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Occurrence of Cladocera and the genetic diversity of *Daphnia cucullata* in the pelagic zone of Latvian salmonid lakes

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Abstract. Cladocerans are a considerable food source for such planktivorous fish as salmonids. In Latvia 26 lakes are categorized as priority fish lakes for salmonids and therefore studies on cladocerans as salmonid fish prey are of particular interest. For the study of salmonids' food base, i.e. zooplankton diversity, and the genetical diversity of *Daphnia cucullata* in four Latvian lakes zooplankton samples were taken in the summers of 2010 and 2011. The most dominant species of Cladocera were *Diaphanosoma brachyurum*, *Daphnia cucullata*, *Bosmina crassicornis*, *Bosmina longispina*, and *Bosmina longirostris*. The highest diversity and biomass of cladocerans were observed from June to late July. This can be explained by seasonality. The common cladoceran species such as *Daphnia cucullata* may be used as a good model organism for ecological genetics research. We found *D. cucullata* in all the investigated lakes. The genetic structure and plasticity in *D. cucullata* were studied using nuclear random amplified polymorphic DNA (RAPD). Carl Roth random primers PCR were used for the amplification of DNA samples. The DNA markers were polymorphic segments with band sizes from 500 to 3000 bp. The number of polymorphic DNA bands of *D. cucullata* in the four investigated lakes was different.

Key words: zooplankton, Cladocera, *Daphnia cucullata*, RAPD, diversity, salmonid lakes.

INTRODUCTION

Lakes are significant resources for the development of any area. They are especially important for the development of human settlements, tourism and recreation, fisheries, and other industries. About 40% of all lakes in Latvia are located in Latgale in the Augšzeme Highland. According to the quality indicators, they are clean lakes with low trophic state indexes (Urtāne, 1998; Latvijas ezeru, 2002). Salmonid fish lakes are one of the priority water bodies in Latvia. Latgale has a high percentage of lakes that fall into this category; however, there have not been any extensive ecological studies of these lakes in the region.

In accordance with the Regulations of the Cabinet of Ministers No. 118, Appendix 2 of 2002 there are 26 salmonid lakes in Latvia. One salmonid species found in these lakes is vendace (*Coregonus albula*), which is a planktophagous fish. Vendace was found in 30 lakes of Latvia in the 1930s, in 11 lakes in the 1950s–

1960s, and only in 5 lakes in the 1990s. This means that this economically important species is gradually disappearing from the Latvian lakes. Since 1995, vendace has been included into the Red Data Book of Latvia as rare species of the 3rd category. Vendace is also included in the lists of the specially protected species. Since vendace mainly feeds on zooplankton, we chose zooplankton as a major research object for our paper.

Zooplankton (e.g. Cladocera) is an important feeding base for juvenile fish and planktophagous fishes such as salmonids (Hebert, 1982; Malone & McQueen, 1983; Pinel-Alloul, 1995; Cimdiņš, 2001; Wetzel, 2001; Chang & Hanazato, 2004) and plays an essential role in the transformation of substances and energy in water bodies. Zooplankton controls the number of bacteria and algae, contributing to the biological self-purification process of water.

A zooplankton community is a dynamic system in which the species composition may change significantly during the season. Temporal changes of the zooplankton species found in temperate lakes are influenced by many factors, including temperature, food, competition, and predation (Hebert, 1982; Malone & McQueen, 1983; Dodson, 1984; Larsson & Dodson, 1993; Weider & Pijanowska, 1993; Pinel-Alloul, 1995; Cimdiņš, 2001; Wetzel, 2001; Chang & Hanazato, 2004; Harris et al., 2012). It is a well-known fact that zooplankton organisms are very sensitive to the biotic and abiotic influences, which lead to structural and functional changes on a polymorphism level (De Meester et al., 1995). This makes them good bioindicators for the evaluation of water quality and toxicity as well as for experimental purposes in ecology and genetics (Sloka, 1998; Dussart & Defaye, 2001). During our research (Brakovska & Škute, 2007, 2009; Brakovska & Paidere, 2012; Brakovska et al., 2012; Jurevičs et al., 2012) we found that *Daphnia cucullata* is among dominants in the Cladoceran community of Latvian salmonid lakes. It forms also an important part of the vendace food (Viljanen, 1983; Sutela & Huusko, 1997). Therefore we have decided to study for the first time in Latvia the genetic diversity and plasticity of *D. cucullata* in Latvian salmonid lakes as so far the investigations of zooplankton species in Latvian lakes have been based only on morphology.

Cladocera genera (e.g. *Daphnia*) have frequently been used as model organisms for ecological genetic research for more than 150 years (e.g. Lubbock, 1857; Colbourne & Hebert, 1996; Harris et al., 2012). It should be noted that *Daphnia* as a model organism is also used in other scientific disciplines, including chemistry and physiology. Thanks to Winfried Lampert and his colleagues all around the world, *Daphnia* has become a model organism in the international freshwater ecology (Larsson & Weider, 1995; Lampert, 2006). *Daphnia* has also been used in studies of the predator-induced polyphemism (Ebert, 2005; Stollewerk, 2010). In addition, *Daphnia* has become a kind of convergence model organism with adaptive features in radically different habitats (Colbourne et al., 1997); as a result, it has been considered to be a test organism in fresh water (Dodson & Hanazato, 1995).

There are numerous publications where *Daphnia* is used as a research object; for example, a number of studies have been performed in Europe and North America with *Daphnia* as a pelagic feeding base in lakes and ponds (Lampert, 1985, 2006; Sterner, 1989; Larsson & Weider, 1995; Colbourne et al., 1997; Tessier et al., 2000; Weisse, 2006). Before 1855 *Daphnia* was mentioned in more than 4000 ecological studies as a model organism, but since 1855 in more than 7000 studies (Shaw et al., 2008). Fundamental researches into *Daphnia*'s molecular phylogenesis in different geographical areas, such as Europe (Schwenk et al., 2000), North America (Colbourne & Hebert, 1996), South America (Adamowicz et al., 2004), and Australia (Colbourne et al., 2006) are of particular interest. *Daphnia* has been used in a series of population genetics studies (Schwenk et al., 1998; Hellsten & Sundberg, 2000; Atienzar & Jha, 2004; Mergeay et al., 2005; Picado et al., 2007; Martins et al., 2009).

The aim of our study was to reveal the diversity of the Cladocera species in some Latvian salmonid lakes during the summer season and to investigate the polymorphism of *Daphnia cucullata*, one of the leading Cladocera species in these lakes, with the help of molecular genetic techniques.

MATERIAL AND METHODS

Study sites

Our investigated lakes belong among the deep transparent mesotrophic and mesoeutrophic lakes (Urtāne, 1998). Morphometric features of the studied lakes are presented in Table 1. All of them are located in the eastern part of Latvia. According to the Regulations of the Cabinet of Ministers No. 118 of 2002, all the studied lakes are included in the list of priority fish lakes of Latvia.

Lake Drīdzis is the deepest lake in Latvia as well as in the Baltic countries (Brakovska & Škute, 2007; www.ezeri.lv.database (accessed 30.06.2013)). Lake Drīdzis is situated on the Hillock of Dagda of the Latgale Highland, in Skaista and Kombuļu parishes, Kraslava Region. It is an area of Natura 2000.

Lake Geraņimovas-Ilzas is the fifth deepest Lake in Latvia. It is located on the top of Feimanu Hill at 150.3 m above sea level, in Kastulini Municipality in Kraslava Region (Fig. 1) (Eipurs, 1995).

Table 1. Morphometric features of lakes Svente, Riča, Drīdzis, and Geraņimovas-Ilzas

Lake	Coordinates X/Y	Average depth, m	Maximum depth, m	Surface area, km^2
Drīdzis	705390.852/ 208462.077	12.8	65.1	7.53
Geraņimovas-Ilzas	696251.015/ 228167.042	9.8	46	3.28
Svente	647412.511/ 192388.091	7.8	38	7.35
Riča	670715.594/ 175721.067	9.7	39.7	12.86*

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* In Latvia 5.88 km^2, in Belarus 6.98 km^2.

Fig. 1. Location of the studied lakes.

Lake Svente is the tenth deepest lake in Latvia (Tidriķis, 1998). The lake is located in the SE part of Latvia and it is included in the special area of conservation *Svente Nature Park*. Moreover, it is a European special area of conservation (Natura 2000).

Lake Riča is situated on Skrudaliena Hillock in Augšzeme, on the border of Latvia and Belarus (Fig. 1). It is the ninth deepest Lake in Latvia. Besides, the surroundings of Lake Riča are a complex protected area of landscape and an area of Natura 2000 (Tidriķis, 1997; Brakovska & Škute, 2007).

Physico-chemical measurements

Physico-chemical parameters of water (water temperature (°C), dissolved oxygen (mg L^{-1})) were determined in the deepest site of each lake using a HACH DS5 probe with 1 m interval from the bottom towards water surface. Water transparency was measured using a Secchi disk (Wetzel & Likens, 2000).

Collection and analyses of zooplankton samples

The collection of the zooplankton samples and their quantitative and qualitative analyses were performed using the APHA standard methods procedure for water and wastewater analyses (Wetzel & Likens, 2000; APHA, 2005).

For the taxonomic and quantitative study of zooplankton and the analysis of genetic variation in the *Daphnia cucullata* populations in lakes Svente, Riča, Drīdzis, and Geraņimovas-Ilzas the zooplankton samples were taken in July 2010 and 2011. Depth-integrated zooplankton samples were taken from the deepest site of each lake with a Hydro-bios Apstein type plankton net with an opening–closing mechanism (mesh size 64 µm), preserved with 37–40% formaldehyde solution (4% final concentration), and stored in 0.33 L bottles. The samples collected for the study of genetic biodiversity in *Daphnia cucullata* were preserved with 70–98% ethanol immediately after collecting to prevent individuals from biochemical and molecular degradation (Harris et al., 2005).

The zooplankton samples were analysed by using a Zeiss Primo Star upright light microscope (100–400× magnification). Per sample, six 1 mL subsamples were analysed in a Gridded Sedgewick Rafter counting chamber with the volume of 1 mL (Wetzel & Likens, 2000). The zooplankton organisms were enumerated and identified to species, genera, or families. For identification we used the following zooplankton guides: Manujlova, 1964; Kutikova, 1970; Flössner, 1972, 2002; Pontin, 1978; Sloka, 1981; Krauter & Streble, 1988; Scourfield & Harding, 1994; Segers, 1995; Dussart & Defaye, 2001; Dumont & Negrea, 2002; Nogrady & Segers, 2002; and Paidere & Škute, 2011.

The following formula was used to calculate the number of organisms:

$$N = \frac{a \times b \times 1000}{c \times d}, \tag{1}$$

where N is the number of organisms per m^{-3}, a is the average number of organisms in the subsample volume, b is the volume of the concentrated sample, c is the subsample volume, and d is the volume of filtered water.

The zooplankton biomass in a sample was calculated as follows:

$$B = \frac{a \times b}{1000}, \tag{2}$$

where B is the biomass of organisms per m^{-3}, a is the number of organisms per m^{-3}, and b is the individual biomass of organisms (mg) in the wet weight sample.

The individual biomass values for the zooplankton organisms were obtained from the available information in the literature (Kisilev, 1956; Bottrell et al., 1976; Ruttner-Kolisko, 1977). The proportions of Cladocera species in the zooplankton community were calculated as the percentages in the total zooplankton abundance and biomass in each sample.

Dominance (D) frequency was calculated by the following formula:

$$D = 100 \times (a/b), \tag{3}$$

where a is the number of individuals of a certain species and b 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).

DNA was isolated using the modified method by Harris et al. (2005). The polymerase chain reaction (PCR) was performed in 12 μL. The composition of the PCR was 20 ng of genomic DNA sample, 10 × Taq Buffer with KCl, 25 mM $MgCl_2$, 2 mM dNTP Mix, 0.06 U μL^{-1} Taq DNA polymerase (MBI Fermentas, Vilnius, Lithuania), and 1 pmol μL^{-1} RAPD primer (Carl Roth, Germany).

We used the following amplification cycle: denaturation – 94 °C 3 min; 46 cycles: 94 °C 20 s (denaturation), 40 °C 30 s (solicitation or primer annealing), 72 °C 1 min (synthesis); 72 °C 10 min; 4 °C (cooling). After the PCR amplification the samples were stored in a refrigerator (4 °C) until the analytical separation in agarose gel.

The RAPD–PCR fragments were separated (fractionated) in 1.4% agarose gel with TBE buffer (0.045 M Tris, 0.001 M EDTA, 0.045 M H_3BO_3, pH 8.3–8.4) with regime 4.3 V cm^{-1} 15 min, 6.5 V cm^{-1} 2 h. The RAPD–PCR products were separated in agarose gel using horizontal electrophoresis equipment (Cleaven Scientific).

Before applying the gel a buffer (50% glycerin, 0.1 M EDTA, 0.002% bromophenol blue) was added to the PCR products for the degradation of the sample and tracking the electrophoresis time in the gel. RAPD–PCR products were used for analysing the whole PCR reaction volume (12 μL) (Fig. 2). The DNA marker GeneRuler™ 100 bp DNA Ladder Plus (MBI Fermentas, Vilnius, Lithuania) was used to identify the size of the RAPD–PCR fragments.

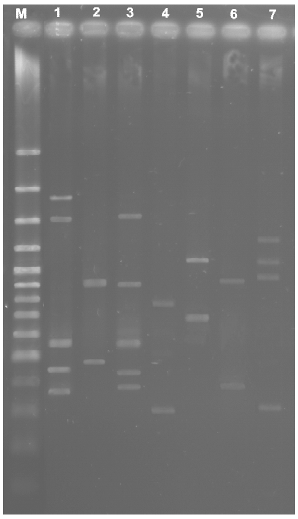

Fig. 2. Reproducibility of RAPD fingerprinting. DNA fingerprints from different samples of *Daphnia cucullata* were obtained by PCR with primers ROTH A03 and ROTH A05 (M – marker, 1–7 runners – different samples of *Daphnia cucullata*).

The genetic structure of the population of *Daphnia cucullata* in lakes Svente, Riča, Drīdzis, and Geraņimovas-Ilzas was investigated based on the nuclear DNA polymorphism. DNA polymorphism was investigated by the randomly amplified sequences (RAPD method). Thirty random primers from A, B, C, and F sets (Carl Roth, Germany) were tested for this investigation.

The amplification products were separated (by size) electrophoretically in gel where the presence or absence of a band of a specific molecular weight was used to assay genetic variation between clones of populations (Grosberg et al., 1996; Hellsten & Sundberg, 2000).

The amplified bands were scored for their presence (1) or absence (0). The presence or absence of the fragment in each sample was assessed and the data were assembled into a binary matrix. DNA bands of equal mobility were treated as identical. Mean bandsharing similarity indices were calculated within (S_i) and between populations (S_{ij}) for all possible comparisons, according to Lynch (1990). The resulting genetic data were statistically analysed using 'GENALEX 6' (Peakall & Smouse, 2006) and SPSS Statistics 20 software.

The number of polymorphic loci, pairwise similarities Dice coefficient (S), and genetic diversity were detected in each investigated population. Pairwise similarities between specimens were calculated based on the presence and absence of RAPD bands using the Dice coefficient (S) (Schwenk et al., 1998; Krebs, 1999; Hellsten & Sundberg, 2000):

$$S = \frac{2a}{2a + b + c}, \tag{4}$$

where a is the presence of a fragment in both individuals, b is the presence in one but not the other, and c is the opposite of b.

RESULTS

Diversity and density of zooplankton in the four studied Latvian lakes

The mean transparency of the studied lakes was 5.27 m (max 7.5 m, min 3.15 m), and they were stratified during summer. The temperature below the metalimnion boundary was 9–10 °C and in the deep layers of the hypolimnion 4–5 °C. The dissolved oxygen concentrations were more variable over the season and depth. For example, dissolved oxygen levels ranged from 0.63 mg L^{-1} (in the hypolimnion) to 9.20 mg L^{-1} (in the epilimnion), but over the season from 3.09 to 7.03 mg L^{-1}.

Rotifera, Cladocera, and Copepoda were present in all studied lakes with Cladocera having the leading role in the zooplankton. The number of cladoceran species varied from 8 to 16 in the lakes (Table 2). *Diaphanosoma brachyurum*, *Daphnia cristata*, *Daphnia cucullata*, *Bosmina crassicornis*, and *Leptodora kindtii* were present in all the lakes (Table 2).

Table 2. Presence of Cladocera species in lakes Svente, Riča, Geraņimovas-Ilzas, and Drīdzis in July 2010 and July 2011

Species	Svente	Riča	Geraņimovas-Ilzas	Drīdzis
Diaphanosoma brachyurum (Liévin, 1848)	+	+	+	+
Ceriodaphnia pulchella Sars, 1862	+	+		+
Ceriodaphnia quadrangula (O. F. Müller, 1785)	+			
Ceriodaphnia reticulata (Jurine, 1820)		+		+
Daphnia (Daphnia) cristata Sars, 1862	+	+	+	+
Daphnia (Daphnia) cucullata Sars, 1862	+	+	+	+
Daphnia (Daphnia) longispina (O. F. Müller, 1776)	+		+	+
Daphnia (Daphnia) sp.			+	
Acroperus harpae (Baird, 1835)				+
Chydorus ovalis (Kurz, 1875)	+			+
Chydorus sphaericus (O. F. Müller, 1776)	+			+
Bosmina (Bosmina) longirostris (O. F. Müller, 1776)	+	+		+
Bosmina (Eubosmina) coregoni Baird, 1857				+
Bosmina (Eubosmina) crassicornis Lilljeborg, 1887	+	+	+	+
Bosmina (Eubosmina) longispina Leydig, 1860	+	+		+
Bosmina (Eubosmina) reflexa Seligo, 1907		+		+
Bythotrephes longimanus Leydig, 1860		+	+	
Polyphemus pediculus (Linnaeus, 1758)				+
Leptodora kindtii (Focke, 1844)	+	+	+	+
Number of species	12	11	8	16

In Lake Riča four cladoceran species, i.e. *Diaphanosoma brachyurum*, *Daphnia cucullata*, *Daphnia cristata*, *Bosmina crassicornis*, made up 16.2% of the total zooplankton abundance in July 2010. In July 2011 seven species of Cladocera were identified, i.e. *Diaphanosoma brachyurum*, *Daphnia cucullata*, *Daphnia cristata*, *Bosmina crassicornis*, *Bosmina longispina*, *Ceriodaphnia pulchella*, and *Leptodora kindtii* (Table 3), comprising 10.1% of the total zooplankton abundance. In Lake Svente four Cladocera species were found in July 2010: *Diaphanosoma brachyurum*, *Daphnia cucullata*, *Bosmina longispina*, and *Bosmina longirostris*. Their share in the total zooplankton abundance was 4.8% (Fig. 3).

Table 3. Dominance and subdominance (%) of Cladocera species in the total zooplankton abundance in lakes Svente, Riča, Geraņimovas-Ilzas, and Drīdzis in July 2010 and July 2011

Species	Svente		Riča		Drīdzis		Geraņimovas-Ilzas	
	2010	2011	2010	2011	2010	2011	2010	2011
Diaphanosoma brachyurum (Liévin, 1848)	25.2	9.14	78.52	40	10.78	7.9	13.3	11
Daphnia (Daphnia) cucullata Sars, 1862	55	5.38	9.7	10.3	25.15	19.4	46.7	
Daphnia (Daphnia) cristata Sars, 1862		1.25	0.88	6.9	13.17	10	23.3	
Daphnia (Daphnia) sp.							16.7	
Daphnia (Daphnia) longispina (O. F. Müller, 1776)								20.37
Ceriodaphnia pulchella Sars, 1862				1.72		0.72		
Chydorus ovalis (Kurz, 1875)					0.6			
Chydorus sphaericus (O. F. Müller, 1776)		0.37			2.99			
Bosmina (Bosmina) longirostris (O. F. Müller, 1776)	16.8	37.5			1.2	5.7		
Bosmina (Eubosmina) longispina Leydig, 1860	2.52	38.42		5.2	36.53	50.36		
Bosmina (Eubosmina) crassicornis Lilljeborg, 1887			10.88	33	9.58	5.75		26
Leptodora kindtii (Focke, 1844)				3.45				1.85
Bythotrephes longimanus Leydig, 1860								1.85

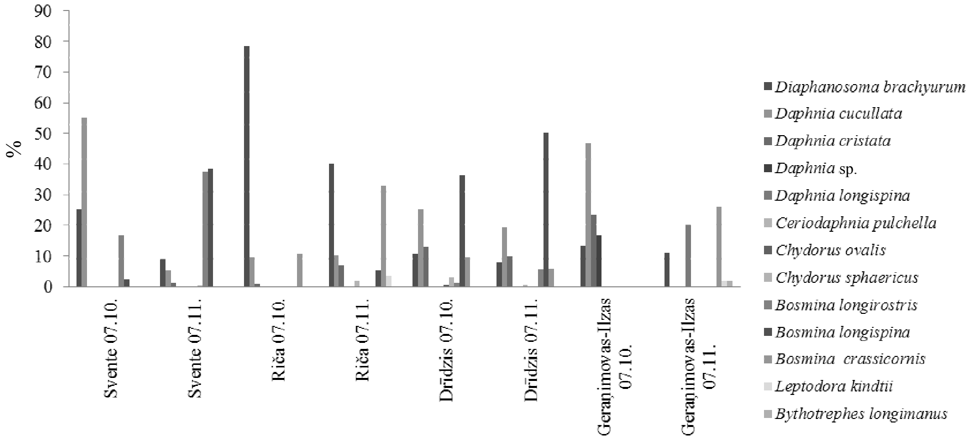

Fig. 3. The proportions of Cladocera species in the total zooplankton abundance in lakes Svente, Riča, Geraņimovas-Ilzas, and Drīdzis in July 2010 and July 2011.

Cladocerans contributed significantly to the total zooplankton biomass (Table 4) in the lakes (for example in Lake Svente min 6.9% in May 2010 (unpublished data of the Institute of Ecology of Daugavpils University, Latvia), max 69.9% in July 2010) (Fig. 4). According to unpublished data of the Institute of Ecology of Daugavpils University, the highest Cladocera biomass was observed from June to late July, which can be explained by seasonality. It is a well-known fact that cladocerans have an important place in the food chain; they regulate bacterial and detrital quantity. Cladocerans are an important component of the food for juvenile fish, plankton-feeding fishes, and many other aquatic animals. The composition and biomass of Cladocera species are often used to characterize the biological productivity of plankton-feeding fishes.

Table 4. Dominance and subdominance (%) of Cladocera species in the total zooplankton biomass in lakes Svente, Riča, Drīdzis, and Geraņimovas-Ilzas in July 2010 and July 2011

Species	Svente		Riča		Drīdzis		Geraņimovas-Ilzas	
	2010	2011	2010	2011	2010	2011	2010	2011
Diaphanosoma brachyurum (Liévin, 1848)	24.39	25.8	83.07	31.31	14.66	13.9	9.03	8.46
Daphnia (Daphnia) cucullata Sars, 1862	73	21	14.28	10.9	49.8	46.9	47.4	
Daphnia (Daphnia) cristata Sars, 1862		4.79	1.3	7.44	26.4	24.3	23.7	
Daphnia (Daphnia) sp.							16.9	
Daphnia (Daphnia) longispina (O. F. Müller, 1776)								22.3
Ceriodaphnia pulchella Sars, 1862				0.39		0.36		
Chydorus ovalis (Kurz, 1875)					0.26			
Chydorus sphaericus (O. F. Müller, 1776)		0.35			1.17			
Bosmina (Bosmina) longirostris (O. F. Müller, 1776)	2	13.85			0.2	1.43		
Bosmina (Eubosmina) longispina Leydig, 1860	0.26	14		0.39	6.74	11.44		
Bosmina (Eubosmina) crassicornis Lilljeborg, 1887		2.66	1.49	3.13	1.76	0.14		2.49
Leptodora kindtii (Focke, 1844)		17.75		47				24
Bythotrephes longimanus Leydig, 1860								1.49

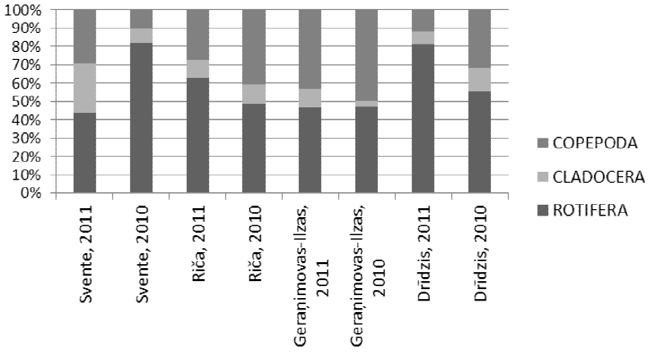

Fig. 4. Percentage distribution of the total abundance of zooplankton groups in lakes Svente, Riča, Geraņimovas-Ilzas, and Drīdzis in July 2010 and July 2011.

Genetic diversity of *Daphnia cucullata* in four Latvian lakes

Seven primers from the set A (OPA-02; OPA-03; OPA-05; OPA-09; OPA-10; OPA-12; OPA-13), three primers from the set B (OPB-03; OPB-07; OPB-08), two primers from the set C (OPC-11; OPC-20), and one primer from the set F (OPF-10) were used for the genetic study of the populations of *Daphnia cucullata* in lakes Svente, Riča, Drīdzis, and Geraņimovas-Ilzas (Table 5). The size of the scored polymorphic DNA fragments ranged from 500 bp to 3000 bp (Table 5).

The number of polymorphic DNA bands of *Daphnia cucullata* in the four investigated lakes was different. The number of amplified bands was the highest in lakes Riča (67) and Geraņimovas-Ilzas (64), whilst the lowest number (49) occurred in Lake Svente (Table 5). The largest number of polymorphic loci was detected in lakes Drīdzis and Geraņimovas-Ilzas (making up 50% and 32.8%, respectively) (Table 5), and the number was the smallest in Lake Svente (13%).

Dice coefficient (*S*) values of *Daphnia cucullata* populations between lakes ranged from 0 to 1 (Table 6). The greatest pairwise similarity (Table 6) was between lakes Riča and Geraņimovas-Ilzas (by the primers OPA-03 – 0.91; OPA-05 – 0.57; OPA-09 – 0.54; OPA-13 – 0.57; OPB-08 – 0.8; OPC-20 – 0.57) and between lakes Svente and Riča (by the primers OPA-02 – 0.8; OPA-09 – 0.54; OPB-03 – 0.73). According to the primer OPB-07, the populations were identical (similarity coefficient 1) (Table 6).

Considering the interpopulation genetic distance data (Table 7), the highest similarities in *Daphnia cucullata* populations were between lakes Svente and Riča (4.98) and between lakes Riča and Drīdzis (4.62). Similarity was the lowest between lakes Svente and Geraņimovas-Ilzas (3.21). By the genomic diversity in the populations of *Daphnia cucullata* in each lake (after *T*-test), Lake Geraņimovas-Ilzas was the most different (Fig. 5). This means that the genome level of *Daphnia cucullata* populations in this lake is more diverse than of the populations of the other studied lakes.

Table 5. Primers used in RAPD analysis and numbers and sizes of general bands

Primer	Primer sequence 5′→3′	Number of DNA fragments								Polymorphic DNA band size range, bp
		Svente		Riča		Drīdzis		Geraņimovas-Ilzas		
		Total	Polymorphic	Total	Polymorphic	Total	Polymorphic	Total	Polymorphic	
Roth A-02	TGC CGA GCT G	3	0	5	0	5	1	3	1	600–3000
Roth A-03	AGT CAG CCA C	4	0	5	1	2	1	8	1	800–3000
Roth A-05	AGG GGT CTT G	4	0	3	2	4	2	6	2	1000–3000
Roth A-09	GGG TAA CGC C	5	2	5	1	3	1	4	2	1000–3000
Roth A-10	GTG ATC GCA G	0	0	4	1	9	6	4	1	900–3000
Roth A-12	TCG GCG ATA G	2	0	2	0	2	1	3	1	900–3000
Roth A-13	CAG CAC CCA C	0	0	4	1	4	1	4	0	1000–3000
Roth B-03	CAT CCC CCT G	5	2	5	1	3	1	7	1	900–3000
Roth B-07	GGT GAC GCA G	5	3	5	2	5	2	5	2	800–3000
Roth B-08	GTC CAC ACG G	4	1	3	3	4	4	2	2	1200–3000
Roth F-10	GGA AGC TTG G	2	2	11	6	7	6	9	7	500–3000
Roth C-11	AAA GCT GCG G	5	0	5	0	4	0	4	0	600–3000
Roth C-20	ACT TCG CCA C	10	3	4	2	6	3	5	1	700–3000
Mean		3.77	1	4.69	1.54	4.46	2.23	4.92	1.61	
Total		49	13	67	20	58	29	64	21	
Polymorphic DNA bands, %			26.50		29.80		50		32.80	

Table 6. Pairwise similarities after Dice coefficient (*S*) between *Daphnia cucullata* populations in lakes Svente, Riča, Drīdzis, and Geraņimovas-Ilzas

	Svente	Riča	Drīdzis		Svente	Riča	Drīdzis
Primer Roth A-02				Primer Roth B-03			
Svente				Svente			
Riča	0.8			Riča	0.73		
Drīdzis	0.67	0.73		Drīdzis	0.5	0.22	
Geraņimovas-Ilzas	0.67	0.5	0.5	Geraņimovas-Ilzas	0.67	0.33	0.22
Primer Roth A-03				Primer Roth B-07			
Svente				Svente			
Riča	0.4			Riča	1		
Drīdzis	0.4	0.28		Drīdzis	1	1	
Geraņimovas-Ilzas	0.36	0.91	0.22	Geraņimovas-Ilzas	1	1	1
Primer Roth A-05				Primer Roth B-08			
Svente				Svente			
Riča	0.4			Riča	0.28		
Drīdzis	0	0.28		Drīdzis	0.4	0.28	
Geraņimovas-Ilzas	0.4	0.57	0.4	Geraņimovas-Ilzas	0.33	0.8	0.33
Primer Roth A-09				Primer Roth F-10			
Svente				Svente			
Riča	0.54			Riča	0.31		
Drīdzis	0.28	0.22		Drīdzis	0.44	0.68	
Geraņimovas-Ilzas	0.5	0.54	0	Geraņimovas-Ilzas	0.2	0.31	0.5
Primer Roth A-10				Primer Roth C-11			
Svente				Svente			
Riča	0			Riča	1		
Drīdzis	0	0.67		Drīdzis	0.89	0.89	
Geraņimovas-Ilzas	0	0.6	0.8	Geraņimovas-Ilzas	0.89	0.89	1
Primer Roth A-12				Primer Roth C-20			
Svente				Svente			
Riča	0			Riča	0.28		
Drīdzis	0.4	0		Drīdzis	0.33	0.4	
Geraņimovas-Ilzas	0.4	0	0.25	Geraņimovas-Ilzas	0.28	0.57	0.36
Primer Roth A-13							
Svente							
Riča	0						
Drīdzis	0	0.4					
Geraņimovas-Ilzas	0	0.57	0.5				

Table 7. Genetic distance of *Daphnia cucullata* between lakes Svente, Riča, Drīdzis, and Geraņimovas-Ilzas

Lake	Svente	Riča	Drīdzis
Svente			
Riča	4.98		
Drīdzis	3.61	4.62	
Geraņimovas-Ilzas	3.21	3.44	3.76

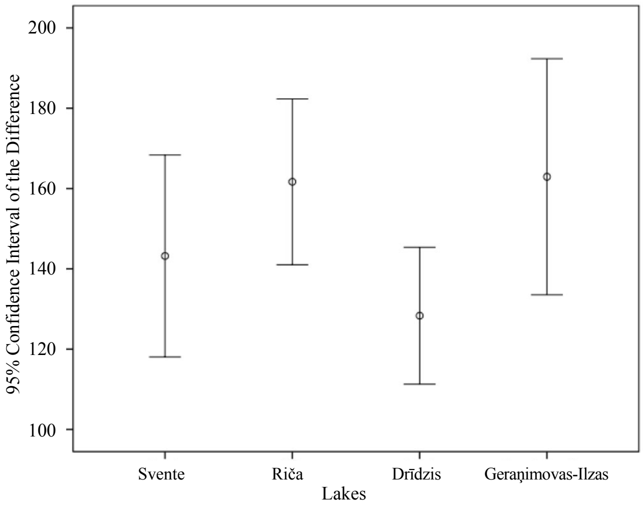

Fig. 5. Genome difference of *Daphnia cucullata* populations (Independent Samples Test (*T*-test)).

DISCUSSION

Numerous authors (Patalas, 1971; Sprules, 1975; Keller & Conlon, 1994; Bertilsson et al., 1995; Pinel-Alloul et al., 1995; Cottenie et al., 2001) have analysed changes in the structure of zooplankton populations within the season and how specimens choose the most optimal ecological niche using various physiological and behavioural mechanisms. Such factors as the light regime, temperature, oxygen content, chlorophyll concentration, macrophyte cover, predator (both invertebrates and vertebrates) presence, and competition among species usually vary over the seasons. Lake morphology and anthropogenic activities in the lake basin as well as the distance between water bodies are also very important. The above-mentioned researchers showed that the structural differences in the zooplankton of a water body are closely related to the differences in the trophic structure and biotic interactions, which complies with the theory of alternative equilibria. Large Cladocera taxa such as *Daphnia* and *Pediculus polyphemus* require water bodies with high transparency, low chlorophyll *a* concentrations, low fish density, and high macroinvertebrate density (Gliwicz & Pijanowska, 1986; Lampert, 1987; Irvine et al., 1989, 1990).

The biomass proportions of zooplankton found by Halvorsen et al. (2004) during their long-term studies in Lake Atnsjøen in the ice-free season (June–October) were very similar to those found by us, i.e. the Cladocera group had the highest percentages, followed by Copepoda and Rotifera. Halvorsen et al. (2004) emphasize that the detection of specific determinants is limited because various factors have a different effect on different species, and each of the factors should be checked under the unchanged conditions for a long period of time. According to several authors (Bottrell et al., 1976; Moore, 1977; Wetzel, 2001; Halvorsen et al., 2004), the main factor that affects the physical, chemical, and biological processes in lakes is the water temperature. However, other authors (Brettum & Halvorsen, 2004) point out that some specific phytoplankton species have a strong effect on some zooplankton species. Dimante-Deimantovica et al. (2012) emphasize in their research on the zooplankton fauna in deep Latvian lakes that according to the RDA analysis the species composition of zooplankton is closely related to the temperature, oxydation–reduction potential, chlorophyll *a*, and conductivity.

Many authors (Brooks & Dodson, 1965; Larsson & Dodson, 1993; Halvorsen et al., 2004; Saksgård & Hesthagen, 2004) state that planktofagous fishes, in our case vendace, have an effect on zooplankton. It has been experimentally proved that if there are more planktofagous fish in a lake, this lake will have a higher diversity of zooplankton species or species with some morphological adaptations (such as smaller size) compared with the lakes where no planktofagous fish is observed (De Meester et al., 1995; Bohn & Amundsen, 1998). This may explain the fact that among our studied lakes, lakes Drīdzis and Svente had a lower diversity of cladoceran species than the other lakes where *Coregonus albula* was not found, and the specimens were really smaller.

In comparison with the surveys carried out in previous years (Brakovska & Škute, 2007, 2009), the composition of Cladocera species and physico-chemical parameters of water had not changed significantly. According to literature data (Kačalova & Laganovska, 1961; Sloka, 1981), *Daphnia cucullata*, *Daphnia cristata*, and *Leptodora kindtii* are typical widespread pelagic species. In all the investigated lakes and sampling localities Daphniidae, Bosminidae, and Sididae dominated in the Cladocera group. The cosmopolitan cladoceran genus *Daphnia* is considered as a taxonomically difficult complex due to its variable morphological features. The reasons for morphological variations in *Daphnia* species are not clear.

The density of different Cladocera species, e.g. of *Daphnia cucullata*, was very variable in the vertical water column during the investigated season. It is known that *Daphnia* populations may consist of a few to several thousand clones and that rapid changes in clonal frequencies are common (Carvalho & Crisp, 1987; Matthes, 2004). However, vertical clonal coexistence has not been described. In general, *Daphnia* reproduce parthenogenetically in most time of the year. A population of *Daphnia* can contain a few dominant and many rare clonal groups (Carvalho & Crisp, 1987). In our research, the highest level of polymorphism during the summer season was observed in lakes Drīdzis (50%) and Geraņimovas-Ilzas (33%). The polymorphism levels in lakes Svente and Riča were from 26% to 29%. Haag et al. (2005) showed that older populations have a higher genetic diversity and that genetic differentiation among pools decreases with population age. They assumed that the bottleneck effect may be twofold: namely decreasing genetic diversity and population-wide inbreeding. Subsequent immigration may not only introduce new genetic material, but also lead to the selection of non-inbred hybrids, which may cause immigrant alleles to increase in frequency, thus leading to an increase in the genetic diversity in the older population.

The water temperature in July was equal in lakes Svente, Riča, Geraņimovas-Ilzas, and Drīdzis, being on average approximately 5 °C in the deep water and on average 23 °C in the upper layers. By contrast, the dissolved oxygen concentration in all water layers was 0.15 mg L^{-1} in Lake Svente, 0.16 mg L^{-1} in Lake Riča, 0.20 mg L^{-1} in Lake Geraņimovas-Ilzas, and 0.18 mg L^{-1} in Lake Drīdzis.

It is known that sexual phases are restricted to distinct periods when environmental conditions deteriorate (e.g. in autumn). Under stress conditions, parthenogenetic *Daphnia* switches to sexual reproduction, which leads to the production of diapausing eggs. A number of factors inducing sexual reproduction in Daphniidae have been proposed, including temperature, photoperiod, population density (Carvalho & Crisp, 1987; Korpelainen, 1989; Hobaek & Larsson, 1990), as well as fish exudates (Ślusarczyk, 1995). The induction of diapause in *Daphnia* seems to be maternally controlled (Alekseev & Lampert, 2001).

It may be assumed that the low temperature and low population density lead to sexual reproduction in deep water layers in the middle of summer. Earlier studies showed a temporal separation between the periods of sexual reproduction of *Daphnia* species in the field (Wolf, 1987). Additional laboratory experiments detected a large inter- and intraclonal variation in susceptibility to environmental incentives (i.e. photoperiod, shifts in population density, presence of food or predators) that induce sexual reproduction of *Daphnia* species in the field (Spaak, 1995). Contrary to the findings of Wolf (1987) and Spaak et al. (2004) we did not detect a separate extensive sexual phase of *Daphnia cucullata* in early summer. In the excellent work by Spaak et al. (2004) the distribution of sexual and asexual forms of *Daphnia* in the water column (20 m) was studied from April to December and from May to October at different depths. Sexually reproducing animals were found, with the exception of June, only during autumn and early winter with a time lag between the first occurrence of males and ephippial females. At that time, up to 50% of the extorted *Daphnia* population consisted of sexual morphs. Consequently, it is possible that in addition to the clones we found there are various other clones of *Daphnia cucullata* in lakes Svente, Riča, Drīdzis, and Geraņimovas-Ilzas.

The genetic structure of metapopulations offers insights into the genetic differentiation and it shows consequences of local extinction and recolonization. Research on allozyme variation in the metapopulation of rock pools showed that the genetic differentiation among pools of metapopulation is strong (Haag et al., 2005). It is assumed that the genetic structure of a population in the metapopulation is largely explained by three consequences of the founder events: strong drift during colonization, subsequent immigration, and effects of selection through hitching of neutral genes with linked loci under selection.

In general, analysis of Cladocera species in the pelagic zones of lakes Svente, Riča, Drīdzis, and Geraņimovas-Ilzas in July 2010 and July 2011 did not reveal significant differences in the qualitative and quantitative composition of species in comparison with earlier studies (Brakovska & Škute, 2007, 2009; Brakovska & Paidere, 2012; Brakovska et al., 2012). Comparison of the morphological characteristics of Cladocera species in the four studied lakes allows us to agree with the statement that the more planktofagous fish are in a lake, the smaller the size of zooplankton organisms is in comparison with other lakes with fewer planktofagous fish or none at all (De Meester et al. 1995; Bohn & Amundsen 1998). Namely, the size of Cladocera specimens in lakes Svente and Drīdzis was smaller in places where the number of planktofagous fish was greater, whilst in lakes Riča and Geraņimovas-Ilzas Cladocera specimens were larger and there were fewer planktofagous fish. Also the earlier finding that populations of *Daphnia cucullata* have genetic differences in different lakes and even within one lake (Carvalho & Crisp, 1987; Wolf, 1987; Spaak, 1995; Matthes, 2004; Haag et al., 2005) was confirmed in our study: *Daphnia cucullata* populations in our studied lakes showed genetic differentiation. Therefore more detailed research into the genetics of *Daphnia cucullata* populations in Latvian lakes needs to be performed.

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