

Vertical variability of pelagic zooplankton fauna in deep Latvian lakes, with some notes on changes in ecological conditions

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Abstract. Vertical structure of zooplankton communities from five deep Latvian lakes during the late summer and early autumn season was analysed. Changes in species composition, abundance, and dominant species assemblages were assessed in relation to temperature, oxygen, pH, chlorophyll *a*, oxidation reduction potential, and conductivity. Where possible, comparison with historical data was made.

No significant changes of ecological conditions and annual dynamics of zooplankton diversity and abundance during the last 50 years were observed. However, a decrease of oxygen concentration occurred in deep lakes, caused probably by the pressure of human induced eutrophication. Also, slight differences were observed in the species composition, which most likely mark changes in the trophic status.

A total of 24 to 38 Rotifera and Cladocera species were found during investigations from all lakes. The dominant species were *Conochilus hippocrepis*, *Keratella cochlearis*, *Polyarthra vulgaris*, *Filinia longiseta*, *Kellicottia longispina*, *Daphnia (Daphnia) cucullata*, *Diaphanosoma brachyurum*, *Bosmina (Eubosmina) crassicornis*, and *B. (Eubosmina) longispina*.

Zooplankton communities can be defined as distinct groups both at species and higher levels on the basis of seasonal stratification in deep lakes.

Temperature, oxidation reduction potential, and chlorophyll *a* concentration were found to be statistically the most influential environmental factors in the vertical distribution of zooplankton. Also sampling date and depth showed strong trends concerning zooplankton abundance and species composition. Vertical segregation between samples occurred within water layers of 0–10 m, 10–20 m, and below 20 m depth. The samples collected at the beginning of the sampling season assembled into a separate group.

Key words: zooplankton, community structure, vertical variability, seasonal dynamics.

INTRODUCTION

A combination of light, temperature, oxygen and other abiotic variables, food resources, competition and predation (both by fish and invertebrates) affects the seasonal vertical structure of freshwater zooplankton. Many reviews and investigations emphasize this (e.g. Stich & Lampert, 1981; Primicerio & Klemetsen, 1999; Primicerio, 2000; Kehayias et al., 2004; Kessler & Lampert, 2004; Pinel-

Alloul et al., 2004; Ka et al., 2006; Trifonova & Makartseva, 2006; Adamczuk, 2009; Doulka & Kehayias, 2011).

Seasonal stratification is considered to be the primary factor affecting zooplankton species composition and biomass succession (Ortega-Mayagoitia et al., 2000; Ringelberg, 2010). Variation in physical and chemical conditions impacts zooplankton both at population and individual levels, providing unique, species-specific and predictably changing (see Hutchinson, 1957), but not necessarily stable niches. Besides the constantly changing environment due to seasonality some environmental conditions can become more influential than others. For example, competition for food resources is more important than predator avoidance in the vertical habitat segregation of cladocerans (Adamczuk, 2009). Time of starvation and ability to store resources may affect an individual's success in variable environments (Kirk, 2002). In fresh waters many zooplankton species are competing for limited resources (Hebert, 1982), and the outcome for coexistence among species is largely dependent on the fluctuations of biotic and abiotic factors and vertical segregation (Jacobs, 1977; Primicerio, 2000). The complexity of zooplankton species is very dynamic between different biotopes within a lake, with no clear delineations due to ecological conditions as one species complex is replaced by another (Line, 1966). Typically the zooplankton vertical distribution is shown to be more uniform before stratification and more differentiated during the summer stratification time (Primicerio, 2000; Hudcovicová & Vranovsky, 2006; Zadereev & Tolomeyev, 2007; Doulka & Kehayias, 2011).

About 1.5% of the area of Latvia is occupied by lakes (Glazaceva, 2004). Most of the Latvian lakes are shallow and eutrophic (70% of the lakes have an average depth of 1–5 m). Only seven Latvian lakes are deeper than 40 m and like shallow lakes tend to become shallower due to eutrophication and sedimentation impacts (Klavins et al., 2002; Glazaceva, 2004).

Dridzis is the deepest lake in Latvia (and the Baltic States). It is of great ecological importance like lakes Rica and Svete as they are located in protected natural parks and are also included in NATURA 2000 (network of protected areas in the European Union). Lake Rica is located in the border area of Latvia and Belarus and is protected in both countries. In accordance with regulations of the Cabinet of Ministers of the Republic of Latvia No. 118 'On surface and groundwater quality' of 12.03.2002 four of the investigated lakes (Dridzis, Svete, Rica, and Geranimova) are categorized as priority fish lakes for salmonid fish species. Therefore the current assessment of zooplankton, which is an important fish prey, is of particular interest.

Latvian freshwater zooplankton studies have so far mostly focused on upper water layers. Little is known about the seasonal vertical distribution of zooplankton in deep Latvian lakes. The deepest parts of the hypolimnion of the lakes have begun to be explored only recently. The aim of this study was therefore to describe patterns of the vertical dynamics of the zooplankton population and species interactions in the late summer to early autumn period in relation to environmental variables from five deep lakes in Latvia (Dridzis, Svete, Geranimova, Rica, and Garais). We also examined changes in zooplankton populations over the last 50 years where relevant data were available.

MATERIAL AND METHODS

The study was carried out in five lakes situated in the southeastern part of Latvia (Fig. 1). All lakes are located in the Latgale territorial unit (more than 40% of all Latvian lakes are located in this region (Glazaceva, 2004)). Latgale is characterized by relatively deep, clear lakes, some of which can still be considered as mesotrophic water bodies with some oligotrophic features. The lakes investigated are similar in their physical and some ecological features (dimictic, mesotrophic lakes with comparatively eutrophic bays) (Table 1).

Presence, diversity, and abundance of zooplankton were assessed in relation to temperature, pH, conductivity, dissolved oxygen content, oxidation reduction potential (ORP), and chlorophyll *a* content, which were recorded using a HACH DS5 Multiprobe.

Zooplankton was sampled from fixed stations (pelagic zone) in daytime. Samples were taken from July to September 2007 with two to four week intervals. For lakes Svente and Rica an additional sampling was made in September. Samples were collected using an Apstein type net (mesh size 64 μm) from various depths with sampling range of 10 m from the surface to the bottom. Samples were fixed with 4% formalin solution. The volume of subsamples was 3×2 mL (from 100 mL samples). In cases the density of specimens was high, the volume of samples was increased up to 200 mL. Subsamples were counted using a Carl Zeiss Jena 'Amplival' microscope ($\times 160$ magnification).

Individuals of Rotifera and Cladocera were identified to species level where possible. Two genera of copepods, of which only one was identified to species, were enumerated. All other copepods were recorded as nauplii, copepodites, and adults. Species were identified according to Kutikova (1970), Flossner (2000), Sloka (1981), Manujlova (1964), and Einsle (1993).

For comparing zooplankton communities between lakes, Sørensen's similarity index (QS) for species diversity between lakes was calculated: $QS = 2C/(A + B)$,

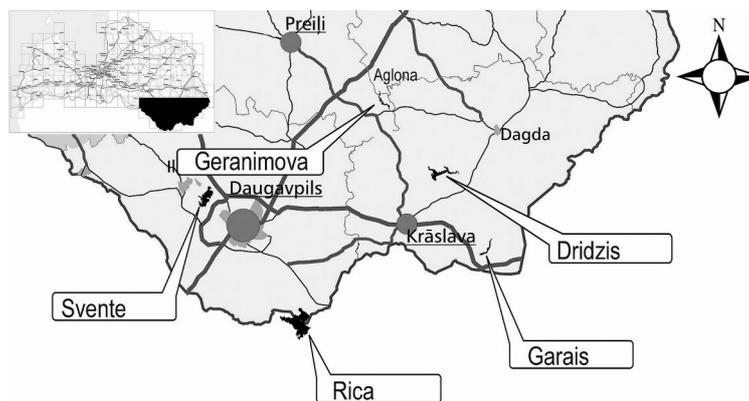


Fig. 1. Location of the study area and sampling sites (Latgale region, southeastern Latvia).

Table 1. Physical and ecological features of the investigated lakes

	Rica	Svente	Geranimova	Dridzis	Garais
Location	X670715.594 Y175721.067	X647412.511 Y192388.091	X696251.015 Y228167.042	X705390.852 Y208462.077	X717935.687 Y192640.366
Max length, km	6.0	5.3	8.1	9.8	3.4
Max width, km	4.0	2.8	0.8	2.4	~0.35
Surface area, km ²	12.86*	7.35	3.28	7.53	0.7
Average depth, m	9.7	7.8	9.8	12.8	16.5
Max depth, m	51.9**	38.0	46.0	65.1	56.0
Sampling depth, m	20	30	40	60	40
Notes on ecology	Mesotrophic	Eutrophic	Transition from mesoeutrophic to eutrophic	Mesotrophic	Mesotrophic

* In Latvia 5.88 km², in Belarus 6.98 km².

** The area of max depth is located in Belarus.

Coordinate system used for localities is LKS92. All data except for sampling depth are from the literature. For more information see Spuris (1951), Eipurs (1995a, 1995b, 1995c), Tidrikis (1997, 1998), Glazaceva (2004), and Society 'Latvian lakes' database.

where A and B are species numbers from two separate lakes, and C is the number of species shared by those lakes (Guhl, 1987). For Sørensen's similarity index calculations only Cladocera and Rotifera species were used.

In order to estimate dominance (D), frequency was calculated by the formula $D = 100 \times (X/Y)$, where X is the number of individuals of a certain species and Y is the total number of all individuals in the sample. The D values >10% indicate dominant species and 5–10% indicate subdominant species (Schwerdtfeger, 1975). Dominance was calculated separately for Cladocera and Rotifera (for species) and Copepoda (for nauplii, copepodites, and adults).

Finally, redundancy analysis (RDA) run in CONOCO 4.5 (ter Braak & Smilauer, 1998) was used to analyse the covariance structure of interspecies and environmental variables. Zooplankton species were scored as presence/absence and abundance records from different depths for each lake. Rare species were down-weighted.

RESULTS

Environmental variables

Temperature showed a clear summer stratification pattern (Fig. 2). Differences in temperature between the epilimnion and hypolimnion were most pronounced in

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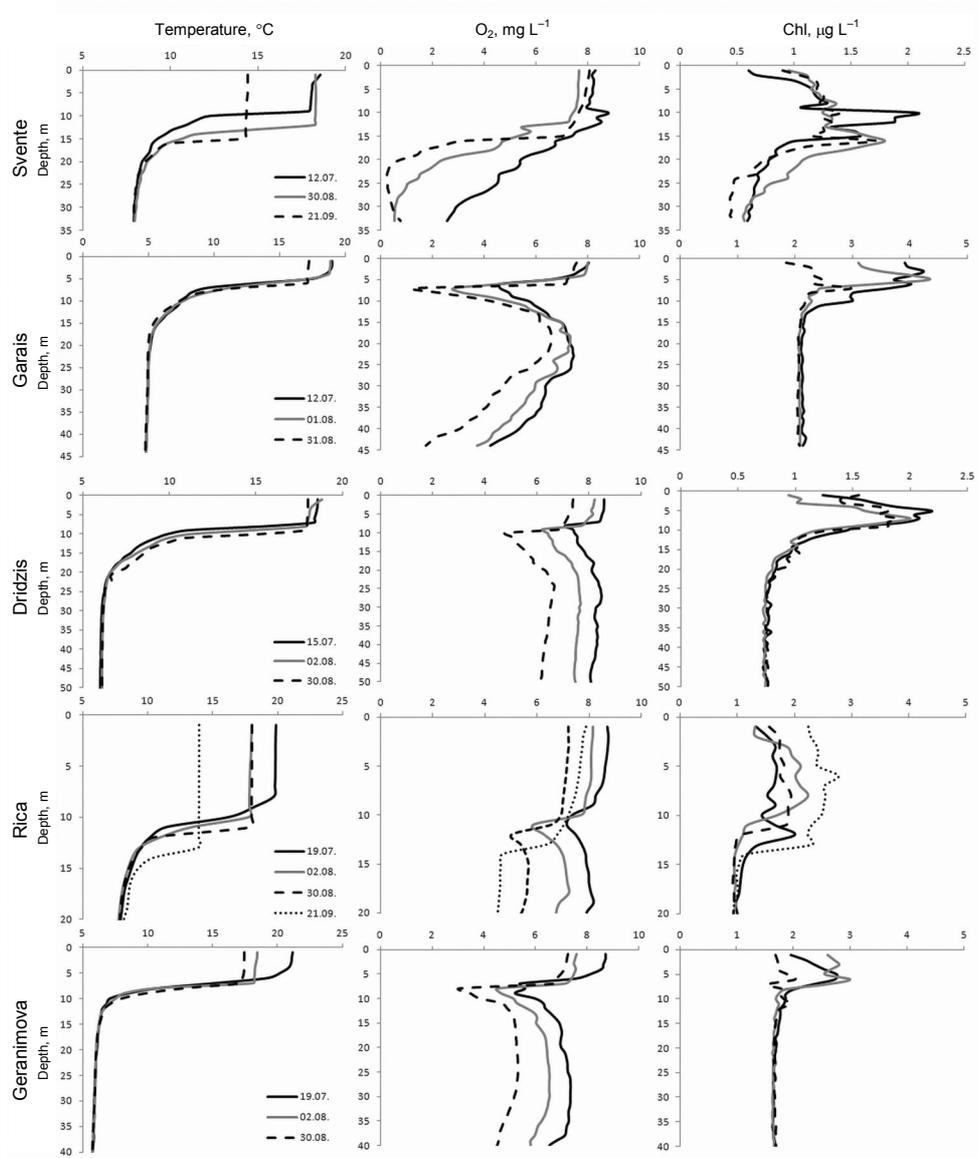


Fig. 2. Vertical profiles of temperature and dissolved oxygen and chlorophyll *a* concentration during the sampling period (2007) in the studied lakes.

lakes Garais and Geranimova in July, being 18.9°C and 21.2°C at the surface and 4.8°C and 5.7°C at the bottom, respectively.

The vertical oxygen gradient in Lake Svente demonstrated the classical negative heterograde curve for deep eutrophic lakes, with dissolved oxygen near the bottom close to 0 mg L⁻¹ in September (Fig. 2). The oxygen conditions were suitable for zooplankton during the whole sampling period in lakes Dridzis, Rica,

and Geranimova. Lake Garais experienced oxygen limitation at the end of summer at 7–8 m ($1.3\text{--}2.2\text{ mg L}^{-1}$) and below 42 m (less than 2 mg L^{-1}) depth.

A maximum for chlorophyll *a* concentration was detected in the upper water layer. In lakes Svente and Dridzis the highest concentrations were measured in July (2.1 and $2.2\text{ }\mu\text{g L}^{-1}$, respectively), in lakes Garais and Geranimova at the beginning of August (4.3 and $3\text{ }\mu\text{g L}^{-1}$, respectively). In Lake Rica the highest concentration of chlorophyll *a* was at the end of September ($2.7\text{ }\mu\text{g L}^{-1}$). For all lakes except Svente the chlorophyll *a* maximum was detected within the upper 10 m. In Lake Svente the chlorophyll *a* maximum reached ~ 15 m depth. Later during autumn a chlorophyll maximum was detected deeper than during summer (all lakes except Rica) (Fig. 2).

The average conductivity found for all lakes was between 226 and $320\text{ }\mu\text{S cm}^{-1}$. The highest average value was observed in lakes Garais and Geranimova (about $320\text{ }\mu\text{S cm}^{-1}$) and the lowest in Lake Svente ($226\text{ }\mu\text{S cm}^{-1}$).

The average pH for all lakes varied between 7.76 and 8.18 .

The ORP conditions in all lakes, except for Svente, were similar. In July we observed about 450 mV in the epilimnion, after which the ORP increased up to 500 mV in the metalimnion, and slightly decreased towards the bottom. In August and September the ORP decreased to about 350 mV in the epilimnion, increased in the metalimnion to almost 400 mV , and remained at that level down to the bottom. In Lake Svente the ORP increased in the metalimnion in July and remained at that level until the hypolimnion. During August and September the ORP decreased considerably, reaching values below 200 mV in the hypolimnion.

Diversity, abundance, and vertical distribution of zooplankton

The total number of Rotifera species found from the five lakes studied was 20 and that of Cladocera, 26 (Table 2). The highest zooplankton diversity was detected in lakes Svente and Dridzis (38 species), the lowest in Lake Garais (24 species). Lakes were similar in species composition (similarity varied from 69.8% between lakes Garais and Svente to 88.9% between lakes Rica and Geranimova according to Sørensen's similarity index).

The highest abundance of individuals was detected from lakes Svente and Dridzis (Fig. 3). In all lakes the abundance of zooplankton was higher in August than in July. The decreasing abundance in September was mainly due to the decreasing abundance of rotifers. There was no discernible maximum for Cladocera in lakes Dridzis, Svente, and Rica. In Lake Svente there was no explicit peak for Copepoda either. However, in Lake Geranimova cladocerans were more abundant in July, especially in the upper water layer, and decreased in autumn. This seasonal pattern contrasted with that of rotifers in Lake Geranimova. The total number of the rotifers in Lake Garais increased in August, reaching the maximum at the end of the month, while cladocerans and copepods increased at the beginning of August and then decreased at the end of the month. In Lake Dridzis the proportion of copepods increased towards the end of August while the opposite trend was observed for rotifers. Within Copepoda nauplii contributed

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Table 2. Pelagial zooplankton species composition from the studied lakes (R – Rica, S – Svente, GR – Geranimova, D – Dridzis, G – Garais) from July to September 2007. Average species dominance values during the sampling period: xxx > 10%, xx 5–10%, x < 5%

Taxon	Abbreviation	R	S	GR	D	G
Rotifera						
<i>Anuraeopsis</i> sp.					X	
<i>Ascomorpha ecaudis</i> Perty	<i>AscEca</i>	x		x	x	x
<i>Asplanchna</i> sp.	<i>Asp</i>	x	x	x	x	x
<i>Brachionus</i> sp.			x	x	x	
<i>Conochilus (Conochilus) hippocrepis</i> (Schrank)	<i>ConHip</i>	x	x	x	x	x
<i>Euchlanis</i> sp.					x	
<i>Filinia longiseta</i> (Ehrenberg)	<i>FilLon</i>	x	x	x	x	xx
<i>Kellicottia longispina</i> (Kellicott)	<i>KelLon</i>	x	xx	x	xxx	xx
<i>Keratella cochlearis</i> (Gosse)	<i>KerCoc</i>	xxx	xxx	xx	xxx	xxx
<i>Keratella quadrata</i> (Müller)	<i>KerQua</i>	x	x	x	x	x
<i>Lecane</i> sp.			x		x	
<i>Polyarthra vulgaris</i> Carlin	<i>PolVul</i>	xx	xx	x	x	x
<i>Polyarthra major</i> Burckhardt	<i>PolMaj</i>	x		x	x	
<i>Polyarthra remata</i> Skorikov				x	x	
<i>Pompholyx sulcata</i> Hudson	<i>PomSul</i>	x	x	x	x	x
<i>Synchaeta</i> sp.	<i>Syn</i>	x	x	x	x	
<i>Testudinella truncata</i> (Gosse)	<i>TesTru</i>	x	x	x	x	x
<i>Trichocerca capucina</i> (Wierzejski & Zacharias)	<i>TriCap</i>	x	x	x	x	x
<i>Trichocerca tigris</i> (Muller)	<i>TriTig</i>	x	x	x	x	x
<i>Trichotria pocillum</i> (Muller)			x			
Cladocera						
<i>Alona</i> sp.			x			
<i>Alona affinis</i> (Leydig)	<i>AloAff</i>	x	x	x	x	x
<i>Alonella nana</i> (Baird)					x	
<i>Bosmina (Eubosmina) coregoni</i> Baird					x	x
<i>Bosmina (Eubosmina) longispina</i> Leydig	<i>BosLons</i>	x	x	x	x	
<i>Bosmina (Bosmina) longirostris</i> (Muller)	<i>BosLongr</i>	x	x	x	x	x
<i>Bosmina (Eubosmina) crassicornis</i> Lilljeborg	<i>BosCra</i>	x	x	x	x	x
<i>Bosmina (Eubosmina) reflexa</i> Seligo		x				
<i>Bythotrephes longimanus</i> Leydig	<i>BytLon</i>	x	x	x	x	
<i>Ceriodaphnia pulchella</i> Sars			x		x	
<i>Ceriodaphnia reticulata</i> (Jurine)	<i>CerRet</i>	x	x	x	x	x
<i>Ceriodaphnia</i> sp.	<i>Cer</i>	x	x	x	x	x
<i>Chydorus ovalis</i> Kurz					x	
<i>Chydorus sphaericus</i> (Muller)	<i>ChySph</i>	x	x	x	x	
<i>Chydorus</i> sp.	<i>Chy</i>	x	x	x	x	
<i>Daphnia (Daphnia) cristata</i> Sars	<i>DapCri</i>	x	x	x	x	x
<i>Daphnia (Daphnia) cucullata</i> Sars	<i>DapCuc</i>	x	x	x	x	xxx
<i>Daphnia (Daphnia) longispina</i> Muller	<i>DapLon</i>	x	x	x	x	x
<i>Daphnia (Daphnia) pulex</i> Leydig				x		
<i>Daphnia (Daphnia)</i> sp.			x			
<i>Diaphanosoma brachyurum</i> (Lievin)	<i>DiaBra</i>	xx	x	x	x	x
<i>Holopedium gibberum</i> Zaddach			x			
<i>Kurzia latissima</i> Kurz		x	x			
<i>Leptodora kindti</i> Focke	<i>LepKin</i>		x	x	x	x
<i>Polyphemus pediculus</i> (Linnaeus)	<i>PolPed</i>	x	x			
<i>Sida crystallina</i> (Muller)	<i>SidCry</i>		x			
Copepoda						
<i>Eudiaptomus</i> sp.	<i>Eud</i>	x	x	x	x	x
<i>Limnocalanus macrurus</i> Sars			x			
Total species number		31	38	32	38	24

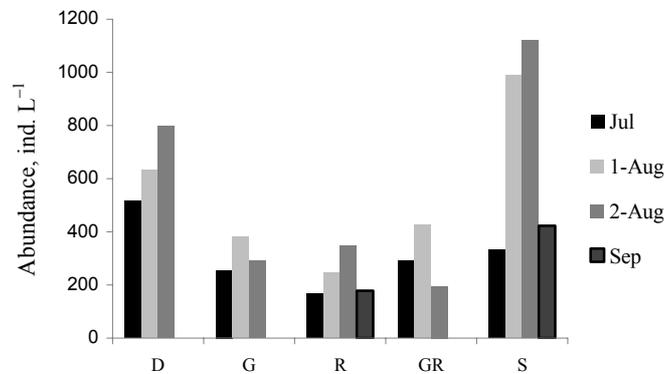


Fig. 3. Zooplankton abundance (average of all sampling layers) during the sampling period (July to September 2007) in the studied lakes: D – Dridzis, G – Garais, R – Rica, GR – Geranimova, S – Svente, 1-Aug – beginning of August, 2-Aug – end of August.

the most to their total amount in all lakes. Copepods comprised 72% of the total zooplankton abundance in Lake Geranimova during the observed season and did not exceed 49% in the other lakes (the lowest was 31% for Lake Svente).

The highest abundance was in the water layer of 0–20 m for all zooplankton groups with some exceptions. Zooplankton individuals from this water layer contributed on average 61–78% of the total zooplankton abundance. For the lakes with the greatest maximum depths, Dridzis and Garais, the share was 61% and 69%, respectively. For the shallower lakes Geranimova and Svente the zooplankton abundance of the water layer of 0–20 m made up 75% and 78% of the total abundance, respectively. Cladocerans tended to be located in the 0–10 m layer in lakes Dridzis and Svente. Rotifers were more abundant in the water layer below 10 m. The species diversity of the Rotifera showed high similarity between lakes. For all lakes *Keratella cochlearis* was the most common species and was found during every sampling visit (Table 2). In lakes Geranimova and Svente *K. cochlearis* was especially abundant below 20 m depth.

The second most abundant Rotifera species from lakes Dridzis, Garais, and Svente was *Kellicottia longispina*, appearing as dominant during July and at the end of August, especially below 10 m depth. Both species, *K. cochlearis* and *K. longispina*, co-occurred as dominants for a period in August.

Polyarthra vulgaris occasionally dominated in lakes Svente, Garais, Rica, and Geranimova. The dominance of this species increased in late summer and in autumn.

The common species included also *Conochilus (Conochilus) hippocrepis* and *Filinia longiseta*. The former appeared as a subdominant and dominant species in lakes Svente and Rica during summer months, but not during September. The latter was a dominant in some samples from deeper water layers (10–45 m) in Lake Garais.

There was a distinct vertical and seasonal pattern between the rotifer species *K. longispina* and *P. vulgaris* in all lakes. Except for Rica, the same pattern was

also found between *K. longispina* and *Pompholyx sulcata*. The species abundance peaks did not overlap and co-existence was not observed during the species maxima. However, no correlation was found between the species. While *P. vulgaris* correlated with sampling time, *K. longispina* showed a clear correlation with temperature and depth (in lakes Rica, Dridzis, and Geranimova).

Cladocera represented comparatively low proportions with the lowest (12%) in Lake Geranimova and the highest (23%) in Lake Garais. *Daphnia* (*Daphnia*) *cucullata* and *Diaphanosoma brachyurum* were the most common and dominant cladocerans in all lakes (Table 2). *Bosmina*, especially *Bosmina* (*Eubosmina*) *crassicornis* and *B. (Eubosmina) longispina*, were also common in all lakes except Lake Garais. In Lake Garais *D. (Daphnia) cucullata* can be detected as periodically dominant and *D. brachyurum* as periodically subdominant.

Vertical segregation between Cladocera species was not as apparent as for Rotifera. High numbers of *B. (Eubosmina) crassicornis*, *D. (Daphnia) cucullata*, and *D. brachyurum* were mostly found within the water layer of 0–10 m, and occasionally also at 10–20 m. However, the same pattern was not found in all lakes. In Lakes Dridzis and Geranimova *D. brachyurum* and *D. (Daphnia) cristata* preferred the upper water layer, while *B. (Bosmina) longirostris* preferred deeper layers during daytime.

Predatory cladocerans, including *Polyphemus pediculus*, *Leptodora kindti*, and *Bythotrephes longimanus*, were present in very low numbers.

Redundancy analysis (RDA)

RDA revealed that temperature, ORP, chlorophyll *a* concentration, and conductivity contributed significantly ($p < 0.01$, Monte Carlo test) to the spatial distribution, abundance, and species composition of the zooplankton. Environmental variables explained 47.5% of the total variance of zooplankton abundance and 26.7% of species diversity. The first axis explained 60.2% of the variation for abundance, whereas the second axis explained 19.9%, for species diversity (based on presence/absence records) 32.4% and 29.4%, respectively. No clear and significant effects of dissolved oxygen and pH were observed.

However, the ordination plot scores for zooplankton abundance and of environmental variables (Fig. 4) show that most Rotifera and Crustacea species correlated highly with temperature and pH. The microcrustacean species *D. (Daphnia) cristata*, *D. (Daphnia) longispina*, *Ceriodaphnia reticulata*, *Sida crystallina*, *P. pediculus*, *B. (Eubosmina) longispina*, and *B. (Bosmina) longirostris* displayed a strong relationship with oxygen and chlorophyll *a*.

Also, as expected, a correlation was detected between the sampling date and zooplankton abundance and species number and also between the depth and zooplankton abundance.

The RDA ordination plots for zooplankton specimen abundance and species composition displayed groups representing the relevance of sampling time. Species and individuals from July assembled into a separate group (Fig. 5). Depth

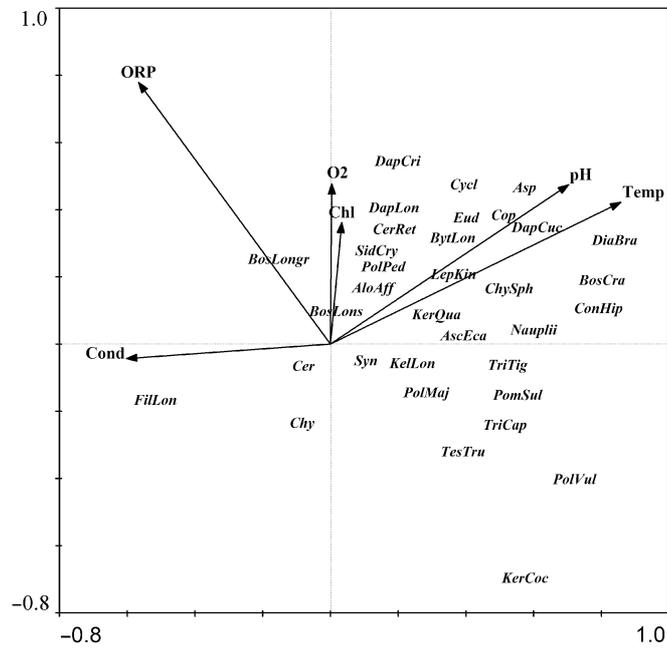


Fig. 4. Redundancy analysis (RDA) ordination plot for zooplankton abundance and scores of environmental variables (rare species were downweighted). Abbreviations: Cond – conductivity, ORP – oxidation reduction potential, O₂ – oxygen, Chl – chlorophyll, Temp – temperature, Cop – copepodites, Cycl – adult Cyclopidae. For abbreviations of species see Table 2.

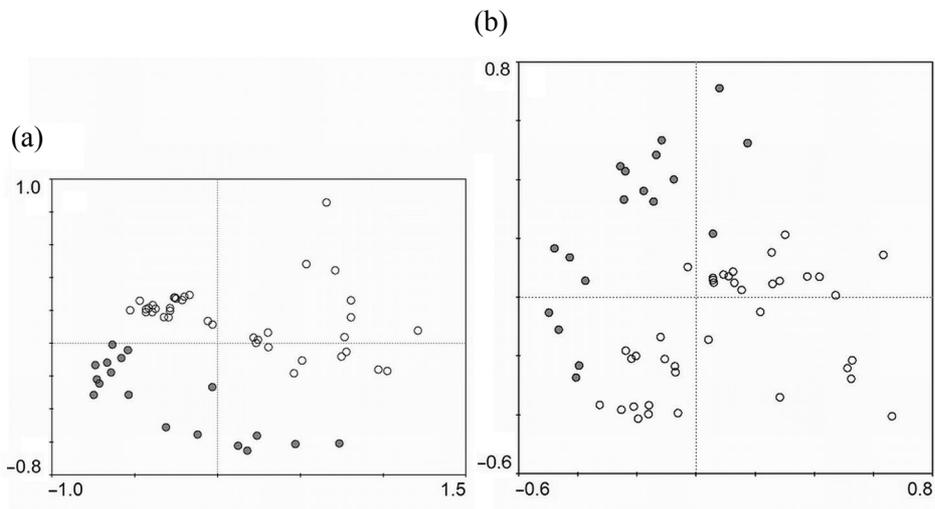


Fig. 5. Redundancy analysis (RDA) ordination plot showing July 2007 sample assemblages (filled circles) compared to samples from August and September 2007 (open circles): (a) – zooplankton abundance, (b) – species composition. Sampling sites: lakes Rica, Drīdzis, Garais, Svente, and Geranimova. All lakes are represented with samples from different dates and depths.

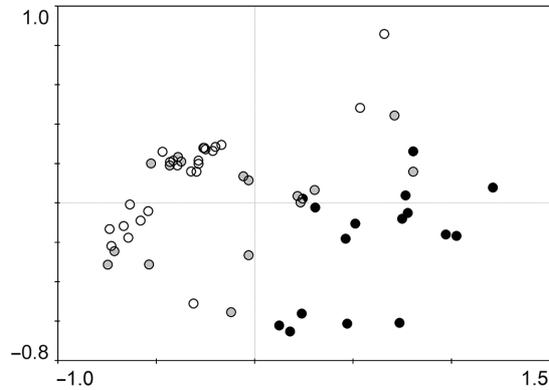


Fig. 6. Redundancy analysis (RDA) ordination plot for zooplankton abundance from lakes Rica, Dridzis, Garais, Svente, Geranimova during the sampling period of July to September 2007. Filled black circles – samples from 0–10 m depth; filled grey circles – samples from 10–20 m depth; open circles – samples below 20 m depth.

can also be seen as a determinant for zooplankton abundance. Samples according to depth were arranged along the first RDA axis. A group of samples from the water layer 0–10 m was followed by a group of samples from 10–20 m, and most of the samples below 20 m formed one more group (Fig. 6). Samples from the water layer of 0–10 m together with the rest of the samples from the lakes where the sampling site depth was up to approximately 30 m (Rica and Svente) formed a separate group.

DISCUSSION

Environmental variables

Despite nearly anoxic conditions in deeper layers of lakes Svente and Garais during the sampling time in August and September, there was neither statistically significant impact of low oxygen concentration on zooplankton fauna nor any obvious difference between lakes with varying oxygen conditions. Several authors describe rotifers' and crustaceans' response to decreasing oxygen concentration (Infante, 1993; Zadereev & Tolomeyev, 2007) and mention oxygen as an important environmental variable influencing zooplankton (Elliott, 1977; Field & Prepas, 1997). The vertical oxygen profile can limit the depth at which zooplankton species occur. For most zooplankton species 2–3 mg L⁻¹ of oxygen is the limiting amount for survival (Dodson, 2005). However, some zooplankton species have adapted to hypoxic conditions (Kizito & Nauwerck, 1995). Berzins & Pejler (1989b) and Bertilsson et al. (1995) reported on the relationships of rotifers and microcrustaceans with oxygen concentration from more than 500 freshwater Swedish localities and concluded that the range of occurrence is wide for most rotifers and microcrustaceans, although there can be marked differences in tolerance for low oxygen

concentrations. For example, *P. vulgaris*, *P. remata*, *P. major*, *A. priodonta*, and *K. longispina* can tolerate oxygen conditions of 2 mg L^{-1} and sometimes even levels close to 0 mg L^{-1} , although their maximum abundance occurs at more or less the same optimal oxygen level for all investigated rotifer species: $\sim 8\text{--}9 \text{ mg L}^{-1}$ (Berzins & Pejler, 1989b). In contrast, Elliott (1977) showed that for *P. vulgaris* the preferable oxygen range is significantly lower than for *K. longispina* and *K. cochlearis*. In the present study in lakes limited by oxygen (Svente and Garais), *P. vulgaris* abundance fluctuated before or after low oxygen conditions. *Asplanchna* sp. is also sensitive to oxygen limitation (Elliott, 1977; Mikschi, 1989). In the present research *Asplanchna* sp. reached its highest densities in the well oxygenated upper layer (0–10 m), especially during July when the best oxygen conditions occurred.

Oxygen depletion occurred in Lake Svente as early as 1952 (Per & Skolnikova, 1955). Zooplankton's ability to adapt to long-term low oxygen concentrations may have reduced researchers' readiness to detect a correlation between oxygen concentration and zooplankton abundance and species diversity.

The pH values recorded were optimal for most zooplankton (7.76–8.18). In accordance with rotifer species' pH optima by Berzins & Pejler (1987), species having pH optima below 7.0 (e.g. *C. (Conochilus) hippocrepis*, *Ascomorpha ecaudis*, *P. remata*) and above 7.0 (such as *Trichocerca capucina*, *P. sulcata*, *K. quadrata*) were detected during the present study. Most of the cladocerans found in lakes in the present study have a pH median optimum between 6.8 and 7.2 (Berzins & Bertilsson, 1990), which is below the actual pH in these five lakes.

Temperature had the most significant effect on the distribution, abundance, and species composition. Temperature conditions and the thermocline depth during summer have not changed notably in the lakes investigated in the last 50 years. In the present study rotifer abundance was found to decrease at higher temperatures in the epilimnion in all lakes except Svente. Most rotifers and microcrustaceans have a wide temperature tolerance range, with rotifers generally having lower optimal temperature preference (Kizito & Nauwerck, 1995) than microcrustaceans (Berzins & Pejler, 1989a; Bertilsson et al., 1995). Both in the epilimnion and hypolimnion rotifer species with a wide thermal tolerance range such as *K. longispina* (Bushman & Rusanova, 1976) as well as species with a narrower thermal tolerance range such as *P. sulcata*, *T. capucina*, and *B. (Eubosmina) crassicornis* (Berzins & Pejler, 1989a; Bertilsson et al., 1995) were found. Our results showing that the vertical distribution of species was limited by the lack of mixing of water during thermal stratification rather than individual thermal preferences of species agree with Berzins & Pejler (1989a).

Species diversity, abundance, and vertical distribution of zooplankton in deep lakes

The assemblage of dominant species as well as the number of crustacean (cladoceran) and rotifer species recorded from the pelagic zone have not changed appreciably during the last 50 and more years in lakes Dridzis, Geranimova, and

Svente compared to earlier reports (Berzins, 1949; Selkere, 1955; Kumsare & Laganovska, 1959; Line, 1966; Vadzis et al., 1976; Brakovska & Skute, 2007).

Deep lakes (mean depth >9 m) and medium deep lakes (mean depth 5–9 m) in Latvia have lower numbers of zooplankton species compared to shallow lakes (mean depth <5 m). Line (1966) reported in a study of Latvian lakes that a typical number of zooplankton species (Cladocera, Copepoda, Rotifera) found in deep lakes is between 24 and 46 (maximum 85) and for medium deep lakes between 22 and 33 species (maximum 91). For shallow lakes that are also nutrient-enriched lakes the total number of zooplankton species found is between 30 and 64 (maximum 116) (Line, 1966). In the present study from 24 up to 38 species of Rotifera and Cladocera were found from the pelagic samples of all lakes. The species *K. cochlearis*, *K. longispina*, *F. longiseta*, *P. vulgaris*, *D. (Daphnia) cucullata*, *B. (Eubosmina) crassicornis*, *B. (Eubosmina) longispina*, and *D. brachyurum* were still dominant in most of the investigated lakes. Those are species mentioned by Line (1966) as characteristic for deep and medium deep lakes. In shallow lakes fewer typical pelagic cladoceran species are present, except *D. (Daphnia) cucullata* and *B. (Eubosmina) longirostris* (Line, 1966). All dominant species from the present study are common and widely distributed in Latvian lakes (Line, 1966; Sloka, 1981; Paidere & Skute, 2011).

Slight changes in the species composition were observed in some of the investigated lakes. For instance, since 1955 *C. (Conochilus) hippocrepis* has appeared and replaced *C. (Conochilus) unicornis* (in lakes Rica and Svente, in the former both species coexist in the Belarusian part of the lake (V. Vezhnavecs, pers. comm.), whereas in the latter *C. (Conochilus) unicornis* has been replaced by other species). In Lake Geranimova *C. (Conochilus) hippocrepis* was only occasionally found in 1960–1962 (Line, 1966). Similarly, *B. (Eubosmina) coregoni* found earlier by Selkere (1955) and Vadzis et al. (1976) was no longer found in high numbers in the present study. The abundance of *B. (Eubosmina) coregoni*, as well as the abundance of copepods in general, has decreased in Lake Dridzis. This is most likely due to the influence of planktivorous fishes. In 1953 species such as *Coregonus albula*, *Osmerus eperlanus*, and *Alburnus alburnus*, which feed mainly on *B. (Eubosmina) coregoni* and *Cyclops*, *Diaptomus*, and *Eurytemora* species, were found (Selkere, 1955). According to data on industrial fishing in 1950–2007 (provided by the Latvian Fish Resources Agency), *O. eperlanus* is dominating among fish species, while *C. albula* is found in comparatively low numbers.

Certain differences in the species composition were most likely caused by the changing trophy. During 1938–1940 Lake Dridzis was a moderately oligotrophic lake with a high oxygen concentration throughout the water column, low zooplankton densities, and absence of eutrophic species. Lake Geranimova was described as a moderately eutrophic lake with a rich plankton, rotifer species characteristic for eutrophic conditions, and little oxygen in the deeper waters (Berzins, 1949). Comparison of the present species composition for Lake Dridzis with that from the sampling period in 1938–1940 (Berzins, 1949) shows that at least five species indicative of eutrophy (Hakkari, 1972; Karabin, 1985) have

appeared. Those include *D. (Daphnia) cucullata*, *K. quadrata*, and *P. sulcata*. Species indicating oligotrophy such as *Gastropus stylifer* (in lakes Svente and Geranimova) and *Ploesoma hudsoni* (in lakes Dridzis and Geranimova) have disappeared. However, in lakes Svente and Geranimova changes in the ratio of species indicating oligotrophy and eutrophy are not so evident. For example, for *Daphnia* spp. abundance decreases with decreasing trophy (Kohler et al., 2005). There was no information available on the earlier abundance of *Daphnia* spp.; however, according to the present investigation, *Daphnia* spp. proved to contribute on average 2.9% of the total zooplankton abundance in Lake Dridzis, 4.6% in Lake Geranimova, and reached the maximum of 12.7% in Lake Garais.

Karabin (1985) suggested that Cladocera dominate the zooplankton community biomass in low-trophic-state lakes and decline in dominance in eutrophic lakes. The proportion of copepods (in the abundance of total zooplankton) in Lake Dridzis decreased from 56% in 1954 (Kumsare & Laganovska, 1959) to 40% in 2007 and that of cladocerans from 23% to 13%. At the same time the proportion of Rotifera increased. In contrast, in Lake Geranimova the abundance of copepods and cladocerans showed an increase, and the zooplankton is dominated by copepods. Urtane (1998) found significant changes in the ratio between Cladocera and Copepoda only in highly eutrophic and dystrophic lakes. The ratio of Rotifera to Crustacea increases significantly from 0:1 in mesoeutrophic and poorly eutrophic lakes up to 1:1 and higher in hypereutrophic Latvian lakes (Urtane, 1998). This ratio of these taxa was also pronounced in the lakes of the present study, especially for lakes Geranimova (~1:5) and Garais (~1:3). This suggests a more or less explicit shift in the trophic state of the lakes and demonstrates zooplankton communities' response to changing environmental conditions. A certain pattern in relation to trophy can be observed based on the concentration of chlorophyll *a*. The lowest average seasonal concentration of chlorophyll *a* was observed in Lake Dridzis ($0.96 \mu\text{g L}^{-1}$), followed by Lake Svente ($1.03 \mu\text{g L}^{-1}$), Lake Rica ($1.54 \mu\text{g L}^{-1}$), and Lake Geranimova ($1.8 \mu\text{g L}^{-1}$). Lake Garais had the highest concentration ($2.33 \mu\text{g L}^{-1}$). According to the trophic classification of lakes based on chlorophyll concentration (Cimdins, 2001; Klavins & Cimdins, 2004), all the studied lakes are more towards oligotrophic type except Lake Garais, which agrees more to mesotrophic features.

The most abundant species in all lakes included *K. longispina* and *P. vulgaris*. The two did not overlap during the sampling period. The same pattern was observed for *K. longispina* and *P. sulcata*. Laxhuber (1987) described a rapid decline in the *Polyarthra* sp. population accompanied by a gradual increase of *K. longispina* and vice versa. However, this is not a constant and always clear pattern (Grundström, 1987; Primicerio & Klemetsen, 1999). A similar segregation pattern between *K. longispina* and *P. sulcata* was also detected by Doulka & Kehayias (2011): the species did not coexist during their density maxima. Doulka & Kehayias (2011) showed vertical segregation between *K. longispina* and other rotifer species, with *K. longispina* avoiding the surface layer during all seasons, also when stratification occurs. In the present study the surface avoiding behaviour was not detected, possibly due to the sampling methodology. However, the highest

abundance of *K. longispina* was detected below 10 m. Such pattern is to some extent caused by the species' temperature preferences. Being a cold-stenothermal species *K. longispina* has lower temperature optima compared to those of *P. vulgaris* and *P. sulcata* (Berzins & Pejler, 1989a). Consequently, it reaches higher densities at lower temperatures and its number is determined by seasonal variability. To some extent the seasonal dynamics of species abundance mentioned above can be explained by the predation risk as there are considerable differences in the morphology: *Polyarthra* sp. is a softer-bodied organism and hence more vulnerable to predation than species with spines such as *K. longispina* (Brandl, 2005).

The structure of zooplankton populations in deep lakes was comparatively dynamic during late summer to early autumn. Our findings demonstrate the importance of season for the vertical distribution of zooplankton individuals and species abundance. The differences in the vertical distribution and species diversity are directly related to the influence of lake stratification. A connection was detected between the sampling period and species diversity, between the sampling period and number of individuals, and finally between the depth and number of individuals.

We did not observe any dramatic decline in ecological conditions based on temperature, oxygen, pH, chlorophyll *a*, ORP, and conductivity. However, a slight decrease in the oxygen concentration in some of the investigated deep lakes during the last 50 or more years parallels a trend toward a zooplankton species composition characteristic of mesotrophy. Still, of all the investigated lakes, Dridzis appeared to be one of the least impacted by eutrophication. Considering the present ecological conditions of all investigated lakes we assume that in more eutrophic lakes under more or less the same conditions, environmental deterioration occurs over longer periods and therefore it is particularly important to ensure appropriate management and legislative protection for deep lakes considering their ecological requirements for sustainable existence in the future.

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Pelaagilise zooplanktoni vertikaalne varieeruvus Lāti sügavates järvedes mõnede märkmetega ökoloogiliste tingimuste muutumise kohta

Inta Dimante-Deimantovica, Arturs Skute ja Renate Skute

On vaadeldud Lāti viie sügava järve zooplanktoni leviku hilissuvist ja varasügist vertikaalset struktuuri. Uuriti, kuidas veetemperatuur, hapnik, pH, klorofüll *a*, redokspotentsiaal ja juhtivus seostuvad muutustega tänapäevaste ning andmete olemasolul ka ajalooliste zooplanktoni liigilise koosseisu ja arvukuse domineerimissuhetega. Viimasel 50 aastal ei täheldatud olulisi muutusi ökoloogilistes tingimustes ja zooplanktoni mitmekesisuse ning arvukuse sesoonses muutlikkuses. Inimtekkelisest eutrofeerumisest põhjustatud järvevee hapnikukontsentratsioonide langus tõi kaasa väikesed muudatused zooplanktoni liigilises koosseisus. Uuringu käigus leiti kokku 24 Rotifera ja 38 Cladocera taksonit. Domineerivad liigid olid *Conochilus hippocrepis*, *Keratella cochlearis*, *Polyarthra vulgaris*, *Filinia longiseta*, *Kellicottia longispina*, *Daphnia (Daphnia) cucullata*, *Diaphanosoma brachyurum*, *Bosmina (Eubosmina) crassicornis* ja *B. (Eubosmina) longispina*. Eristusid selged zooplanktoni kooslused nii liigilise koosseisu kui ka kõrgemate taksonite põhjal ja erinevate koosluste taga olid erisused järvede sesoonses stratifikatsioonis. Veetemperatuur, redokspotentsiaal ja klorofüll *a* avaldasid kõige suuremat mõju zooplanktoni vertikaalsele levikule. Olulisteks keskkonnamuutujateks olid ka proovikogumise kuupäev ja sügavus. Selgelt eristusid 0–10 m, 10–20 m ja 20 m suurema sügavusega veekihid. Selgelt eristusid ka proovid, mis koguti hooaja algul.