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LIMNOLOGY

# How are spring zooplankton and autumn zooplankton influenced by water temperature in a polymictic lake?

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**Abstract.** We singled out spring (season with a water temperature of 4–15 °C) and autumn (15–4 °C), i.e. the seasons with the most variable meteorological conditions, in order to study the development of zooplankton as well as concurrent meteorological conditions (air and water temperature, ice conditions) and their relationships in these seasons. The aims of this study were (1) to review the spring zooplankton versus autumn zooplankton of a shallow polymictic lake; (2) to assess how much the zooplankton of the transition seasons, i.e. spring and autumn, is influenced by water temperature; (3) to clarify what factors are the main drivers of water temperature in such type of lakes. Proceeding from these aims, a long-term (1965–2014) study was conducted in the shallow (mean depth 2.8 m) polymictic Lake Võrtsjärv (Estonia). The main drivers of water temperature were air temperature and ice conditions. The water of the lake warmed up from 4 °C to 15 °C within 48 ± 2 days in spring and it cooled down from 15 °C to 4 °C during 57 ± 1.5 days in autumn. Both the air temperature in the territory of the studied lake and the water temperature in the lake increased while the duration of an ice cover on the lake decreased during the study period. The abundance of zooplankton in the seasons with the highly variable water temperature was also variable and largely dependent on the water temperature. In spring the effect of water temperature was greater than in autumn. Statistical analysis showed that when water temperature rose one degree in spring, the abundance of zooplankton increased by 27%, and when water temperature fell one degree in autumn, zooplankton abundance decreased by 9%. Zooplankton abundance was almost three times as high in spring (922 ind $L^{-1}$) as in autumn (325 ind $L^{-1}$) and was dominated by rotifers, small-bodied cladocerans, and juveniles of cyclopoid copepods. The domination of rotifers was more pronounced in spring (92%) than in autumn (70%). The share of cladocerans was negligible in the spring zooplankton (2%) but appreciable (24%) in the autumn zooplankton. The share of copepods in the total zooplankton abundance (6%) was modest and similar in both seasons. A shift (i.e. a marked increase in zooplankton abundance, switch from cold-water to warm-water species) in the abundance of spring zooplankton occurred in spring at a water temperature of about 10 °C (critical time window). A comparable but less conspicuous change (decrease in abundance, switch from warm-water species to cold-water species) was found at the same water temperature in autumn. During the 50 study years, the period with a mean water temperature of 10 °C shifted by 7 days to an earlier date in spring and by 6 days to a later date in autumn.

**Key words:** spring zooplankton, autumn zooplankton, water temperature, polymictic lake.

## INTRODUCTION

Climate change is increasingly acknowledged as an important driver of lake ecosystems (Adrian, 1997; Williamson et al., 2009; Kernan et al., 2010; Jeppesen et al., 2014; Izmest'eva et al., 2016). Nevertheless, several authors (Moss et al., 2011; Wagner and Adrian, 2011; Battarbee et al., 2012; Bennion et al., 2012; Hobæk et al., 2012; Nicolle et al., 2012; Yates et al., 2013) have admitted that distinguishing climate impacts on water ecosystems from other drivers is complicated as climate signals are suppressed by other impacts, frequently by

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concurrent eutrophication, or because climate and other pressures may interact. Different types of lakes, as well as lakes located in different geographical and climate regions, respond to weather variations in different ways (Arvola et al., 2010; Nõges et al., 2011; Dokulil et al., 2014); consequently, every lake is unique in this respect. Shallow lakes and deep lakes are differently affected by meteorological conditions; shallow polymictic freshwater ecosystems are particularly susceptible to climate warming (Mooij et al., 2005, 2007; Tuvikene et al., 2011; Jeppesen et al., 2014). Also, it is well documented that the effect of climate warming is more significant in winter and spring conditions (Adrian and Deneke, 1996; Weyhenmeyer et al., 1999; Thompson and Clark, 2008; Nõges and Nõges, 2014). Biological systems can respond to subtle signals in critical seasonal periods, serving as sensitive indicators of climate processes (Taylor et al., 2002; Wagner and Benndorf, 2007; Adrian et al., 2012). This can be explained by the fact that organisms are often adapted to a certain narrow temperature range and their life cycle strategies can be highly sensitive to variations in the ambient water temperature (Chen and Folt, 1996). The probability that future climate warming will cause major changes in the structure and functioning of freshwater ecosystems is very high (IPCC, 2007). The significant effect of water temperature on zooplankton is well known (Gerten and Adrian, 2002; Schalau et al., 2008; Dupuis and Hann, 2009; Straile, 2015).

Considering the above circumstances, we believed that the shallow polymictic Lake Võrtsjärv, which is strongly influenced by climate (Tuvikene et al., 2011; Nõges and Nõges, 2014), was a proper medium for studying spring zooplankton and autumn zooplankton and their relationship with meteorological conditions.

The first data on the zooplankton of Lake Võrtsjärv were presented in a monograph of Mühlen and Schneider (1920), where the lake was already classified as a eutrophic Chydorus-lake. Since 1965 up to the present (50 years) the zooplankton of the lake has been monitored monthly (in some years weekly and biweekly). Several authors have appreciated long-term ecological research into ecosystem's responses to environmental changes (Magnuson, 1990; Arvola et al., 2010; Kernan et al., 2010; Barr et al., 2013).

In Lake Võrtsjärv zooplankton abundance has been relatively high (annual average 757 ind $L^{-1}$) while its biomass has been low (0.874 mg $L^{-1}$), which is characteristic of highly eutrophic water bodies with zooplankters of small weight (Andronikova, 1996). In Lake Võrtsjärv, on average a rotifer weighed 0.7 µg, a cladoceran 9 µg, and a copepod 6 µg (Haberman and Haldna, 2014). Conditions for zooplankton are unfavourable in this lake. Phytoplankton is dominated by filamentous cyanobacteria (*Aulacoseira* spp. in spring, and *Limnothrix planctonica*, *L. redekei*, and *Planktolyngbya limnetica* in summer and in autumn), which are regarded as unsuitable food for zooplankton. Only 10% of the algae fall into the size fraction (<30 µm) edible for zooplankton, and about 2% of the energy assimilated by the algae reaches zooplankton. As small-bodied zooplankton cannot effectively graze on large algae, there is no clear-water period in late spring in Lake Võrtsjärv (Nõges et al., 2004). According to Ger et al. (2014), cyanobacteria provoke selection in zooplankton and only more adapted species can live simultaneously with cyanobacteria. In Lake Võrtsjärv zooplankton is dominated by rotifers, by small-bodied bakteriovorous cladocerans (*Chydorus sphaericus*, *Bosmina longirostris*), and by juveniles of cyclopoid copepods (Haberman, 1998).

All phytoplankton-based water quality indices, tested in long-term data, indicated deterioration in the water quality while none of them reflected a decline in the nutrient loadings to the lake in the 1990s. It seems that in Lake Võrtsjärv the situation represents an expression of morphometric hypertrophy where the phytoplankton species indicating hypertrophy are favoured by changes in the water level (light limitation) rather than by changes in the nutrient content (Tuvikene et al., 2011). It has also been shown that an increase in water temperature plays an important role in the proliferation of cyanobacteria (Paerl and Huisman, 2008; Battarbee et al., 2012; Deng et al., 2014). Obviously, the prospect of improvement in the feeding conditions of zooplankton is low in Lake Võrtsjärv.

According to some studies (Agasild et al., 2007; Zingel et al., 2007), the ciliate community of the lake is extremely rich (up to 191 cells $mL^{-1}$, usually >50% of the total zooplankton biomass). It has been found that ciliates consume about 20% of the standing stock of nanoplankton and almost 100% of the biomass production of bacteria during the growing season. As powerful predators on bacteria and small algae, ciliates can be strong food competitors for poorly fed cladocerans in this lake. Also, large predacious ciliates (haptorians) can reduce the abundance of small metazoans, such as rotifers (Nõges et al., 2016). Aberle et al. (2012) reported that climate warming may be favourable to ciliates. It should also be noted that the water of the shallow and wind-stirred Lake Võrtsjärv is rich in detritus, which may harm grazing cladocerans by clogging up their filter apparatus (Lougheed and Chow-Fraser, 1998). As zooplankton in Lake Võrtsjärv is poor, the pressure of fish on it may be appreciable (Ginter et al., 2011).

The aims of this study were (1) to review the spring zooplankton and autumn zooplankton of a shallow polymictic lake; (2) to assess how much the zooplankton of the transition seasons, i.e. spring and autumn, is influenced by water temperature; and (3) to clarify the factors that are the main drivers of water temperature in such lakes.

## STUDY SITE

The shallow (mean depth 2.8 m, maximum 6 m) large (270 $km^2$) eutrophic polymictic Lake Võrtsjärv is situated in South Estonia. The volume of the lake is 0.75 $km^3$ and the water residence time is about 1 year. The mean transparency in the ice-free period is typically less than 1.0 m but may be only 10–15 cm after storms. The water level of Lake Võrtsjärv fluctuates strongly (3.2 m) and the ecosystem of the lake is highly sensitive to these fluctuations, which follow the pattern of the North Atlantic Oscillation (NAO) index (Järvet, 2004; Tuvikene et al., 2011). Temperature in Lake Võrtsjärv is usually the highest (about 20 °C) in the second half of July or early August. The period with rather high water temperatures (for example 27.5 °C on 16 July 1994) has lasted since 1988. During most of the ice-free period the lake water is well oxygenated while rare winter anoxia has occurred in winters with extremely low water level. The water is alkaline (pH 8.0–8.6) with a great buffering capacity. Palaeodata demonstrated that the ecological status of Lake Võrtsjärv deteriorated already in the 1960s; the process continued in the 1970s (Leeben et al., 2013), peaked in the 1980s (total phosphorus concentration (TP) 53 mg $L^{-1}$), showed a small decline in the 1990s (TP 51 mg $L^{-1}$) and declined in the 2000s (TP 43 mg $L^{-1}$, Haberman and Haldna, 2014). The average TP concentration in the water of the lake was 42 mg $L^{-1}$ in spring and 56 mg $L^{-1}$ in autumn; the respective data of total nitrogen concentration (TN) were 1414 mg $L^{-1}$ and 822 mg $L^{-1}$.

## MATERIAL AND METHODS

The current study is based on long-term (1965–2014) research into spring zooplankton and autumn zooplankton and concurrent meteorological conditions (air and water temperature, ice phenomena) in the shallow polymictic Lake Võrtsjärv (Estonia). Quantitative zooplankton samples were collected monthly (in some years weekly or biweekly) at a permanent monitoring site, located between the Centre for Limnology and Tondisaar Island (58°12′40″N, 26°06′20″E), in the pelagial of the lake. The methods of collecting and treating zooplankton samples were described earlier in detail by Haberman and Haldna (2014). The data of daily water temperature, air temperature, and ice cover conditions were obtained from the Estonian Environmental Research Agency.

In the present study, we divided the year into climatic (thermal) seasons by threshold water temperatures according to Järvet (2004). By spring we refer to the period with water temperature ranging from 4 to 15 °C, and by autumn to the period with water temperature from 15 to 4 °C. When gathering zooplankton data the water temperature of the sampling time was used. Long-term data of the NAO index for the winter months (January–February) were drawn from the webpage http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml. A shift detection calculator (SDC) (Rodionov, 2004) was used to expose significant changes in climate and zooplankton. To detect relationships between the weather variables (annual mean air and water temperature for different months, the duration of the ice cover, and winter NAO), correlation analysis (CA, $N = 50$) was used. Regression analysis (RA) was used to estimate long-term trends. Contrasts between cold water and warm water were calculated using ANOVA model (AOV) for zooplankton taxa and groups. Zooplankton data were performed as follows: for total abundance of zooplankton and zooplankton groups, logarithmic; for species abundances, square root. All other calculations were carried out using the R package (R Development Core Team, 2011).

## RESULTS AND DISCUSSION

### Air temperature

The long-term (1965–2014) average air temperature in South Estonia, where Lake Võrtsjärv is located, was 5.2 °C in April (quartile range 1.9–7.6 °C) and 11 °C in May (8.7–13.4 °C). In autumn the average values were 11 °C (8.7–13.4 °C) in September, 5.7 °C (3–8.7 °C) in October, and 0.6 °C (from –2 to +4 °C) in November. The annual mean air temperature increased during the study period by an average (mean ± standard error) of 0.47 ± 0.04 °C per decade. The greatest estimated rise (RA, $p < 0.0001$) for the 50 years occurred in January (5.5 ± 0.05 °C) and in April (3 ± 0.03 °C, Fig. 1a). A marked regime shift (about 2 °C, from 3.8 °C up to 6 °C) in the mean April temperature took place in 1989, the year with the highest value of the winter NAO index. The effects of the winter NAO are highly pronounced in the case of spring air temperatures ($r = 0.41$, $p = 0.03$). It is well known that the climate of both winter and early spring is strongly influenced by the oscillation patterns of the North Atlantic (Straile and Adrian, 2000; Jaagus, 2006; Kļaviņš et al., 2007; Nõges et al., 2007). During the 50 years the average

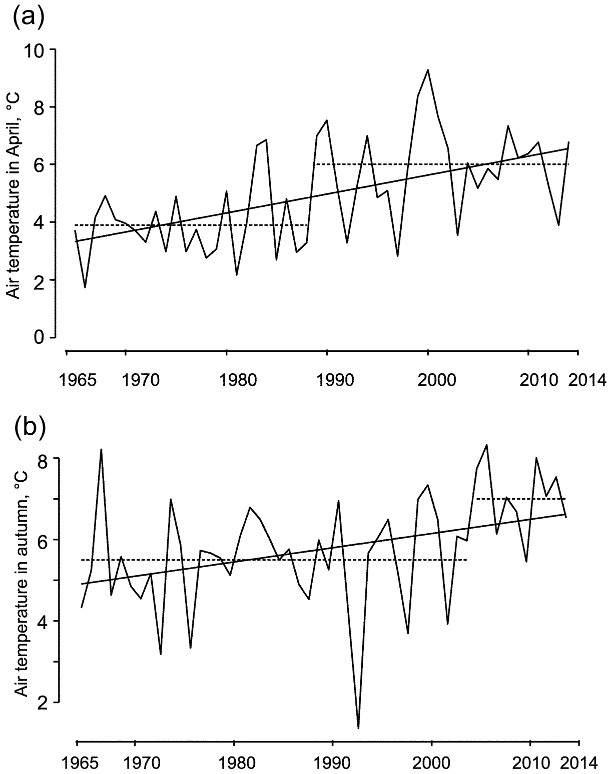


**Fig. 1.** Long-term changes with significant shifts (dashed line) in the mean air temperature, a – spring, b – autumn.

air temperature for the three autumn months also showed an increasing trend while the estimated rise was twice lower than for April, being on average 1.5 °C (RA, $p = 0.008$, Fig. 1b).

In the neighbouring regions (i.e. the regions influenced by the Baltic Sea), changes in annual air temperatures were synchronous with the increase starting in 1988 (Spriņģe et al., 2007; Kriauciuniene et al., 2012). In Latvia (1851–2006), the increase of the average air temperature was 1.4 °C (Lizuma et al., 2007), in Lithuania (1970–1990) 0.5–0.9 °C (Pernaravičiūtė, 2004), and in Poland 0.8–1.0 °C (Dabrowski et al., 2004). Nõges and Nõges (2014) found that in Estonia the mean air temperature increased by 0.09 °C per decade from 1866 and by 0.44° per decade from 1961 and that in terms of seasons the most significant change occurred in spring. According to IPCC (2007), the global average annual air temperature increased about 0.6–0.9 °C from the end of the 19th century to the end of the 20th century. Mooij et al. (2007) supposed that the average air temperature increased about 0.6 °C during the last century and will increase 1.4–5.8 °C by 2100 (0.07–0.29 °C per decade). On the basis of an earlier study (Jaagus, 2006), the annual air temperature in Estonia increased 1.0–1.7 °C (0.2–0.34 °C per decade) in the second half of the 20th century, and the most significant increase in the air temperature, i.e. 0.4–0.66 °C per decade, was typical of spring.

### Water temperature

According to Mooij et al. (2005), water temperature is among the most relevant climate factors in shallow lakes. In Lake Võrtsjärv, spring lasted generally from 10 April to 31 May and autumn lasted from 12 September to 7 November (Fig. 2). The water temperature in April was (mean ± SE) 4.6 ± 1.4 °C, in May 12.3 ± 1.5 °C, in September 13.2 ± 1.4 °C, in October 6.7 ± 1.6 °C, and in November 2 ± 1.2 °C. On average, the water of Lake Võrtsjärv warmed up from 4 °C to 15 °C during 48 ± 2 days in spring and it cooled down from 15 °C to 4 °C during 57 ± 1.5 days in autumn. The change per day was slower in autumn (0.18 °C) than in spring (0.2 °C; RA, $p < 0.0001$). According to statistical analysis, the most marked rise in water temperature occurred in April and the most marked fall in October; the mean change per decade was about 0.3 °C (RA, $p < 0.001$) for both months.

In 1965–1980, spring with a water temperature of 4 °C began on average on 13 April while in 2000–2014 spring with such water temperature began on average on 7 April. For the same time periods, autumn terminated on 1 November and 6 November, respectively. The beginning of spring shifted to an earlier date and the end of autumn, to a later date. A sharp rise in water temperature in April occurred in 1989 when, compared to the previous April, it increased more than 5 °C; the average level of temperature was continuously about 1.2 °C higher in the following 24 years (SDC, $p < 0.001$, Fig. 3a). In autumn the increase in water temperature was also essential (Fig. 3b). A similar stepwise increase of water temperature in the 1980s has also been observed by other researchers (Livingstone, 1997; Pernaravičiūtė, 2004; Spriņģe et al., 2007; Nõges et al., 2010; Dokulil et al., 2014; Straile, 2015).

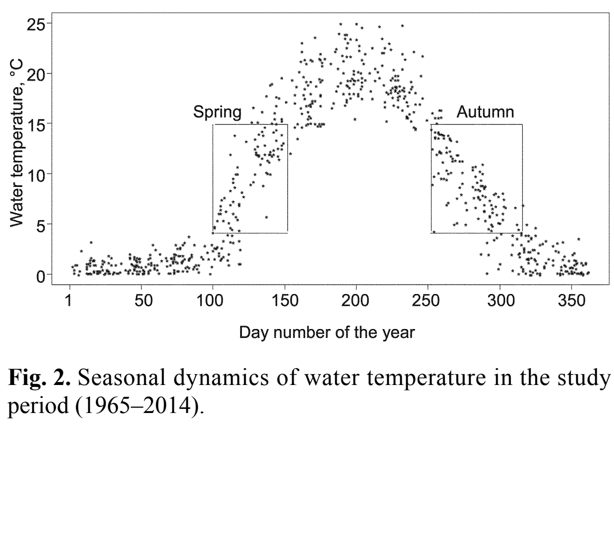


**Fig. 2.** Seasonal dynamics of water temperature in the study period (1965–2014).

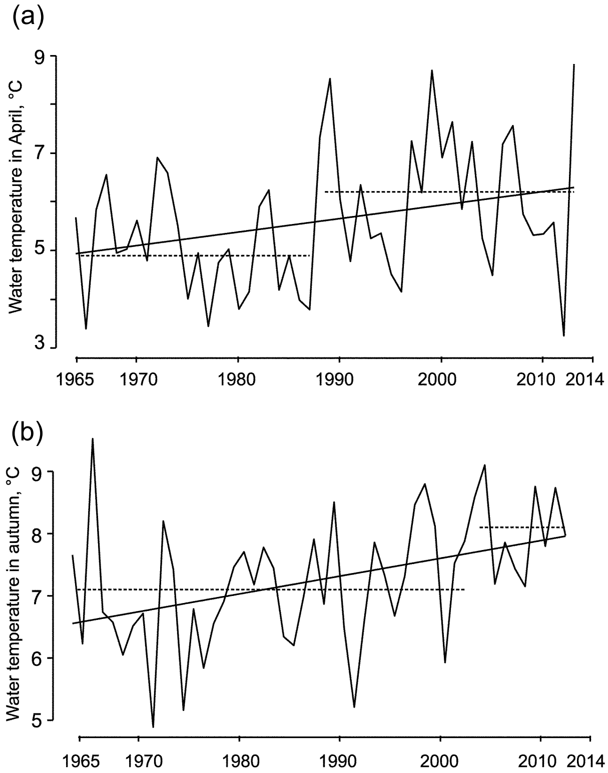


**Fig. 3.** Long-term changes with significant shifts (dashed line) in the mean water temperature: a – spring, b – autumn.

The water temperature in shallow polymictic lakes is tightly coupled to the air temperature (Livingstone and Dokulil, 2001; Mooij et al., 2005; Nõges and Nõges, 2014). Also in Lake Võrtsjärv, a strong positive correlation was found between the water temperature and air temperature (April $r = 0.65$, May $r = 0.54$, September $r = 0.62$, October $r = 0.6$). A negative correlation was found between the water temperature, on the one hand, and the first ice-off day ($r = -0.71$) and ice cover duration, on the other hand ($r = -0.42$).

## Ice phenomena

The condition of the ice cover on the lake is an important sensitive indicator of the regional climate and its change (Magnuson et al., 2000; Mooij et al., 2005; Arvola et al., 2010; Dokulil et al., 2014; Choinski et al., 2015). As an average for 50 years (1965–2014), Lake Võrtsjärv was covered with ice from 28 November to 7 April, i.e. 130 days per year. It is consistent with earlier data on the duration of the ice cover on the lake (Järvet, 2004; Dokulil et al., 2014; Nõges and Nõges, 2014). The earliest ice-on occurred on 8 October and the latest, on 22 November; the earliest ice-off took place on 23 March and the latest, on 5 May. The ice-off shifted by 18 days to an earlier date (RA, $p = 0.001$) and the ice-on shifted by 17 days to a later date (RA, $p = 0.001$).

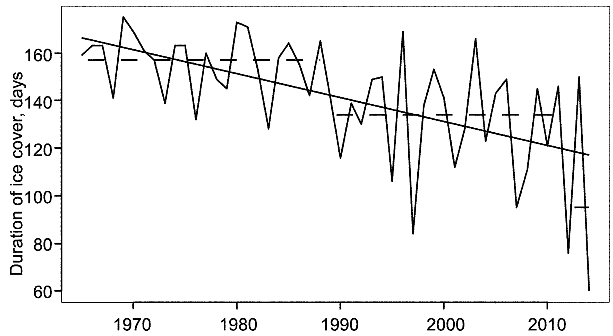


**Fig. 4.** Long-term changes with significant shifts (dashed line) in the ice-cover duration.

The duration of the ice cover was quite variable and became 35 days shorter during the study period (RA, $p = 0.0003$; Fig. 4). A decrease in the duration of ice at a rate of about 0.5 days per year was found for Neusiedler See, Lake Balaton, and for several Polish shallow lakes (Dokulil et al., 2014). Choinski et al. (2015) found for 18 Polish lakes that the duration of ice cover decreased by 5.6 days per decade during 1961–2010. Magnuson et al. (2000) reported a 6.5 days earlier ice-break in lakes in the Northern Hemisphere in the past 100 years in response to an air temperature increase of 1.2 °C. The timing of ice-on and ice-off is driven by several meteorological variables of which air temperature has been shown to be the most important one (Livingstone, 1997; Weyhenmeyer et al., 2008; Nõges and Nõges, 2014). In Lake Võrtsjärv, the date of ice-on was most correlated with air temperature in December (CA, $r = 0.98$, $p = 0.002$). The frequency of ice-free winters, particularly in large lakes, is known to have increased (Weyhenmeyer et al., 2008); large Lake Peipsi was ice-free in winter 2007/2008 (Laugaste et al., 2010).

## Zooplankton taxa

Altogether 45 zooplankton taxa were found in the pelagial of L. Võrtsjärv in spring: 11 cladocerans (24%), 10 copepods (22%), and 24 rotifers (54%). The respective data for autumn were 11 (27%), 8 (19%), and 22 (54%, Table 1). During the 50 years, essential changes occurred in the zooplankton composition of the lake. Already in the 1960s–1970s, i.e. at the time of the first signs of eutrophication (Leeben et al., 2013), species characteristic of oligo-mesotrophic waters (*Asplanchna herricki*, *Bythotrephes longimanus*) disappeared from the zooplankton. In the 1980s–1990s, in the period of the highest trophy of the lake (TP > 50 mg $L^{-1}$) and a stepwise rise in the water temperature (Nõges, 2009; Nõges and Nõges, 2014), species preferring lower trophy (*Bipalpus*

**Table 1.** Frequency and abundance of zooplankton in spring and in autumn (1965–2014). Percentages indicate the share in total zooplankton abundance

| Taxon | Spring ($N$ = 91) | | | Autumn ($N$ = 119) | | |
|---|---|---|---|---|---|---|
| | Frequency, | Abundance | | Frequency, | Abundance | |
| | % | ind L$^{-1}$ | % | % | ind L$^{-1}$ | % |
| Total zooplankton | | 922.3 | | | 324.6 | |
| Rotifera | | 849.3 | 92.1 | | 227.5 | 70.1 |
| *Anuraeopsis fissa* (Gosse) | 15.1 | 31.7 | 3.4 | 11.7 | 23.5 | 10.3 |
| *Ascomorpha ecaudis* Perty | 1.9 | 0.5 | 0.1 | 1.5 | 0.2 | 0.1 |
| *Asplanchna girodi* de Guerne | 7.5 | 0.2 | 0.0 | 0.7 | 0.1 | 0.0 |
| *Asplanchna priodonta* Gosse | 30.2 | 3.7 | 0.4 | 51.8 | 3.2 | 1.4 |
| *Bdelloida* gen. sp. | 5.7 | 0.3 | 0.0 | 4.4 | 0.2 | 0.1 |
| *Bipalpus hudsoni* (Imhof) | 2.8 | <0.1 | 0.0 | 4.4 | <0.1 | 0.0 |
| *Brachionus angularis* Gosse | 8.5 | 0.4 | 0.0 | | 0.0 | 0.0 |
| *Brachionus c. calyciflorus* Pallas | 26.4 | 2.5 | 0.3 | 12.4 | 0.9 | 0.4 |
| *Conochilus unicornis* Rousselet | 17.9 | 9.9 | 1.1 | 5.8 | 0.6 | 0.3 |
| *Filinia longiseta* (Ehrenberg) | 52.8 | 5.7 | 0.6 | 33.6 | 4.4 | 1.9 |
| *Gastropus stylifer* Imhof | 10.4 | 0.9 | 0.1 | 8 | 1.3 | 0.6 |
| *Kellicottia longispina* (Kellicott) | 23.6 | 11.2 | 1.2 | 5.8 | 0.1 | 0.0 |
| *Keratella cochlearis* (Gosse) | 90.6 | 394.1 | 42.7 | 70.0 | 42.0 | 18.5 |
| *Keratella hiemalis* Carlin | 15.1 | 2.5 | 0.3 | 1.5 | 0.1 | 0.1 |
| *Keratella quadrata* (Müller) | 85.8 | 126.7 | 13.7 | 51.8 | 10.8 | 4.7 |
| *Notholca labis* Gosse | 0.9 | <0.1 | 0.0 | 0.7 | 0.1 | 0.0 |
| *Notholca squamula* (Müller) | 7.5 | 0.4 | 0.0 | | | |
| *Polyarthra dolichoptera* Idelson | 74.5 | 144.4 | 15.7 | 26.3 | 16.1 | 7.1 |
| *Polyarthra luminosa* Kutikova | 41.5 | 89.6 | 9.7 | 74.5 | 109.5 | 48.1 |
| *Synchaeta verrucosa* Nipkow | 44.3 | 12.9 | 1.4 | 16.8 | 1.9 | 0.8 |
| *Trichocerca porcellus* (Gosse) | 2.8 | 0.4 | 0.0 | 4.4 | 0.6 | 0.3 |
| *Trichocerca rousseleti* (Voigt) | 9.4 | 10.7 | 1.2 | 13.9 | 10.2 | 4.5 |
| *Trichotria tetractis* (Ehrenberg) | 1.9 | <0.1 | 0.0 | 1.5 | <0.1 | 0.0 |
| *Trichotria pocillum* (Müller) | 1.9 | <0.1 | 0.0 | 0.7 | <0.1 | 0.0 |
| Cladocera | | 19.0 | 2.1 | 0.7 | 77.1 | 23.8 |
| *Alona guttata* Sars | 0.9 | <0.1 | 0.0 | 0.7 | <0.1 | 0.0 |
| *Alona costata* Sars | 0.9 | <0.1 | 0.0 | 20.4 | 0.8 | 0.3 |
| *Alona rectangula* Sars | 0.9 | <0.1 | 0.0 | 39.4 | 1.4 | 0.6 |
| *Alonella nana* (Baird) | 6.6 | <0.1 | 0.0 | 8.8 | 0.1 | 0.0 |
| *Bosmina berolinensis* Imhof | 14.2 | 0.3 | 0.0 | 28.5 | 0.6 | 0.2 |
| *Bosmina c. coregoni* (Baird) | 39.6 | 1.8 | 0.2 | 63.5 | 7.5 | 3.3 |
| *Bosmina longirostris* (O.F. Müller) | 63.2 | 5.0 | 0.5 | 78.1 | 8.0 | 3.5 |
| *Bosmina obtusirostris* Sars | 2.8 | <0.1 | 0.0 | 5.1 | <0.1 | 0.0 |
| *Chydorus sphaericus* (O.F. Müller) | 74.5 | 10.0 | 1.1 | 95.6 | 55.1 | 24.2 |
| *Daphnia cucullata* Sars | 10.4 | 0.1 | 0.0 | 33.6 | 1.4 | 0.6 |
| *Leptodora kindti* (Focke) | 8.5 | 0.1 | 0.0 | 1.5 | <0.1 | 0.0 |
| Copepoda | | 54.1 | 5.9 | | 20.0 | 6.2 |
| Copepodites | 93.4 | 14.8 | 1.6 | 84.7 | 12.1 | 5.3 |
| Nauplii | 91.5 | 33.6 | 3.6 | 73.7 | 6.2 | 2.7 |
| *Acanthocyclops viridis* (Jurine) | 2.8 | 0.1 | 0.0 | 1.5 | <0.1 | 0.0 |
| *Cyclops kolensis* Lilljeborg | 16 | 1.7 | 0.2 | 0.7 | 0.0 | 0.0 |
| *Eucyclops macrurus* (Sars) | 0.9 | 0.1 | 0.0 | | 0.0 | 0.0 |
| *Eucyclops serrulatus* (Fischer) | 3.8 | <0.1 | 0.0 | 0.7 | <0.1 | 0.0 |
| *Eudiaptomus gracilis* (Sars) | 15.1 | 0.3 | 0.0 | 16.8 | 0.6 | 0.2 |
| *Mesocyclops crassus* (Fischer) | 13.2 | 0.3 | 0.0 | | | |
| *Mesocyclops leuckarti* Claus | 47.2 | 1.8 | 0.2 | 18.2 | 0.9 | 0.4 |
| *Mesocyclops oithonoides* Sars | 35.8 | 1.2 | 0.1 | 5.1 | 0.1 | 0.0 |

*hudsoni*, *Conochilus unicornis*, *Kellicottia longispina*, *Bosmina berolinensis*, *Cyclops kolensis*, *Eudiaptomus gracilis)*, which had been present in the 1960s–1970s, had disappeared. Despite the decrease in the loadings as well as in in-lake nutrient concentrations (Nõges et al., 2007; Haberman and Haldna, 2014), these species did not reappear.

It is well known that zooplankton responds to changes in the trophic state of a water body with a certain lag (Jeppesen et al., 2002; Carvalho et al., 2012); however, as climate warming promotes eutrophication it is very difficult to distinguish interactions between trophic state and warming (Moss et al., 2011; Wagner and Adrian, 2011; Bennion et al., 2012). In Lake Võrtsjärv, the genus *Daphnia* was only represented by *D. cucullata*, a character species for eutrophic water bodies. Thermophilous *D. cucullata*, appearing in spring zooplankton at a water temperature of about 12–13 °C, was never abundant in the spring zooplankton but was still relatively numerous in the autumn plankton. However, in the 1990s this species almost disappeared from the lake. This can be explained by unfavourable feeding conditions (Claska and Gilbert, 1998; Carvalho et al., 2012) and by strong fish predation (Ginter et al., 2011). Also *Bosmina coregoni*, which was relatively abundant in the 1960s–1970s, disappeared from the zooplankton starting from the 1990s and had not reappeared by the end of the study period. At the same time, the cladoceran community became dominated by small-bodied *B. longirostris*. Davidson et al. (2011) described a similar change from Lake Søbygaard (Denmark), where it was most likely due to increased fish predation. Starting from the 1990s, the abundance of the rotifer genus *Brachionus* (*B. calyciflorus, B. angularis*) increased in Lake Võrtsjärv. Evidently, this was supported by the rich community of ciliates (Mohr and Adrian, 2002) in this lake. During the 50 years the average annual number of zooplankton species decreased in both seasons about 1.4 species per year (RA, $p < 0.05$, Fig. 5). Several

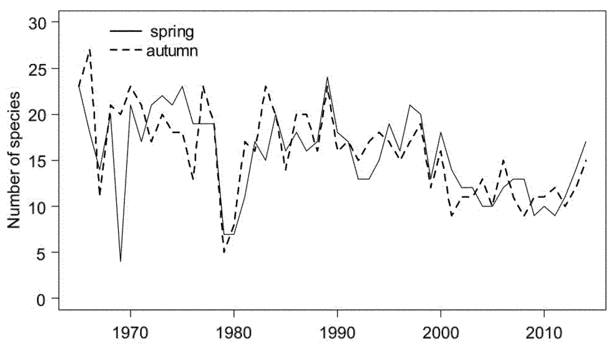


**Fig. 5.** Long-term changes in the number of zooplankton taxa in spring and autumn.

researchers (Wrona et al., 2006; Shurin et al., 2010; Haberman and Haldna, 2014) are of the opinion that freshwater species are at high risk of extinction and that the most influential drivers are related to climate induced stress.

## Frequency of zooplankton taxa

In spring, the most frequent (>70% of all collected samples) zooplankton taxa were *Keratella cochlearis*, *Keratella quadrata*, *Polyarthra dolichoptera*, *Chydorus sphaericus*, and copepodites and nauplii of cyclopoid copepods (Table 1). To resist unsuitable water temperature in winter, dormancy is common for zooplankton species (Sarvala, 1979; Ricci, 2001; De Stasio, 2004). Rotifers and cladocerans overwinter as resting eggs, while copepods mainly overwinter as fifth-stage copepodites. At proper water temperature and light conditions (Vandekerkhove et al., 2005; Dupuis and Hann, 2009), they will continue rapid development in spring. Copepod juveniles and species of the genus *Bosmina* were among the earliest zooplankters in Lake Peipsi (Laugaste et al., 2010), while *D. cucullata* was always among the latest (Haberman and Virro, 2004). According to Gulati (1978), the genus *Bosmina* is usually common in temperate lakes in early spring. In Lake Võrtsjärv the most frequent zooplankters in autumn were *C. sphaericus*, *B. longirostris*, *Polyarthra luminosa*, *K. cochlearis*, and copepodites and nauplii of cyclopoid copepods (Table 1). The most characteristic cladoceran in Lake Võrtsjärv was *C. sphaericus*. It usually appeared in May and disappeared in November; however, a few individuals may have been present in winter plankton. The species was found at water temperatures of 0.8–27.6 °C. Another dominating cladoceran in Lake Võrtsjärv, *B. longirostris*, was also found at water temperatures of 0.8–27.6 °C. The species appeared as single individuals already in April, being, as a rule, the earliest among the cladocerans (Haberman and Virro, 2004).

## Dominating taxa

Domination was calculated as the percentage of each zooplankton taxon of total zooplankton abundance (Green, 1993). In Lake Võrtsjärv, the zooplankton species accounting for at least 20% of the total zooplankton abundance were considered dominants. Molina-Navarro et al. (2012) used the categories 'low' (0–5% of total zooplankton abundance), 'mid' (5–15%), 'high' (15–40%), and 'very high' (>40%) to estimate the share of zooplankton species in the total zooplankton abundance. In spring, zooplankton abundance was mainly built of *K. cochlearis*, *P. dolichoptera*, and *K. quadrata*. In autumn, zooplankton abundance was mainly formed by

*P. luminosa*, *K. cochlearis*, and *C. sphaericus* (Table 1). A great majority of the zooplankton species of Lake Võrtsjärv were of minor importance, with only a few (1–2) dominating species, which is characteristic of strongly eutrophic water bodies (Andronikova, 1996). The so-called functioning load was divided unevenly between species, which is quite expected for such water bodies. The number of dominants increases in parallel with a decrease in the trophic state of lakes. In the oligotrophic Lake Saimaa (Finland), the mean number of dominating species varied between 4 and 8 (Hynynen et al., 1999).

**Abundance**

As spring and autumn (transition seasons) are the seasons with the most variable in-season water temperature conditions (continuous rise in spring and fall in autumn), also the in-season zooplankton was highly variable. In spring the abundance of zooplankton fluctuated between 61 and 3800 ind $L^{-1}$ (95% tolerance limits), being on average about three times as high as in autumn (43–1056 ind $L^{-1}$, Table 1).

In the strongly eutrophic Lake Võrtsjärv zooplankton abundance was overwhelmingly dominated by rotifers. The share of rotifers in the zooplankton community was considerably larger in spring than in autumn, with a mean difference of 26% (AOV, $p < 0.0001$, Table 1). The high population growth potential of rotifers, owing to the short development time and parthenogenetic reproduction, allows them to respond quickly to favourable changes in a lake (Allan, 1976; Adrian et al., 2006). In spring food competition and mechanical interference by cladocerans should be negligible in view of their low abundance (Table 1). Predation by cyclopoid copepods may be strong (Brandl, 2005); however, in spring, when among copepods there are numerous non-predatory nauplii and copepodites, their impact on rotifers cannot be essential in Lake Võrtsjärv. Also fish larvae prey on rotifers (Telesh, 1993), but at least in early spring this cannot be of significance, either. Rotifers are the first resource for newly hatched fish, and the advance in their phenology might affect fish recruitment negatively (Nicolle et al., 2011). Nicolle et al. (2012) suggested that rotifers may be a suitable indicator group for detecting changes in temperature regimes in freshwater ecosystems. The role of thermophilic cladocerans in the zooplankton abundance in spring was unimportant and significantly smaller than in autumn. The share of copepods (dominated by juveniles of cyclopoid copepods) in the total zooplankton abundance was modest and similar in both seasons (Table 1). Several studies (Talling, 2003; Sommer and Lengfellner, 2008; Straile, 2015) point to a possible mismatch between zooplankton and their food (algae) in spring. Cladocerans, dominating in Lake Võrtsjärv, are prevalently bacteriovorous, and their relationship with algae is weak. At the same time, bacteria are known to boost as a result of a rise in water temperature (Sand-Jensen et al., 2007).

The impact of temperature on the development of zooplankton abundance was essential: a significant correlation (CA, $p < 0.01$) was found between the water temperature and the abundance of cladocerans ($r = 0.47$), copepods ($r = 0.62$), and rotifers ($r = 0.53$). The in-season distribution of zooplankton species also demonstrates close relationship between water temperature and zooplankton taxa (Fig. 6, Table 2). Zooplankton was influenced the most by average water temperature of 5 days preceding sampling. The influence of water temperature was more marked in spring than in autumn, and zooplankton was more stable in autumn (Fig. 6, Table 2). Statistical analysis showed that when water temperature rose one degree in spring, the abundance of zooplankton increased on average 27%, and when water temperature fell one degree in autumn, zooplankton abundance decreased 9% (RA, $p = 0.001$). According to Adrian et al. (1999), because of the low heat storage capacity of shallow lakes, the effects of winter on plankton communities in spring are short-lived and are soon overtaken by prevailing weather and by biotic interactions. Herzig (1994) indicated that abiotic factors (e.g. temperature) exert the most important impact on the zooplankton community in spring and autumn while biotic factors (e.g. food, predation) play a significant role in the summer months. Dupuis and Hann (2009) showed, on the basis of zooplankton hatching experiments, that the development of the zooplankton population within 60 days was promoted at temperatures of 12 °C, and a longer period was required at lower (6 °C, 9 °C) temperatures. Because water temperature is perceived differently by species with different thermal tolerance, we distinguished so-called 'winners' and 'losers' (Domisch et al., 2011) for cold-water versus warm-water periods of spring as well as for autumn (Table 2).

In Lake Võrtsjärv, the species of spring zooplankton and autumn zooplankton can be divided into three groups: (1) eurytherms, which make up an overwhelming part of the zooplankton; (2) cold-water stenotherms *K. hiemalis*, *P. dolichoptera*, *Synchaeta verrucosa*, and (3) warm-water stenotherms *Anuraeopsis fissa* and *Daphnia cucullata* (Tables 1, 2).

A shift (i.e. a marked increase in zooplankton abundance, switch from cold-water to warm-water species) in the abundance of spring zooplankton occurred in Lake Võrtsjärv at a water temperature of about 10 °C (critical time window). In autumn a comparable but less conspicuous change (a decrease in abundance, switch from warm-water species to cold-water species) was found at the same water temperature (Fig. 6, Table 2).

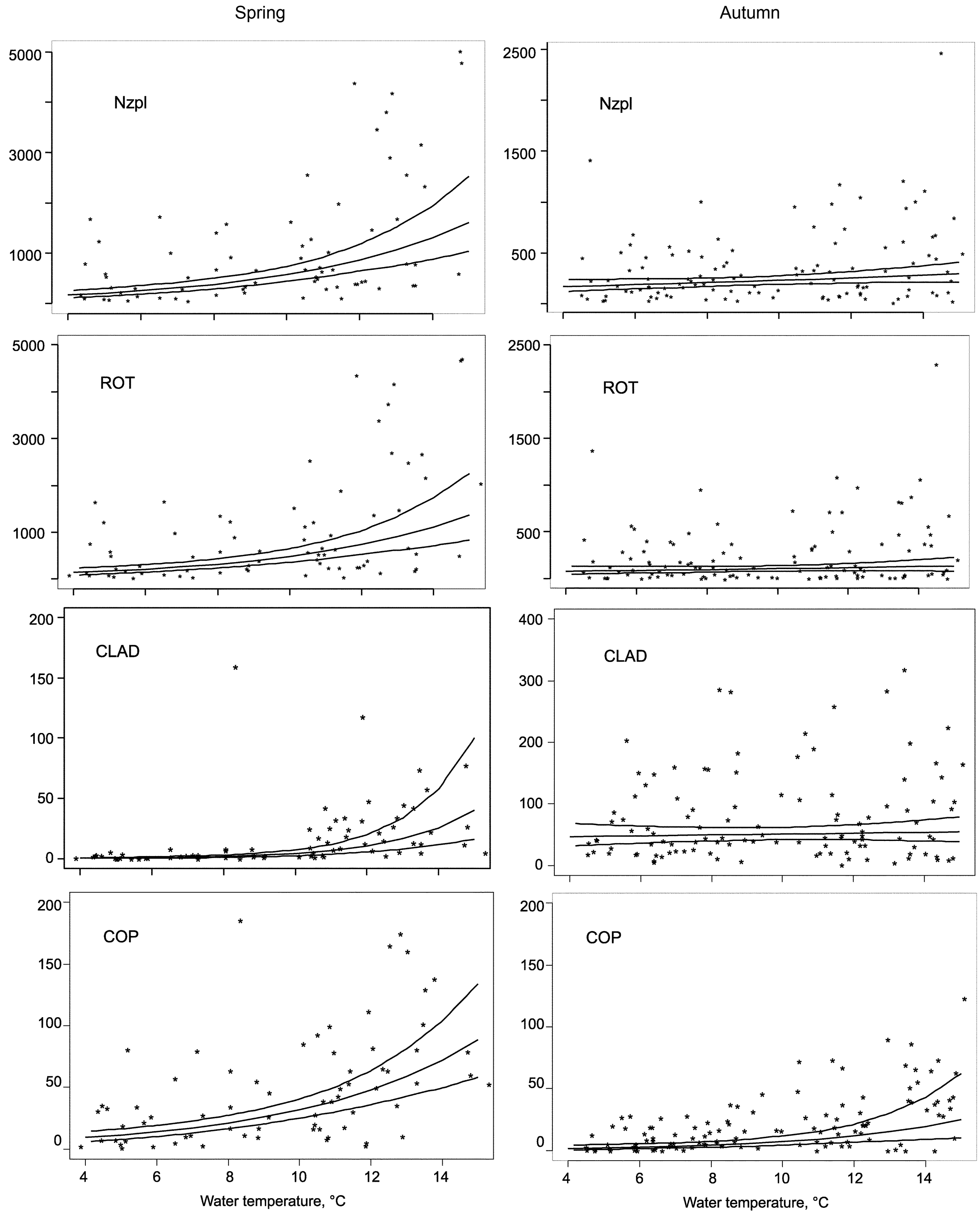


**Fig. 6.** Relationships between water temperature and zooplankton abundance (ind $L^{-1}$), Nzpl – total zooplankton; ROT – rotifers; CLAD – cladocerans; COP – copepods. Predicted means with 95% confident intervals.

**Table 2.** Comparison of zooplankton abundances for cold-water (4–9.9 °C) spring and autumn and for warm-water (10–15 °C) spring and autumn. Only statistically significant differences are presented (estimated contrasts of ANOVA model)

| | Mean abundance, ind $L^{-1}$ | | Results of the tests | | |
|---|---|---|---|---|---|
| | Cold-water | Warm-water | Difference | Ratio | *p*-Value |
| | | | SPRING | | |
| | *N* = 34 | *N* = 57 | | | |
| Total zooplankton | 437.85 | 1325.66 | 882.24 | 3.03 | <0.0001 |
| Copepods | 18.62 | 79.17 | 57.58 | 4.25 | <0.0001 |
| Rotifers | 417.02 | 1218.77 | 790.24 | 2.92 | 0.0002 |
| Cladocerans | 2.21 | 27.73 | 34.42 | 12.54 | <0.0001 |
| Copepodites | 6.71 | 20.04 | 13.63 | 2.98 | 0.0003 |
| Nauplii | 9.56 | 51.96 | 39.12 | 5.44 | <0.0001 |
| *Bosmina berolinensis* | 0.01 | 0.62 | 0.61 | 51.67 | 0.0132 |
| *Bosmina coregoni* | 0.21 | 3.03 | 3.44 | 14.59 | 0.0166 |
| *Bosmina longirostris* | 0.89 | 8.33 | 7.13 | 9.34 | <0.0001 |
| *Chydorus sphaericus* | 0.99 | 13.17 | 20.20 | 13.29 | 0.0019 |
| *Mesocyclops oithonoides* | 0.44 | 1.40 | 1.11 | 3.16 | 0.0104 |
| *Asplanchna priodonta* | 0.13 | 6.93 | 5.47 | 51.75 | 0.0043 |
| *Keratella cochlearis* | 119.70 | 597.47 | 478.02 | 4.99 | 0.0005 |
| *Keratella hiemalis* | 5.49 | 0.48 | –5.13 | 11.44 | 0.0062 |
| *Polyarthra luminosa* | 1.13 | 163.76 | 173.04 | 144.67 | 0.002 |
| *Synchaeta verrucosa* | 27.29 | 2.86 | –25.07 | 9.54 | <0.0001 |
| | | | AUTUMN | | |
| | *N* = 72 | *N* = 47 | | | |
| Copepods | 12.51 | 33.96 | 24.51 | 2.71 | <0.0001 |
| Copepodites | 7.38 | 20.92 | 16.44 | 2.84 | <0.0001 |
| Nauplii | 3.77 | 10.75 | 7.35 | 2.85 | <0.0001 |
| *Daphnia cucullata* | 0.46 | 3.33 | 2.82 | 7.33 | <0.0001 |
| *Anuraeopsis fissa* | 2.61 | 60.80 | 52.53 | 23.28 | 0.0004 |
| *Polyarthra dolichoptera* | 25.06 | 0.05 | –25.01 | 472.85 | 0.0042 |
| *Synchaeta verrucosa* | 2.92 | 0.00 | –2.92 | | 0.02 |

Several studies (Wagner and Benndorf, 2007; Wagner and Adrian, 2011; Adrian et al., 2012) emphasize that records of ecological processes should be not only sufficiently long but also collected at an appropriate temporal resolution as lake ecosystems respond to short-term weather conditions during critical time windows in the year. In Lake Võrtsjärv rotifers showed the most significant increase in abundance at a water temperature of 10 °C. Consequently, as spring zooplankton consists mainly of rotifers, they also increased the response of the total zooplankton to the rise in water temperature. Similarly, Chen et al. (2012) recorded a marked increase of rotifer densities at 10 °C in spring. As rotifers and cladocerans have a relatively short development period, a rise in water temperature can result in their increased abundance in only a few days. At the same time, the effect of temperature may be delayed in the case of copepods, which have a long development period and undergo multiple stages before adulthood (Adrian et al., 2006; Nicolle et al., 2012). As an average, a water temperature of 10 °C occurred in Lake Võrtsjärv on 8 May in spring and on 10 September in autumn. During the 50 study years the period with a water temperature of 10 °C shifted by 7 days (RA, $p = 0.04$) to an earlier date in spring and by 6 days ($p = 0.08$) to a later date in autumn.

## CONCLUSIONS

The long-term (1965–2014) study on spring (season with a water temperature of 4–15 °C) versus autumn (15–4 °C) zooplankton and on concurrent meteorological (air and water temperature, ice phenomena) conditions in the shallow (mean depth 2.8 m) polymictic Lake Võrtsjärv (Estonia) allowed us to draw the following conclusions:

1. The main drivers of water temperature were air temperature and ice conditions;
2. Both air temperature in the territory of Lake Võrtsjärv and water temperature in the lake increased, while the duration of the ice cover on the lake decreased;

3. The beginning of spring shifted to an earlier date and the end of autumn, to a later date;
4. The abundance of zooplankton in the seasons with highly variable water temperature was also variable and largely dependent on water temperature. Zooplankton was influenced the most by average water temperature on 5 days preceding sampling and was more affected by water temperature in spring than in autumn. Autumn zooplankton was more stable than spring zooplankton;
5. A shift in the abundance of zooplankton in spring and to a lesser degree in autumn occurred at a water temperature of 10 °C (critical time window). During the 50 study years, the period with a mean water temperature of 10 °C shifted by 7 days to an earlier date in spring and by 6 days to a later date in autumn;
6. During the 50 years, the number of zooplankton species declined in both seasons. In the 1980s–1990s, i.e. the period of the highest trophy of the lake and a stepwise rise in water temperature, the species preferring lower trophy disappeared from the zooplankton;
7. Zooplankton abundance was three times as high in spring as in autumn and was dominated by rotifers, small-bodied cladocerans, and juveniles of cyclopoid copepods. The domination of rotifers was more pronounced in spring (92%) than in autumn (70%). The share of cladocerans was negligible in the spring zooplankton (2%), but appreciable (24%) in the autumn zooplankton. The share of copepods in the total zooplankton abundance (6%) was modest and similar in both seasons.

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## Kuidas on kevade ja sügise zooplankton mõjutatud veetemperatuurist madalas polümiktilises veekogus?

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Töö eesmärk oli saada ülevaade: 1) kõige muutlikumate meteoroloogiliste tingimustega sesoonide, kevade ja sügise zooplanktonist madalas polümiktilises järves; 2) uurida, kui palju on zooplankton nn ülemineku- (*transition*) sesoonidel mõjutatud veetemperatuurist; 3) millest oleneb seda tüüpi veekogus veetemperatuur.

Kevadena käsitlesime perioodi, mil veetemperatuur on 4–15 °C, ja sügisena perioodi veetemperatuuriga 15–4 °C (joon 3). Viiekümne aasta (1965–2014) materjalide põhjal uuriti madala (2,8 m) polümiktilise Võrtsjärve kevade *versus* sügise zooplanktonit ja neid mõjutavaid meteoroloogilisi tingimusi, vee- ja õhutemperatuuri ning järve jääkatte perioodi. Järve vesi soojenes 4-st 15 kraadini keskmiselt 48 päevaga kevadel ja jahenes 15-st 4 kraadini 57 päevaga sügisel.

Uuringu põhjal võib järeldada:

1) veetemperatuuri põhilisteks kujundajateks kevadel ja sügisel olid õhutemperatuur ning järve jääkatte kestus. Tugev positiivne korrelatsioon oli vee- ja õhutemperatuuride vahel nii kevadel (aprillis $r = 0{,}65$, mais $r = 0{,}54$) kui ka sügisel (septembris $r = 0{,}62$, oktoobris $r = 0{,}6$). Negatiivne korrelatsioon leiti veetemperatuuri ja esimese järve jäävaba päeva ($r = –0{,}71$) ning veetemperatuuri ja jääkatte kestuse vahel ($r = –0{,}42$). Uuringuperioodil veetemperatuur (joon 2) ja õhutemperatuur (joon 1) järve territooriumil tõusid, jääkatte kestus päevades lühenes (joon 4), kevade algus nihkus varasemale ning sügise lõpp hilisemale ajale;
2) kokku leiti Võrtsjärve pelagiaali zooplanktoni kvantitatiivsetest proovidest uurimisperioodil kevadel 45 ja sügisel 41 zooplanktoni taksonit (tabel 1). Aasta keskmine taksonite arv vähenes 50 aasta jooksul nii kevadel kui ka sügisel (joon 5). Aasta kõige muutlikumate meteoroloogiliste tingimustega sesoonidel, kevadel (õhu- ja veetemperatuuri tõus) ja sügisel (temperatuuri langus), oli zooplanktoni arvukus väga varieeruv (kevadel 61–3800 ind $L^{-1}$ ning sügisel 43–1056 ind $L^{-1}$). Zooplanktoni arvukus oli kevadel (922 ind $L^{-1}$) peaaegu kolm korda suurem kui

sügisel (325 ind $L^{-1}$). Zooplanktoni arvukuse moodustasid tugevalt eutroofses Võrtsjärves ülekaalukalt (kevadel 92%, sügisel 70%) keriloomad (Rotifera). Vesikirbuliste (Cladocera) osa zooplanktonis oli tühine kevadel (2%), oluliselt suurem (24%) sügisel. Aerjalgsed (Copepoda) olid nii kevadel kui ka sügisel zooplanktoni arvukuses esindatud tagasihoidlikult (6%). Sagedamad ja arvukuselt domineerivad zooplankterid on esitatud tabelites 1 ning 2. Esinenud zooplankteritest oli enamik väikese tähtsusega, domineerisid vaid 1–2 liiki (tabel 1);

3) veetemperatuuri mõju zooplanktonile oli kevadel tugevam kui sügisel. Statistiline analüüs näitas, et veetemperatuuri tõus 1 kraadi võrra kevadel suurendas zooplanktoni arvukust keskmiselt 27%, samal ajal 1-kraadine temperatuuri langus sügisel vähendas zooplanktoni arvukust keskmiselt 9%. Märkimisväärne zooplanktoni arvukuse tõus ja langus sügisel toimusid veetemperatuuril 10 °C (*critical time window*, joon 6). Kevadel oli muutus oluliselt suurem kui sügisel. Kriitilise veetemperatuuri periood nihkus 50 aasta jooksul kevadel keskmiselt 7 päeva võrra varasemale ja sügisel 6 päeva võrra hilisemale ajale, mis viitab selgelt kliima soojenemisele.