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Regular research paper

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## INTERACTIONS OF CON-GENERIC *LECANE* SPECIES (ROTIFERA) WITHIN DIFFERENT MACROPHYTE PATCHES IN A SHALLOW LAKE

**ABSTRACT.** The research on the distribution of species of the *Lecane* genus among different types of macrophytes (including rushes, nymphaeids and two zones of submerged macrophytes) in comparison with open water was carried out for three years in a shallow lake (Lake Budzyńskie, western Poland; an area – 17.4 ha, maximum depth – 2.7 m and a mean depth – 1.4 m) in order to determine the possibility of their competition and of co-existence. The distinct species of submerged macrophytes create separate vegetation beds and patches in the lake. The size of a particular macrophyte bed did not exceed the area of 5 m. Zooplankton samples were collected between 1997 and 1999 (from April to October, at about 2-week intervals) in the shallow part (approx. 1m deep) of a lake. Nymphaeids were only sampled during the 1998 and 1999. Samples were taken at each site using a plexiglass core sampler (Ø 50-mm). Subsamples of a volume of about 1.5 l from the surface layer (0–1.5 m) were sampled from randomly chosen places within each macrophyte patch.

Six *Lecane* species were analysed (*Lecane bulla* (Gosse), *L. clostercerca* (Schmarda), *L. flexilis* (Gosse), *L. furcata* (Murray), *L. luna* (Müller) and *L. lunaris* (Ehrenberg)). *L. bulla* dominated at most of the examined stations each year. Detailed seasonal analysis of the abundance of particular species of the *Lecane* genus in most cases revealed the replacement character of their oc-

currence. The sudden increase in the numbers of one species caused a simultaneous decrease of another within the same macrophyte stand. A distinct replacement pattern was observed for *L. bulla*, which was replaced by *L. clostercerca* or *L. luna* and for another two pairs of species (*L. clostercerca* with *L. furcata* and *L. flexilis* with *L. luna*). At the same time, pairs of species such as *L. clostercerca*–*L. lunaris* (statistically positive correlation was found in the case of *Chara* bed –  $r_s = 0.70$ ;  $P = 0.007$ ), *L. flexilis*–*L. furcata* (within *Typha* –  $r_s = 0.58$ ;  $P = 0.048$ ) and also *L. luna*–*L. furcata* (in the *Myriophyllum* bed –  $r_s = 0.80$ ;  $P = 0.001$ ) exhibited a similar pattern of seasonal changes without, however, revealing the exchange occurrence between each other.

The pattern of species replacement within a genus is an example of the competitive exclusion of closely related species. The nature of the seasonal distribution of species of the *Lecane* genus, replacing each other over a period of time, may be connected with the niche overlap of particular species, which results in time segregation. Exploitative competition cannot be excluded when describing such behaviour.

**KEY WORDS:** rotifers, macrophytes, *Lecane*, niche overlap, related species, shallow lake

## 1. INTRODUCTION

Rotifers including the Lecanidae are able to inhabit a variety of environments and are mostly typically littoral forms (Pejler 1995). The behaviour of rotifers inhabiting the pelagic area of lakes has been extensively investigated (Herzig 1987), while the littoral zone still requires greater attention. The fitness of particular species among macrophytes is modified by a combination of abiotic and biotic factors, such as temperature, light, oxygen as well as food, invertebrate and fish predation (Pejler and Bērziņš 1989, Lauridsen *et al.* 1994, 1996, Theil-Nielsen and Søndergaard 1999). Moreover, when analysing rotifer behaviour, the effect of competition among rotifer species and competition between them and crustaceans cannot be neglected (Leibold 1991, Rozenzweig 1991, Sarma *et al.* 1996). The initial causes of intraspecific competition are usually limited environmental resources. It may be supposed that related organisms living in the same habitat will interfere with each other, which may result in changes in the behaviour of the population of one species in the presence of a second species.

Although, the pattern of seasonal distribution of zooplankton within the littoral zone of lakes is recognised to some extent (Kuczyńska-Kippen 2001a, Kuczyńska-Kippen and Nagengast 2006), only a little is known about detailed seasonal changes of related species of the same genus among different types of water vegetation. The macrophyte zone, due to its morphologically and spatially complicated structure, may create numerous ecological niches (Gliwicz and Rybak 1976), which may help zooplankton to co-exist in this environment. Particular plants differ in respect to their architecture, which in turn influences the amount of available food. In the case of the studied lake the *Chara* and *Myriophyllum* beds appeared to be denser and more complicated in shape and also contained richer food resources compared to the *Typha* and *Potamogeton* stands (Kuczyńska-Kippen and Nagengast 2003). The variation in shape and density of particular macrophytes relates also to their

effectiveness as a refuge for zooplankton (Crowder and Cooper 1982, Jeppesen *et al.* 1997, Van de Meutter *et al.* 2005).

The aim of this study was to find out whether in a shallow lake with well-developed macrophyte cover, the co-existence of closely related species, representing the *Lecane* genus, takes place. Thus this work was then undertaken in order to:

- determine the spatial distribution of *Lecane* species in the littoral zone of the lake under study,
- describe a seasonal pattern of the replacement of different rotifer species within a particular macrophyte stand,
- find out whether there are similarities in the seasonal pattern of the sequence between particular species of the *Lecane*.

## 2. MATERIAL AND METHODS

The research was carried out on Lake Budzyńskie, which is a shallow and macrophyte-dominated lake, situated in the southern part of the Wielkopolski National Park (western Poland). It has an area of 17.4 ha, maximum depth of 2.7 m and a mean depth of 1.4 m. It has been a nature reserve since 1957 due to the ecological succession of vegetation.

The lake consists of two basins; the south-east basin is deeper and only partially covered by submerged vegetation (only along the bank) and the north-west basin which is fully overgrown. Between both basins a stand of *Potamogeton natans* L. has developed. A belt of emergent macrophytes (95% of the shoreline) mainly with *Typha angustifolia* L. surrounds the whole basin of the lake. Nearly 75% of the basin is covered by submerged macrophytes, predominantly *Chara tomentosa* L. and *Myriophyllum verticillatum* L. The distinct species of submerged macrophytes create separate vegetation beds and patches in the lake. The size of a particular macrophyte bed has not exceeded the area of 5 m. The macrophyte measures revealed that *Chara tomentosa* was characterised by the longest stems and relatively high biomass in one litre of the lake water. The rush species were of lowest stem lengths and the highest stem biomass. The results obtained for *Myriophyllum* and

*Potamogeton* were alike, reaching the medium values compared to other species (Table 1).

The distribution of *Lecane* species among different types of macrophytes (including rushes, and two zones of submerged macrophytes) and the open water between particular vegetation stands was studied between 1997 and 1999 (from April to October, 2–3 times a month) in the shallow part (approx. 1 m deep) of Budzyńskie Lake. Nymphaeids were only sampled during 1998 and 1999.

Samples were taken at each site using a plexiglass core sampler (Ø 50-mm) (Schriver *et al.* 1995). Subsamples of a volume of about 1.5 l from the surface layer (0–1.5 m) were sampled from randomly chosen places within each station and pooled together into a calibrated vessel. The collected material of the total volume of 10 l was concentrated using a 45-µm plankton net and was fixed immediately with 4% formalin.

Spearman rank correlation was used in order to compare the trends in the % participation of *Lecane* species pairs within a particular habitat. The analysis was made for 1998 data due to the largest amount of material and regularity of sampling ( $n = 13$  for *Myriophyllum* and *Chara*,  $n = 12$  for *Ty-*

*pha* and water area,  $n = 9$  for *Potamogeton* zone).

The analysis of distribution of lecanid numbers representing particular species between particular habitats was conducted using the analysis of variance (ANOVA) along with the Tukey test ( $n = 105$ ).

### 3. RESULTS

In order to analyse the seasonal changes of species within a single genus the *Lecane* spp. was chosen due to the possibility of co-existence of closely related species. *Lecane* was the genus richest in species (20 species) and had high relative abundance (exceeding 5%) compared to other Rotifera genera of Budzyńskie Lake. However, only six species, due to their highest numbers within the *Lecane* genus in the examined lake, were used in the analysis – *Lecane bulla* (Gosse), *L. closterocerca* (Schmarada), *L. flexilis* (Gosse), *L. furcata* (Murray), *L. luna* (Müller) and *L. lunaris* (Ehrenberg). Apart from *L. lunaris* all remaining six species revealed statistically significant differences between particular habitats, irrespective of the sampling season (Table 2). The post-hoc comparisons revealed that apart from *L. luna* in all cases the abundance of rotifer communities in the *Myriophyllum* stand differed from the *Typha* and open water zone and also in most cases from *Potamogeton* ( $P < 0.05$ ). Moreover, rotifer densities within the *Chara* bed differed from those in open water (*L. bulla*, *L. luna*) and from *Typha* station (*L. luna*) ( $P < 0.05$ ) (Fig. 1).

The mean abundance of particular species revealed that *L. bulla* was dominating (Fig. 2). The peak of its appearance in Budzyńskie Lake was found to be in June and July. In the two first years this species dominated ‘unsharably’ at each station, while in 1999 the higher participation of *L. closterocerca* in the zones of open water and *Chara* zones was observed (Fig. 3).

In the first year of examination, apart from the constantly dominating *L. bulla*, in the stands of *Chara* and *Myriophyllum*, the occurrence of *L. furcata* (with the highest numbers in the middle of August; representing 16 and 18% of the *Lecane* spp. densities respectively) and *L. closterocerca*

Table 1. The length of particular macrophyte stems and their biomass adequate to 1 litre of water in Budzyńskie Lake (Kuczyńska-Kippen and Nagengast 2003).

Macrophyte species	Stem length (m)	Stem biomass (g)
<i>Typha</i>	0.69	9.24
<i>Chara</i>	6.78	5.53
<i>Myriophyllum</i>	2.69	4.56
<i>Potamogeton</i>	1.77	4.32

Table 2. Results of analysis of variance of *Lecane* species densities between particular habitats, irrespective of the season.

Species	F <sub>4,100</sub>	P
<i>Lecane bulla</i>	7.6083	0.0000
<i>Lecane closterocerca</i>	7.5938	0.0000
<i>Lecane furcata</i>	3.6299	0.0085
<i>Lecane luna</i>	4.4740	0.0023
<i>Lecane flexilis</i>	6.4126	0.0001
<i>Lecane lunaris</i>	2.2725	0.0667

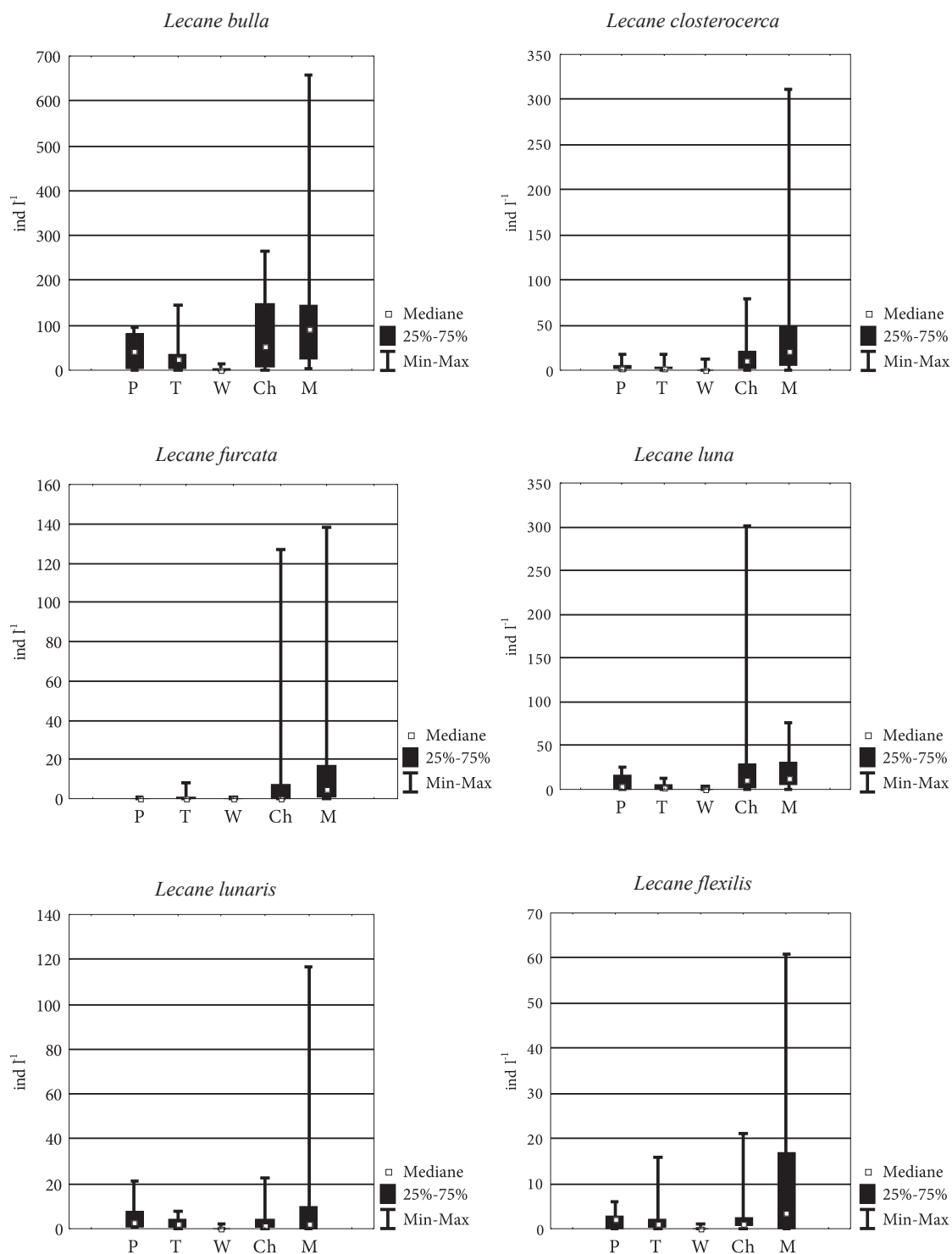


Fig. 1. The numbers of Rotifera (ind l<sup>-1</sup>) of particular *Lecane* species between particular habitats in Budzyńskie Lake (mean values for 1997–1999; P – *Potamogeton*, T – *Typha*, W – Water, Ch – *Chara*, M – *Myriophyllum*).

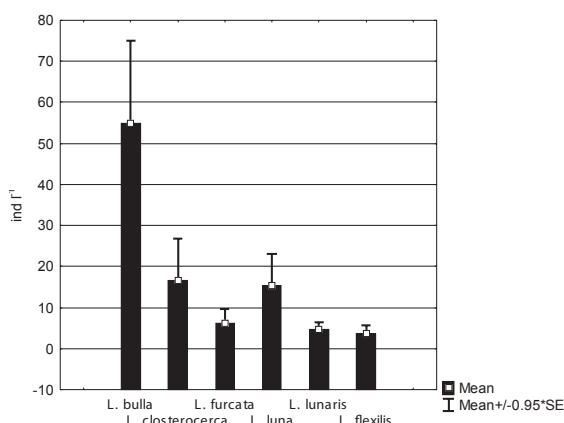


Fig. 2. Mean values of particular *Lecane* species irrespective of the examined stand (mean values for 1997–1999).

(11 and 9% respectively) was noticed (Fig. 3).

In 1998, with the constant domination of *L. bulla*, a higher participation of other species of *Lecane* spp. was recorded. *Lecane luna* dominated in the zones of open water as well as of *Chara* (27 and 31% respectively for both stations) and *L. closterocerca* in the zones of *Myriophyllum*, *Potamogeton* and *Chara* (29, 20 and 17%). Additionally, for 1998 the presence of *L. lunaris* occurring in higher densities in the late-spring season (maximum in *Potamogeton* – 14% of the total numbers of *Lecane* spp.) and *L. flexilis* in the early-spring season (maximum in the *Typha* zone – 14%) was observed (Fig. 3).

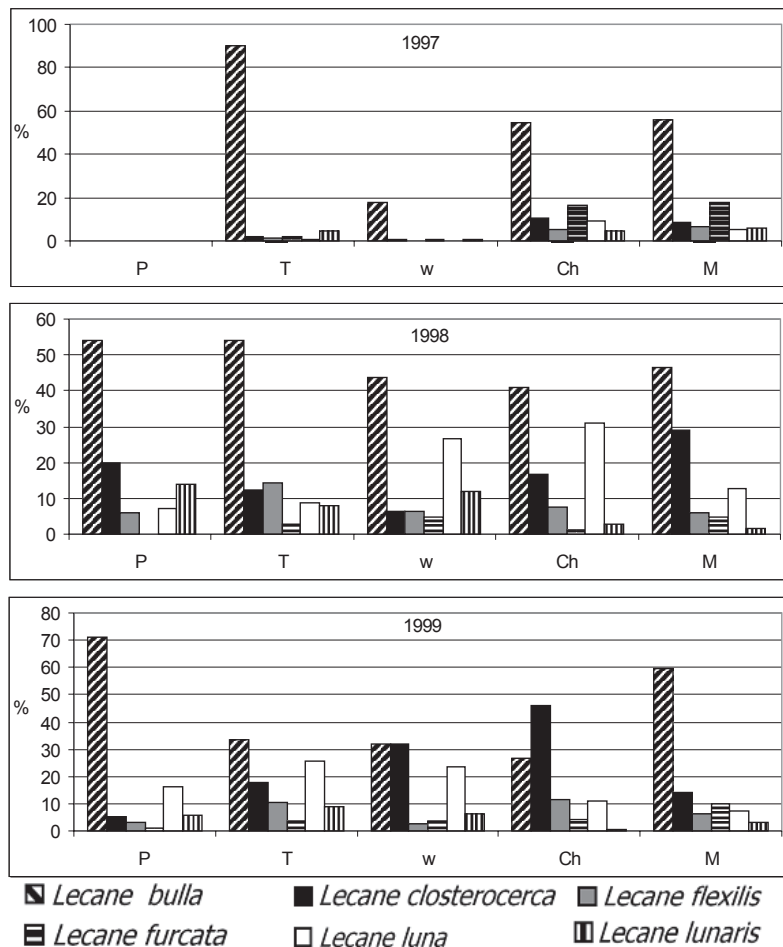


Fig. 3. Mean relative abundance (%) of dominant species in the total numbers of all the *Lecane* spp. (100%) between the years 1997 and 1999 in Budzyńskie Lake. (P – *Potamogeton*; T – *Typha*; w – water; Ch – *Chara*; M – *Myriophyllum*)

In 1999, apart from the dominance of *L. bulla* and *L. closterocerca*, a high participation of *L. luna* in the zones of *Typha* (26%), open water (23%) and *Potamogeton* (16%) was observed. The optimum of the occurrence of *L. closterocerca* and *L. luna* was recorded in the spring and autumn period of the examination (Fig. 3).

The detailed seasonal analysis of the density of particular species of the *Lecane* genus revealed in most cases the replacement character of their occurrence. The sudden increase in the numbers of one species caused a simultaneous decrease of another one or two species (Fig. 4). Due to the most extensive and long-term dominance of *L. bulla* at all the stations, irrespective of the examination year, this species seems to have a decisive influence on the occurrence of the remaining species of the genus *Lecane*. *L. bulla* had mainly negative influence on other species due to negative values of the correlation coefficients (Table 3). Altogether, eight

significant correlations were found when all the pairs of *Lecane* species in particular habitats of Budzyńskie lake were compared for 1998, although the determination coefficient was very high in many other cases. A distinct pattern of competition was observed for *L. bulla*, which was often replaced by *L. closterocerca* (statistically negative correlation was noted for the zone of *Potamogeton* and *Myriophyllum*) or *L. luna* (in the *Chara* bed). Moreover, such a pattern was also recorded for *L. closterocerca* and *L. furcata* (in the *Chara* stand) as well as for *L. flexilis* and *L. luna* (in the open water zone) (Table 3).

At the same time pairs of species *L. closterocerca* with *L. lunaris* (statistically positive correlation was found in the case of *Chara* bed), *L. flexilis* with *L. furcata* (within *Typha*) and also *L. furcata* with *L. luna* (in the *Myriophyllum* bed) exhibited a similar pattern of seasonal changes without, however, revealing the exchange occurrence between each other (Table 3).

Table 3. Correlations between pairs of *Lecane* species in particular habitat (P – *Potamogeton*, T – *Typha*, W – Water, Ch – *Chara*, M – *Myriophyllum*).

Species	P		T		W		Ch		M	
	$r_s$	<i>P</i>	$r_s$	<i>P</i>	$r_s$	<i>P</i>	$r_s$	<i>P</i>	$r_s$	<i>P</i>
<i>L. bulla</i> vs. <i>L. closterocerca</i>	-0.70	0.036	-0.49	0.102	-0.20	0.553	-0.27	0.378	-0.75	0.003
<i>L. bulla</i> vs. <i>L. flexilis</i>	-0.38	0.053	-0.43	0.159	0.00	0.993	-0.23	0.448	-0.38	0.201
<i>L. bulla</i> vs. <i>L. furcata</i>	-0.14	0.725	-0.29	0.358	-0.57	0.068	-0.26	0.309	-0.20	0.523
<i>L. bulla</i> vs. <i>L. luna</i>	0.03	0.931	-0.07	0.836	-0.34	0.312	-0.62	0.024	-0.25	0.415
<i>L. bulla</i> vs. <i>L. lunaris</i>	-0.32	0.404	-0.22	0.490	-0.21	0.543	0.17	0.571	-0.11	0.731
<i>L. closterocerca</i> vs. <i>L. flexilis</i>	0.64	0.061	-0.37	0.239	0.45	0.166	0.44	0.132	0.27	0.374
<i>L. closterocerca</i> vs. <i>L. furcata</i>	-0.41	0.272	-0.43	0.161	0.22	0.518	-0.58	0.036	-0.12	0.687
<i>L. closterocerca</i> vs. <i>L. luna</i>	-0.56	0.117	-0.36	0.256	-0.38	0.246	0.07	0.823	-0.08	0.803
<i>L. closterocerca</i> vs. <i>L. lunaris</i>	0.11	0.781	0.20	0.540	0.09	0.803	0.70	0.007	0.27	0.377
<i>L. flexilis</i> vs. <i>L. furcata</i>	-0.42	0.263	0.58	0.048	0.39	0.241	-0.39	0.190	0.34	0.254
<i>L. flexilis</i> vs. <i>L. luna</i>	0.00	1.000	0.20	0.538	-0.68	0.020	-0.26	0.394	0.34	0.263
<i>L. flexilis</i> vs. <i>L. lunaris</i>	-0.19	0.630	-0.25	0.428	-0.44	0.174	0.17	0.584	-0.45	0.124
<i>L. furcata</i> vs. <i>L. luna</i>	0.42	0.263	0.47	0.120	-0.15	0.656	0.31	0.302	0.80	0.001
<i>L. furcata</i> vs. <i>L. lunaris</i>	0.41	0.270	-0.10	0.752	0.12	0.714	-0.41	0.161	0.02	0.957
<i>L. luna</i> vs. <i>L. lunaris</i>	-0.24	0.537	0.14	0.670	-0.12	0.717	-0.24	0.431	-0.03	0.921

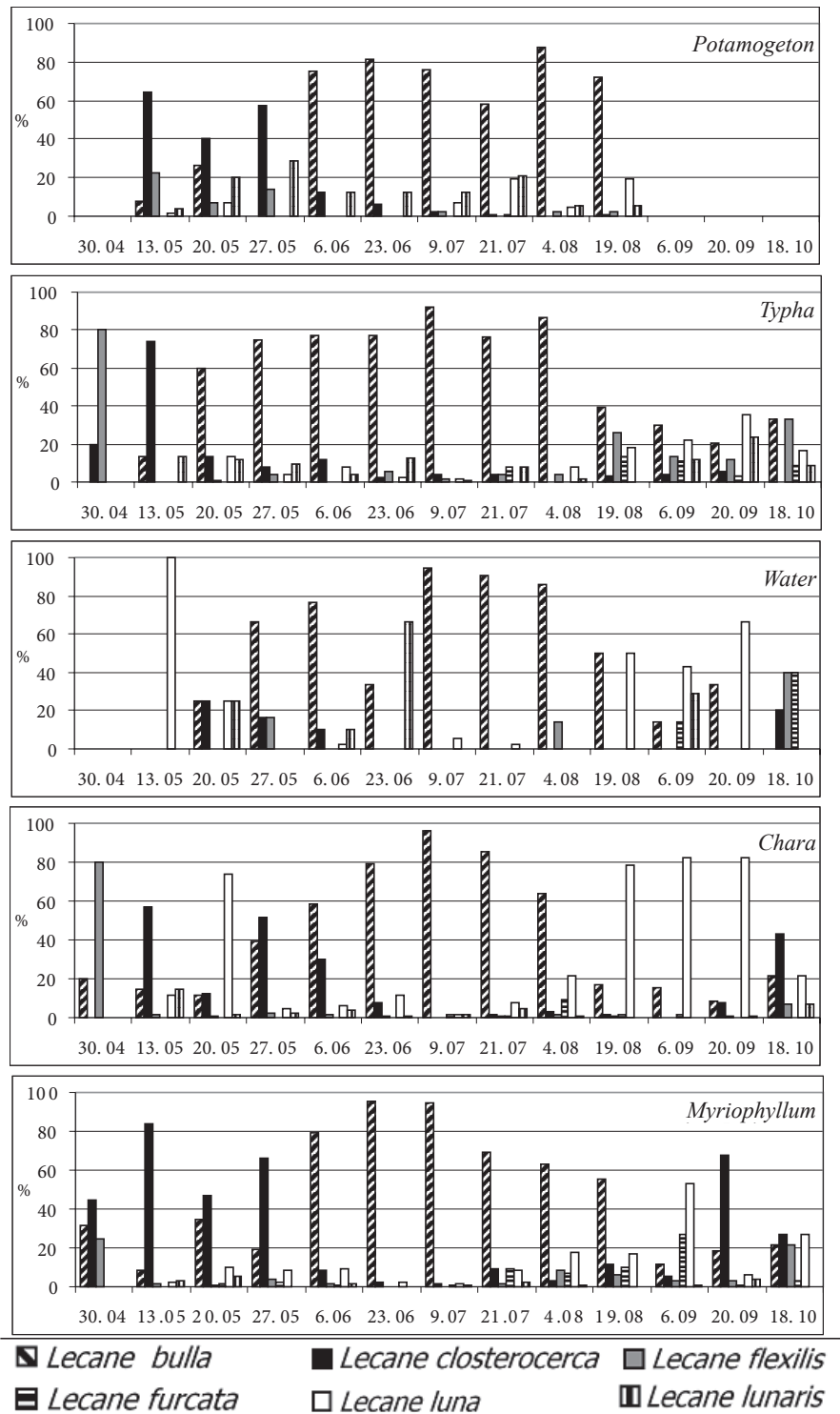


Fig. 4. The participation (in %) of *Lecane* species (100%) in particular zones of Budzyńskie Lake between the years 1997 and 1999.

#### 4. DISCUSSION

The littoral zone is typically characterised by rich and diverse zooplankton communities (Gliwicz and Rybak 1976, Havens 1991). In Budzyńskie lake the most abundant genus was *Lecane*, represented by 20 species. Also Segers *et al.* (1993), examining 13 locations in the Niger delta, including 6 lakes, 4 rivers, rice field and forest pond, revealed the highest species diversity among the *Lecane* spp. This genus is characteristic of littoral environments, inhabiting the zones of nymphaeids, submerged macrophytes as well as helophytes (Pejler and Bērziņš 1994), although some of the species can be frequently found in the pelagic zone of lakes. Some of the *Lecane* species (e.g. *L. bulla*, *L. luna*, *L. closteroerca*, *L. lunaris*) are considered to be among the most common of the rotifer fauna, which appeared to be true in the case of Budzyńskie lake. Moreover, *L. furcata* and *L. flexilis* are described as cosmopolitan, often eurytopic forms (Segers 1995). The above species were analysed seasonally in order to ascertain the pattern of the co-existence of closely related species.

Throughout the three years of examination a replacement pattern of density changes of particular species within the *Lecane* genus was observed. *Lecane bulla* was characterised by the highest level of dominance and therefore it seemed to be the strongest competitor. This species negatively influenced the occurrence of other species of this genus due to mainly negative values of the correlation coefficients. In the first two years this species greatly dominated at all the stations, while in the last year of examination *L. closteroerca* was of higher dominance at the stations of open water and *Chara* bed. At the same time, other species – *L. luna*, *L. lunaris*, *L. flexilis* and *L. furcata* – occurred, revealing the pattern of exchange in time with the above species (*L. bulla* and *L. closteroerca*). Such a pattern, described as a density decrease of one species caused by the increase of another species, was observed for all the years of the examination, however, the statistical analyses were made for 1998, when the samples were collected with highest regularity throughout the spring-summer-autumn seasons. Spearman rank correlation revealed eight

significant relations between pairs of species within a particular habitat. However, the determinant coefficient was high in many cases, which may suggest the presence of a tendency in the relationship between other pairs of *Lecane* species. In the case of *Typha* and *Potamogeton* (both macrophyte zones of sparse stem structure) as well as of open water only one significant correlation was found for each zone, while in *Chara* and *Myriophyllum* (zones of more complicated architecture and dense stem structure due to the longest stems per water unit) three and two respectively. The number of significant correlations seems to be related to increasing density and spatial differentiation of a particular habitat, which led to better refuge conditions and greater numbers of individuals among submerged macrophytes (Kuczyńska-Kippen 2001b, Duggan 2001, Warfe and Barmuta 2004) and therefore stronger competition among inhabiting organisms. Also Lynch (1979), Cooper and Smith (1982) as well as Jiang and Kulczycki (2004) observed that the level of predation may influence the competing abilities of particular organisms.

*Lecane bulla* seemed to have a decisive effect on the occurrence of the remaining species, exchanging with *L. closteroerca* or *L. luna*. A similar distribution pattern was also recorded for two pairs of species: *L. closteroerca*–*L. furcata* and *L. flexilis*–*L. luna*. The nature of the seasonal distribution of species of the *Lecane* genus, representing such a pattern of replacement in time, may be connected with the niche overlap of particular species, which then results in time segregation. It was observed that the optimum of *L. bulla* occurrence at all the stations was ascertained for the summer months, while the remaining species for the spring and autumn season. However, *L. luna* and *L. closteroerca* dominated in both seasons, *L. flexilis* appeared in higher numbers in the spring and *L. furcata* mostly in the autumn. Exploitative competition cannot be excluded when describing such behaviour. This kind of competition for shared food may be manifested in the suppression effect of one species by other species. Gilbert (1988, 1999) and Wickham and Gilbert (1990) described the suppression of rotifers by crustaceans as the effect of exploitative competition for the same food

resources between both groups of animals. Moreover, close relations between two competing species may reduce the population of the weaker through the decrease of its reproduction rate or through mechanical interference (Gilbert 1985, Kirk 2002), however, this has probably not played a role among the group of lecanids. The replacement of species within a genus is a classical example of the competitive exclusion of closely related species within a particular habitat, where two competing species have the same requirements towards the realized ecological niche.

When analysing the seasonal distribution, another group of species of a similar seasonal pattern, was distinguished. These species did not display a characteristic replacement pattern between each other, although periodically they could exchange with the next species – usually *L. bulla*. It was observed that *L. clostercerca*–*L. lunaris* and *L. furcata*–*L. luna* and *L. flexilis*–*L. furcata* had not competed among themselves. In this case such behaviour may be explained by the shared use of a particular niche by both species or by the niche overlap among these pairs of species, which manifests itself in the shared exploitation of the food resources or in their common occurrence in time and space. Two competing species may co-exist only in the case when they differ in their requirements towards the resources. This may be connected with the different kind or size of the available food or with space segregation within the same habitat (species may occupy different parts of a particular macrophyte stand e.g. Kuczyńska-Kippen 2003, 2006), though due to the sampling method used this could not be confirmed. Furthermore, some organisms, as a result of natural selection, may act as various specialists in gaining food in different ways. The lack of evident competitive exclusion of species may also be related to their morphological differentiation.

The seasonal distribution of species of the *Lecane* genus within different types of macrophytes seems to be very complex, mostly related to the exploitative competition for shared food resources between particular species of rotifers, which may then lead to the competitive exclusion of closely related species (Walter 1988). Smiley and Tes-

sier (1998) stated that a food source plays an important role in determining the distribution of zooplankton and may be a factor here also. Moreover, shared exploitation of food resources and the differentiation in size of particular organisms may also play an important role in the occupation of ecological niches and the co-existence of similar species (Peters 1983, Wilson 1990).

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