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Zooplankton structure in architecturally differentiated
macrophyte habitats of shallow lakes in the
Wielkopolska Region, Poland

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Abstract

The aim of this examination was to study the impact of the physical parameters, understood as spatial and morphological features, of two macrophyte habitats created by *Chara tomentosa* and *Typha angustifolia* on the Rotifera and Crustacea communities of three shallow lakes with extensive macrophyte cover.

There were 161 zooplankton species in total identified from three lakes, with over 60% of species common among all lakes. Species richness varied between the sampling stations, with lowest values within the open water zone and highest among macrophyte stands.

Significant differences in zooplankton densities between particular stations for all groups of zooplankton were observed, with the highest values within the most diverse and complex habitat – the *Chara* bed. Furthermore, the distribution of pelagic species between particular stations differed significantly in the case of copepods, with the highest abundance also in the stonewort beds.

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INTRODUCTION

The littoral zone of a lake, the shallow area usually dominated by aquatic vegetation, provides an important habitat for a number of organisms, including rotifers and crustaceans. In shallow water bodies, the large macrophyte-covered areas both support a variety of littoral-associated species and also provide other zooplankters with a spatial refuge, enabling pelagic species to gather in this area (Gliwicz & Rybak 1976, Kairesalo et al. 1998). Furthermore, macrophytes serve as an attachment surface for algae (Gons 1979) and some invertebrates (Duggan 2001), provide a nutritional source for a wide spectrum of animals (Bronmark 1985, Jürgens et al. 1994), and also act as shelter sites for many fish species (Crowder & Cooper 1982, Petr 2000).

Macrophyte species composition, distribution and percentage cover may alter the taxonomic structure and dynamics of a variety of organisms associated with the littoral zone. The spatial arrangement of plant species, usually called plant architecture, has an important impact on the zooplankton inhabiting aquatic vegetation stands. Previous authors have demonstrated that the spatial and morphological structure of the vegetative habitat modifies rotifer and crustacean communities (Downing & Cyr 1986, Walsh 1995). There are different components of a complex macrophyte community in lakes, including submerged plants, floating-leaved plants and emergent macrophytes, which all may create distinct habitats for inhabiting organisms. Plant structure creates spatial complexity and patchiness in the aquatic environment. Each plant is of a different shape, length, width of stem and biomass as measured per lake bottom unit. Broad and dissected leaves of macrophytes provide dense cover and may create favourable concealment conditions for animals. These kinds of plants also provide a wide range of microhabitats for invertebrates and epiphytic algae, as well as serving as spawning substrates for fish and invertebrates (Caffrey 1993). Plants of simpler build, e.g. rush vegetation, will offer minimal cover, and therefore may be less beneficial for their inhabiting organisms. In the three examined shallow lakes of the Wielkopolska region macrophyte parameters revealed significant differences in the stem length between particular stations. The longest stems were found within *Chara* beds when compared to the *Typha* stands (N. Kuczyńska-Kippen, unpublished).

Differentiation in the distribution of organisms between particular zones of the littoral can be found in both animals, vertebrate and invertebrate (Dibble & Harrel 1997, Petr 2000, Balayla & Moss 2003, Tessier et al. 2004) and plants, including phytoplankton and epiphytic communities (Eminson & Moss 1980, Blindow 1987), as has already been demonstrated for the three studied lakes

(Kuczyńska-Kippen et al. 2005, Messyas & Kuczyńska-Kippen 2006, Celewicz et al., manuscript in preparation).

The factors influencing rotifer community structure among macrophytes, apart from food availability and predator avoidance, might also include the different habitat conditions present, providing differences in the suitability for typical littoral and pelagic species (Preissler 1977) and thereby compelling the evolution of morphological adaptations of rotifers inhabiting particular zones of a lake (Preissler 1983).

The aim of the present study was to determine whether, in shallow lakes with well-developed macrophyte cover, zooplankton community structure differs in relation to particular plant species. Thus, this work was undertaken in order to:

- (1) compare the distribution of zooplankton communities between two different stands of aquatic vegetation (*Chara tomentosa* and *Typha angustifolia*) and also compare these to the open water zone,
- (2) analyse the structure of pelagic communities in particular zones,
- (3) compare the structure of dominant species between particular sampling stations.

MATERIAL AND METHODS

The research was conducted in three shallow and typically macrophyte-dominated lakes located within the protected areas of the Wielkopolska region, in the western part of Poland (Lake Wielkowiejskie – 52°17.8'N - 16°40.0'E; Lake Budzyńskie - 52°14.8'N - 16°49.5'E; Lake Dębiniec - 52°28.7'N - 17°13.6'E). All three water bodies were characterised by similar morphometry (they were small and shallow) and displayed a classically developed pattern of water and rush vegetation (Table 1). The basin of each investigated lake was surrounded by helophytes predominately by *Typha angustifolia* L. and *Phragmites australis* (Cav.) Steud. Stands of stoneworts, *Chara tomentosa* L., created large beds, which occupied the shallower parts of each lake compared to

Table 1

Main morphometric features of examined lakes (Jańczak et al. 1996)

parameters	Budzyńskie	Dębiniec	Wielkowiejskie
Surface area (ha)	11.0	15.0	13.3
Max depth (m)	2.7	7.4	2.8
Mean depth (m)	1.4	3.4	1.4
Shoreline length (m)	2900	1600	2300
Special status	National Park	Landscape Park	National Park

other submerged macrophyte species. In Wielkowiejskie Lake, the *Chara* meadows covered extensive parts of the lake bottom and they consisted of separated patches of two species: *Chara tomentosa* and *Ch. hispida* L. In the remaining lakes, stoneworts created single and separated one-species beds.

All three lakes are protected. Lake Dębiniec is situated within a 100% forestry catchment area, while Budzyńskie and Wielkowiejskie Lakes are surrounded by a mixture of forestry and pastoral catchment areas.

The research was conducted in the shallow part (0.5-1.0 m depth) of each lake. The study of the spatial distribution of zooplankton (rotifers and crustaceans) was carried out along a transect that included the rush vegetation (*Typha angustifolia*, *Phragmites australis*), stonewort bed (*Chara tomentosa*) and open water area of each examined lake (Fig. 1). Samples were collected three times, including the spring (April), summer (July) and autumn (September) seasons of 2003, from the same parts of each lake. Three zooplankton subsamples (each of 5 l), randomly selected from each examination station, were collected from each sampling (N=81). The material was taken using a plexiglass core sampler (h = 1 m; \varnothing = 0.05 m), going vertically through the macrophyte stand to about 5-10 cm above the lake bottom. Each subsample was thickened using a planktonic net (45 μ m) and preserved with 4% formaldehyde.

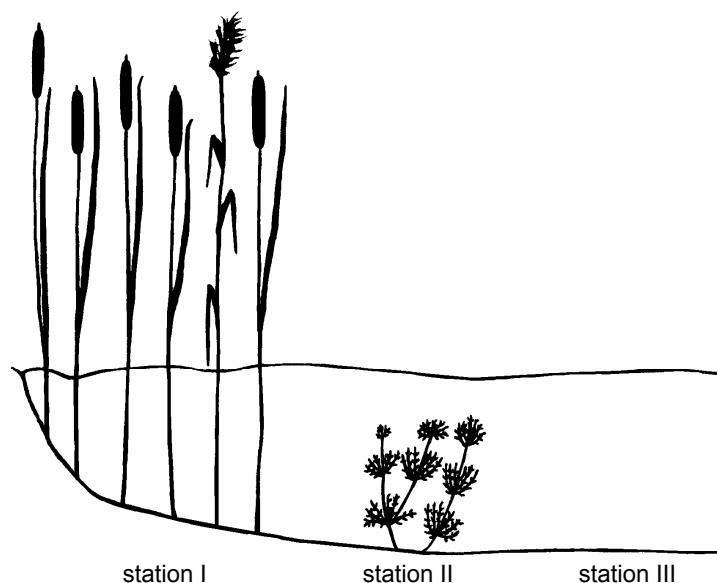


Fig. 1. The sampling stations of zooplankton communities in the examined lakes (station I – *Typha* stand; station II - *Chara* bed; station III – open water zone).

Dominating species were defined as those that reached a minimum of 10% of the total zooplankton densities.

The ANOVA test with *a posteriori* Tukey Test were applied in order to evaluate differences in zooplankton densities between particular stations.

RESULTS

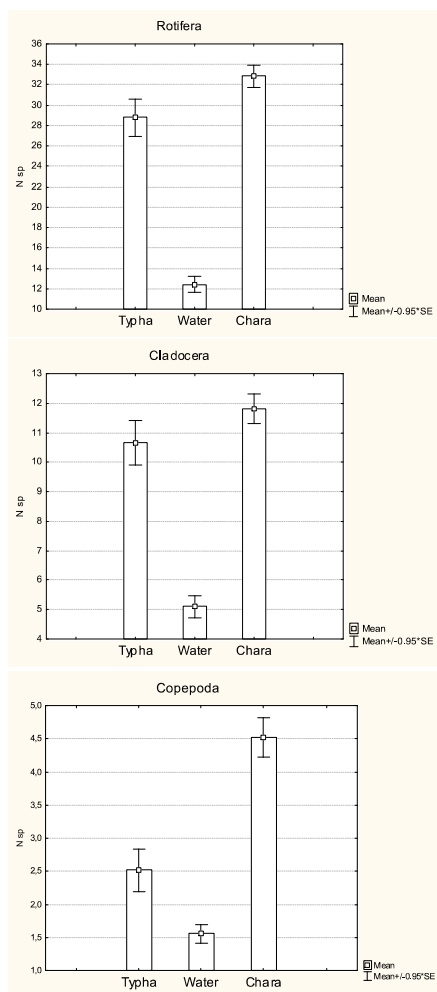


Fig. 2. The number of zooplankton species (Rotifera, Cladocera and Copepoda) at particular stations.

Out of 161 total zooplankton species identified (107 Rotifera, 37 Cladocera and 17 Copepoda), representing 65 genera, 61% of the taxonomic structure of the zooplankton community was common for all three examined lakes (58% within rotifers and 65% within crustaceans). Species richness varied between the sampling stations with lowest values within the open water zone and highest among macrophyte stands (Fig. 2). The mean number of zooplankton species in the *Chara* bed (33 Rotifera and 16 Crustacea) was higher than that within *Typha* (29 Rotifera and 13 Crustacea).

Rotifera dominated over Cladocera and Copepoda at all sampling stations, including both macrophyte zones, comprising between 61 and 99% of the total zooplankton densities of the investigated lakes. Significant differences in total densities between particular stations for all groups of zooplankton were observed. In each case (Rotifera – $F_{2,78}=17.4401$, $p<0.01$; Cladocera – $F_{2,78}=21.1037$, $p<0.01$; Copepoda – $F_{2,78}=48.8265$, $p<0.01$) the abundance of zooplankton within the *Chara* bed was significantly higher than that within the *Typha* and open water stations (Fig. 3). The highest mean numbers were derived from the stonewort bed (2311 ind l⁻¹), while the

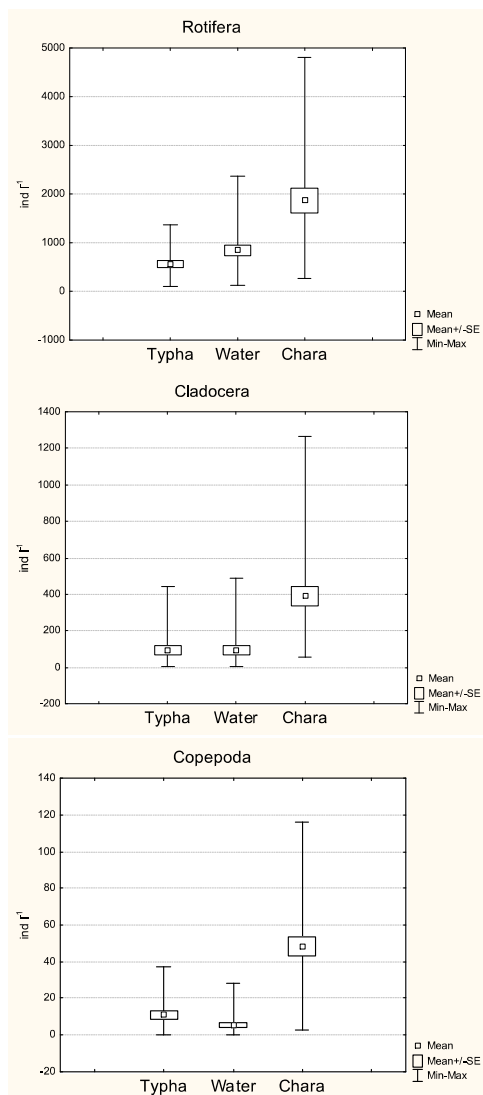


Fig. 3. Mean zooplankton (Rotifera, Cladocera and Copepoda) densities (ind l⁻¹) at particular stations, irrespective of lake and season (N=81).

Voigt, *Keratella quadrata* (O.F. Müller), *Lecane luna* (O.F. Müller), *Lepadella triptera* Ehrenberg and *Trichotria tetractis* (Ehrenberg) and crustaceans *Alonella nana* (Baird) and *Camptocercus rectirostris* Schoedler dominated

lowest from the cattail stand (670 ind l⁻¹).

Pelagic species densities differ significantly between particular stations only in the case of copepods ($F_{2,24}=3.5821$, $p<0.05$), with the highest abundance in the *Chara* bed (Fig. 4). Macrophyte stands were dominated by littoral species, while at the open water station single littoral species occurred only occasionally. In the *Typha* stand, the fraction of pelagic species ranged between 33 and 94%, while in the open water zone between 86 and 100% and lastly in the *Chara* bed, between 9 and 71%.

Of the rotifers, only *Keratella cochlearis* (Gosse) and *Polyarthra remata* (Skorikov) occurred with 100% frequency in the examined material, while *Colurella uncinata* (O.F. Müller) and *P. vulgaris* Carlin from among rotifers and *Bosmina coregoni* Baird and *Ceriodaphnia quadrangula* (O.F. Müller) from among crustaceans occurred with over 90% frequency.

The dominant community was created by 35 zooplankton species (18 of Rotifera and 17 of Crustacea) (Table 2). Of 24 dominating species within the *Chara* bed, rotifers such as *Bdelloidea*, *Cephalodella forficula* (Ehrenberg), *Conochilus natans* Voigt, *Keratella quadrata* (O.F. Müller), *Lecane luna* (O.F. Müller), *Lepadella triptera* Ehrenberg and *Trichotria tetractis* (Ehrenberg) and crustaceans *Alonella nana* (Baird) and *Camptocercus rectirostris* Schoedler dominated

Table 2

Dominating species of zooplankton in particular stations of examined lakes

Lake	Dębiniec			Wielkowiejskie			Budzyńskie		
	sp	su	au	sp	su	au	sp	su	au
Station	T	w	C	T	w	C	T	w	C
Rotifera									
<i>Ascomorpha saltans</i> Bartsch							x		
<i>Bdelloidae</i>							x		
<i>Brachionus angularis</i> Gosse									x
<i>Cephalodella forficula</i> (Ehrenberg)								x	
<i>Colurella uncinata</i> (O.F. Müller)	x	x		x	x	x	x	x	x
<i>Conochilus hippocrepis</i> (Schrank)			x					x	
<i>Conochilus natans</i> Voigt									x
<i>Filinia longiseta</i> (Ehrenberg)									x
<i>Keratella cochlearis</i> (Gosse)	x	x	x	x	x	x	x	x	x
<i>Keratella quadrata</i> (O.F. Müller)					x				
<i>Lecane bulla</i> (Gosse)						x		x	x
<i>Lecane closterocerca</i> (Schmarda)					x			x	
<i>Lecane luna</i> (O.F. Müller)		x						x	
<i>Lepadella triptera</i> Ehrenberg							x		
<i>Polyarthra major</i> Burckhardt			x		x				
<i>Polyarthra remata</i> (Skorikov)		x	x	x	x		x	x	
<i>Trichocerca similis</i> (Wierzejski)									x
<i>Trichotria tetractis</i> (Ehrenberg)							x		
Crustacea									
<i>Acroperus harpae</i> (Baird)	x	x	x	x	x	x	x	x	x
<i>Alona guttata</i> Sars			x						
<i>Alona rectangula</i> Sars							x		
<i>Alonella excisa</i> (Fischer)							x	x	
<i>Alonella nana</i> (Baird)								x	
<i>Bosmina coregoni</i> Baird	x	x	x	x	x	x	x	x	x
<i>Bosmina longirostris</i> (O.F. Müller)								x	x
<i>Camptocercus rectirostris</i> Schoedler				x	x			x	
<i>Ceriodaphnia pulchella</i> Sars	x	x				x		x	x
<i>Ceriodaphnia quadrangula</i> (O.F. Müller)	x	x			x	x	x	x	x
<i>Ceriodaphnia reticulata</i> (Jurine)								x	
<i>Chydorus sphaericus</i> (O.F. Müller)			x			x			x
<i>Daphnia cucullata</i> Sars	x	x							
<i>Diaphanosoma brachyurum</i> (Lievin)	x		x						x
<i>Sida crystallina</i> (O.F. Müller)			x						
<i>Eudiaptomus gracilis</i> (Sars)							x		x
<i>Thermocyclops oithonoides</i> (Sars)					x				

T – Typha; w – open water; C – Chara; sp – spring; su – summer; au – autumn

exclusively in this zone, while *Ascomorpha saltans* Bartsch, *Alona guttata* Sars, *Ceriodaphnia reticulata* (Jurine), *Sida crystallina* (O.F. Müller) and *Thermocyclops oithonoides* Sars (out of 20 species) dominated in the Typha

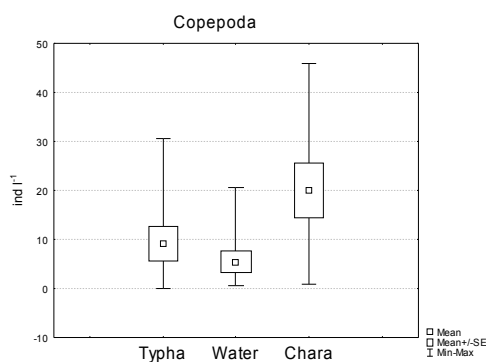


Fig. 4. Mean densities (ind l⁻¹) of pelagic Copepoda at particular stations, irrespective of lake and season (N=27).

Smaller rotifers dominated over larger crustaceans at all sampling stations in the studied lakes. This distribution pattern of particular zooplankton groups is often typical for lake ecosystems and reflects the relationships between planktonic organisms in the trophic pyramid. Zooplankton densities differed significantly between certain stations among each group of animals with the highest mean numbers within the most complex habitat, the *Chara* bed, which is created by a dense structure of stems, and the lowest within the *Typha* stand, whose stems are vertically orientated and create a less complicated habitat. This distribution of zooplankton abundance resembles the model for shallow lakes with fish predation present, where the highest numbers of zooplankton individuals are found among the thick macrophyte beds during the day, as described by e.g. Timms & Moss (1984). Rotifers are preyed upon by many fish, especially during fish young stages, both larval and juvenile (Dibble & Harrel 1997, Petr 2000), and macrophytes may constitute an effective refuge from fish predation for zooplankton (Moss et al. 1998). An alternative explanation for finding such a variety of zooplankters in much greater abundance within the *Chara* bed might be the autecology of numerous littoral species, which derive from littoral organisms in their evolution and hence their densities within vegetated areas of shallow lakes tend to be higher.

stand and, finally, *Brachionus angularis* Gosse, *Filinia longiseta* (Ehrenberg) and *Polyarthra major* Burckhardt from among rotifers and crustaceans *Alona rectangularis* Sars, *Bosmina longirostris* (O.F. Müller) and *Daphnia cucullata* Sars (out of 13 species) dominated in the open water zone.

DISCUSSION

The littoral area of macrophyte-dominated lakes is typically characterised by rich and

Rotifer and crustacean communities in the littoral zone of water bodies consist of various types of organisms, including epiphytic, benthic and numerous pelagic species. Due to such diversity, there are a variety of ways of obtaining food and also of using the macrophyte bed as an anti-predator refuge (Gliwicz & Rybak 1976). In the analysis of the occurrence of pelagic species between investigated sampling stations, it was noted that only in the case of copepods did the densities differ significantly, reaching highest values among stoneworts. Vegetated areas were dominated by littoral species, while the open water zone possessed a rich pelagic community, often reaching 100% of the total zooplankton abundance. However, the participation of limnetic species was also quite high (between 33 and 94%) among the *Typha* stand, and was lower among the *Chara* bed (between 9 and 71%). The observation of a relatively high proportion of pelagic organisms within stands of aquatic vegetation is both due to their search for concealment among morphologically and spatially complicated habitats as well as due to interactions between plant-associated zooplankton and organisms which stay temporarily or permanently in the water within the plant stand (Jeppesen et al. 1998). Additionally, if we take into consideration the findings of some authors (e.g. Preissler 1977, Saunders-Davies 1989) who have stated that the numbers of pelagic species increase with distance from the shore, it can be noticed that in the case of shallow and macrophyte-dominated lakes this does not apply. A greater proportion of pelagic species was found in the nearshore *Typha* stand compared to the *Chara* bed situated in the central part of the examined lakes. This is probably due to the fact that the functioning of aquatic communities in the littoral zone follows different rules in comparison to the pelagic zone. Furthermore, the higher participation of limnetic species in the cattail zone may also have been the result of water movement, as this is often an important factor in determining the horizontal distribution of zooplankton (Saunders-Davies 1989).

In analysing the most frequently occurring zooplankton species, it was found that, apart from *Colurella uncinata*, the remaining species belonged to forms associated with open water (Flössner 1972, Pejler 1995), so their maximum occurrence was found in the pelagic zone. However, as a result of seeking refuge from predation among macrophytes, pelagic species gather in the littoral zone during the daytime (Timms & Moss 1984), and consequently were found in high frequency in the examined material. Furthermore, limnetic species may also occur in the open water area during daylight hours, as some of the rotifer species have evolved special morphological features that could reduce the probability of predator success, such as long, bristle-like spines, which make the capture of prey more difficult (e.g. *K. cochlearis*), rapid escape responses (e.g. *P. vulgaris*) or gelatinous sheaths (e.g. *C. mutabilis*), which offer

greater protection by increasing body size and by making prey appear less distinct (Lampert & Sommer 1993, Pejler 1995). Crustacean zooplankton also protect themselves against attack from predators by employing both behavioural and morphological adaptations. Behavioural studies show vertical or horizontal segregation of animals, which is connected with their diel migrations (e.g. Lampert 1993, Sekino & Yamamura 1999). Morphological defenses are usually reflected in cyclomorphological changes of the body shape or size, where the relative tail spine length or the helmet size changes, or neckteeth in the neck region develop (Spaak & Boersma 1997, Caramujo & Boavida 2000, Kappes & Sinsch 2002, Laforsch & Tollrian 2004).

Dominance is one of the major elements of interaction between particular organisms, as it reflects both behavioural differences and fitness among individuals within a population (Krebs & Davies 1987). Moreover, the structure of dominance exerts an influence on such aspects as habitat selectivity, migrations as well as food availability. In the three examined lakes, the dominant community in all the studied habitats consisted of 35 zooplankton species in total, with 18 of Rotifera and 17 of Crustacea. The most spatially and morphologically diverse habitat, the *Chara* bed, possessed 24 dominating species, while the less diversified habitat, the *Typha* stand, possessed 20 species, and the open water zone was dominated by only 13 species. The most homogenous habitat, the pelagic zone, does not provide the inhabiting organisms with a variety of niches, so the number of species and their trophic requirements may be restricted in such a habitat. In the open water zone, where pelagic species feeding on phytoplankton and detritus prevail, exploitative competition for the same food resources between particular animals may be reflected in the shared use of a particular niche or niche overlap. Competing species may co-occur when their environmental needs differ, such as when they utilise different sizes or kinds of food available, segregate spatially within the same habitat, or specialize in obtaining nutrition in different ways. Moreover, particular dominating species may be subject to time segregation and therefore dominate at alternate times.

The primary factor determining the distribution of rotifer and crustacean communities in two morphologically and spatially differentiated stands of aquatic vegetation and comparatively in the open water area of three shallow lakes seems to be the architecture of a particular habitat. This has also been stated by other authors, who have suggested that plant biomass or morphological differentiation have a crucial impact on the structure of invertebrate (Cyr & Downing 1988, Paterson 1993, van den Berg et al. 1997) as well as fish (Dibble & Harrel 1997) communities, reflecting the potential effectiveness of macrophytes as an anti-predator refuge. In addition, food

sources that may differ between particular macrophyte types in a lake (Jones et al. 2000) may play an important role in determining the distribution of zooplankton. The nutritional base varied in the case of the three investigated lakes, where chlorophyll *a* concentration was significantly higher in the stonewort bed (N. Kuczyńska-Kippen, manuscript in preparation), and the structure of both phytoplankton and periphyton differed between particular stations (Kuczyńska-Kippen et al. 2005, Messyas & Kuczyńska-Kippen 2006, Celewicz et al., manuscript in preparation). Smiley & Tessier (1998) demonstrated that typical littoral representatives of planktonic animals can subsist on nourishment from the pelagic area as well as on the littoral seston, while limnetic species do not flourish successfully on the littoral type of food.

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