULTS

Concentration of chl-*a*, TOC and bacterial abundance were significantly higher at the sites with dense vegetation in comparison with open water or sparsely vegetated sites (for chl-*a*: 41–34 µg l⁻¹, ANOVA *F* = 8.1, *P* = 0.03; for
TOC: 4–2.3 mg l$^{-1}$ C, $F = 8.0$, $P = 0.03$; for bacterial abundance: 6.2–4.6 × 10$^6$ cells ml$^{-1}$, $F = 5.1$, $P = 0.02$, respectively). Remarkably, the highest TOC and bacterial abundance were attained in the middle of the vegetation beds (>3.8 mg l$^{-1}$ C and 6.2 × 10$^6$ cells ml$^{-1}$), and the lowest on the periphery of the macrophyte beds (2.1 mg l$^{-1}$ C and 4.1 × 10$^6$ cells ml$^{-1}$). The concentrations of chl-$a$ and P$_{tot}$ reached the highest values on the periphery of the macrophyte zones (40 µg l$^{-1}$ and 0.270 mg l$^{-1}$, respectively).

Altogether forty two taxa were identified in the investigated lake, with the minimum of 8 taxa in the open-water zone and the maximum among macrophyte stands (28–33 among *Elodea* and *Stratiotes* beds and 14–16 among *Batrachium*, *Phragmites* and *Typha*). For the total ciliate biomass, there was always at least 0.67 µg ml$^{-1}$ C, whereas in the case of the sparse vegetation sites and the open water - usually less than 0.15 µg ml$^{-1}$ C. ANOVA indicated that ciliate abundance and biomass were significantly higher at the sites with most structurally complex plants (*Elodea* and *Stratiotes*) than in the open water or sparsely vegetated sites ($F = 38.3$, $P < 0.05$) (Fig. 1 A–B). There were no significant differences in the abundance and biomass between open water and sparsely vegetated sites, and between the central and peripheral parts of individual beds (Fig. 1 A–B). Furthermore, ANOVA indicated that the mean ciliate size was significantly lower at the dense vegetation sites (the average size = 40 µm) than in the open water or sparse vegetation sites (the average size = 80 µm) ($F = 16.2$, $P < 0.05$). Comparison of the size classes of ciliates between peripheral and central parts of macrophytes’ beds did not show significant differences ($P > 0.05$). In general, the assemblage of ciliates was dominated by Scuticociliatida, followed by Oligotrichida and Heterotrichida. These three orders accounted for about 60% of the total density of ciliates. The most abundant species in macrophyte beds with a definitely complicated structure were *Cinetochilum margaritaceum* (Ehrenberg 1931), *Stylonychia mytilus*-complex and *Euplotes* sp. *Strombidium viride* (Stein 1867) and *Askenasia* sp. were dominant in macrophyte beds with a straight structure and in the open-water zone. The repeated measure ANOVA was applied only to the dominant orders. For bacterivorous Scuticociliatida, the $F$-values indicated a strong effect of microenvironment type (macrophyte beds) and month of collection on their abundance. The interaction of these factors was also significant. Densities of mixotrophic Oligotrichida varied significantly with time. There was also a significant interaction between months and habitat type. Although the effect of zone (central vs. peripheral) was not significant, the highest densities were recorded in the peripheral zones. For the omnivorous Heterotrichida, the effect of month of collection was significant. Additionally, the interactions between months and types of microenvironment, and between months and zones were significant (Table 1).
The RDA diagram indicated that the bacterial abundance and TOC were the most influential water variables, which determine the distribution of ciliates. However, trophic parameters (chlorophyll $a$ and $P_{tot}$) have a lesser influence on the distribution of protozoa. In the central zones, the number of ciliates had the strongest correlation with bacterial abundance and concentration of total organic carbon. Whereas, in the peripheral zone, there was a positive correlation between the number of ciliates and chlorophyll $a$ concentration (Fig. 2).

Fig. 1. Density and biomass of the community of planktonic ciliates within macrophytes beds in the investigated lake (M - middle, E - edge, EL – Elodea, ST – Stratiotes, BA – Batrachium, PH – Phragmites, TH – Typha, OW - open water zone, average values $\pm SD$).
Table 1

Effect of macrophyte beds (1), zone (2) and time (3) and their interactions for three orders of ciliates density.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Scuticociliatida</th>
<th>Oligotrichida</th>
<th>Heterotrichida</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>P</td>
<td>F</td>
</tr>
<tr>
<td>macrophyte beds (1)</td>
<td>6.6</td>
<td>0.0220</td>
<td>6.20</td>
</tr>
<tr>
<td>zone (2)</td>
<td>19.02</td>
<td>0.0001</td>
<td>0.44</td>
</tr>
<tr>
<td>time (3)</td>
<td>2.90</td>
<td>0.0420</td>
<td>2.11</td>
</tr>
<tr>
<td>1 x 2</td>
<td>3.3</td>
<td>0.0250</td>
<td>3.12</td>
</tr>
<tr>
<td>1 x 3</td>
<td>1.31</td>
<td>0.3771</td>
<td>1.03</td>
</tr>
<tr>
<td>2 x 3</td>
<td>1.10</td>
<td>0.3977</td>
<td>2.18</td>
</tr>
<tr>
<td>1 x 2 x 3</td>
<td>0.50</td>
<td>0.7714</td>
<td>0.48</td>
</tr>
</tbody>
</table>

Fig. 2. The RDA ordination diagram showing the relation between zones, environmental variables and common ciliate species (M - middle, E - edge, OW - open water zone); Ask. – Askenasia sp., Asp. – Aspidisca sp., Balan. – Balanion planctonicum, Chil. – Chilodonella uncinata, Cinet. – Cinetochilum marginatum, Cod. – Codonella cratera, Col. hirt. – Coleps hirtus, Col. spat. – Coleps spatulatus, Cycl. – Cyclidium sp., Ench. – Enchelys sp., Eupl. – Euplotes sp., Halt. – Halteria gradinella, Holo. – Holophrya discolor, Hol. – Holosticha pullaster, Par. bur. – Paramecium bursaria, Par. put. – Paramecium putrinum, Prorod. – Prorodon sp., Stent. – Stentor coerulescens, Stok. – Stokesia vernalis, Strom. – Strombidium viride, Str. – Strombilidium sp., Styl. – Stylonychia mytilus-complex, V. com. – Vorticella companula, V. con. – Vorticella convallaria.
DISCUSSION

In the present study, the numbers of ciliate taxa, as well as their density and biomass increase together with the abundance and the level of complicated spatial structure of macrophytes. The evident influence on the density of macrophytes and their structure was also observed in the case of other groups of aquatic organisms (Downing&Cyr 1986, Walsh 1995). The author of this paper observed that the abundance of ciliates within more complex aquatic macrophyte beds was three times higher than in the open water or sparsely vegetated areas. Several mechanisms may account for macrophyte beds being a more favourable habitat for ciliates to develop. As suggested by Jürgens&Jeppesen (1997), macrophyte beds provide protozoa with refuge against the predatory effects of zooplankton. The results of the present study showed that ciliates within more complex vegetation had a smaller average size than ciliates in the open water or among sparse vegetation. Rotifers and larger crustaceans, being visual predators on ciliates, can modify their community size structure. It is highly possible that rotifers and crustaceans reduced the average size of protozoa at more complex vegetation sites, where zooplankton could find refuge. Differentiation in the habitat-related body size of ciliates in the studied lake was consistent with Raffaelli et al. (2000), who suggested that the habitat architecture may constrain the size spectrum of organisms, thus not limiting any possibility of size-differentiation among the inhabiting animals. Higher densities of ciliates inside the plant beds may suggest more advantageous anti-predator refuge and more profitable food conditions. In the present study, a several times higher concentration of total organic carbon and bacterial abundance was recorded in the central part of submerged macrophytes. This may be explained by exceptional abundance of ciliates in the zone analyzed. In the peripheral part, there was a strong correlation between the number of ciliates and the chlorophyll a concentration. A similar situation was observed in a macrophyte-dominated lake (Biyu 2000). As a result of the preferred-habitat analysis for individual species of ciliates, it was revealed that Stylonychia mytilus-complex and Cinetochilum margaritaceum were definitely connected with the central part (high abundance and frequency more than 70% in the samples), whereas two pelagic species, Strombidium viride and Askenasia sp. - with the peripheral part. In the open water area, Strombidium viride was the most numerous one. In the area of submerged vegetation, there was an increased number of epiphytic species. Probably this species must have been detached from the macrophyte substratum through the process of water movement. Many authors have observed a similar situation during the research on rotifers and crustacean zooplankton (Nurminen&Horppila 2002, Kuczyńska-Kippen 2007).
The results of this study demonstrate that ciliates probably use macrophyte vegetation as potential refuge, while at the same time, the habitat complexity, the bacterial abundance and the content of total organic carbon are the factors that influence their occurrence to the greatest extent.

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