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**Seasonal dynamics of zooplankton in two
contrasting lakes of the high Arctic**

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Annotation:

Two arctic lakes differing in depth and other attributes were sampled for zooplankton and phytoplankton during one vegetation season, and their population dynamics and trophic interactions were compared.

Anotace:

Dvě arktická jezera lišící se hloubkou a dalšími vlastnostmi byla vzorkována na zooplankton a fytoplankton během jedné vegetační sezóny a byla porovnána jejich populační dynamika společně s trofickými interakcemi.

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1 General introduction

1.1 Arctic

The Arctic is defined as the area north of the Northern Polar Circle ($66^{\circ}32' \text{ N}$) (Pienitz, Douglas, & Smol, 2007; Schindler & Smol, 2006). This means that in this area there is at least one day without a sunset (polar day) and one day without a sunrise (polar night). The Arctic is characteristic by little precipitation, fishless freshwater lakes, and missing woody plants. A special case is Svalbard. It is an archipelago in the Arctic Ocean located between 74° and 81° N and 10° and 35° E. The largest island is called Spitsbergen. During the Pleistocene the archipelago had been covered by a glacier which started receding some 10 000 years ago (Birks, Jones, & Rose, 2004). This causes the glacial isostatic adjustment and formation of the sea terraces (Saulnier-Talbot, Pienitz, & Vincent, 2003).

1.2 Climate

The local climate on Svalbard is very specific. Because it is located in the high Arctic, the climate is very cold and dry; annual precipitation in the central part of the area reaches 200 mm. April–May tend to be the driest, whereas February–March and August–September are slightly more humid in comparison. The highest precipitation is in the form of snow during December–January. Moreover, there are extreme differences between summer and winter. The annual mean temperature is -5°C (Ingólfsson, 2008). On the other hand, Svalbard is being warmed up by the North Atlantic Current which causes relatively mild winters in the context of the Arctic. The summer mean temperature is $+5^{\circ}\text{C}$ (Bernardová & Košnar, 2012). The sun does not set from April to August which means the growing season lasts 3–4 months (Birks et al., 2004; Zwoliński et al., 2007).

1.3 Lakes

In the area of high Arctic, there are many different kinds of lakes, such as glacial lakes or tundra lakes. Tundra lakes are usually shallow (less than a meter) while glacial lakes are deeper (several meters). The shallow lakes freeze in their entire volume in winter, and in summer they can warm up to more than 10°C . The deep lakes freeze only to some extent and there is liquid water at the bottom at all times. In summer they warm up, and stratification may occur. Our studied lakes were not stratified, however, because thanks to their depth and temperature they were mixed throughout the whole season. Lakes in this area are poor in nutrients, and the food web is very simple (Jónsdóttir, 2005; Nedbalová & Kavan, 2017).

1.3.1 Ebba lake

Ebba lake was created by the glacioisostatic adjustment at the end of the last ice age. This created the sea terrace where Ebba is located. This means that the lake is shallow, more specifically its depth is around 50 cm. In winter it freezes in its whole volume and melts in late spring (May). It belongs to the category of cold polymictic lakes which is mixed by the wind the whole time it is not frozen.

There are no fish in it and the trophic levels are limited to phytoplankton/bacterioplankton -> zooplankton -> invertebrate predator. Phytoplankton is represented by the following groups: *Cyanobacteria*, *Euglena*, *Chrysophyceae*, *Bacillariophyceae*, *Xanthophyceae*, *Dinophyta*, *Cryptophyceae*, *Chlorophyta* and *Streptophyta*. Zooplankton are these species: *Daphnia middendorffiana*, *Cyclops sp. X*, *Chydorus sphaericus*, *Acroperus cf. angustatus*, *Macrothrix hirsuticornis*, *Notholca foliacea* and *Polyarthra dolichoptera*. The only predator here is *Lepidurus arcticus* which is benthic. It can hunt in the whole water column thanks to the shallowness of the lake. The lake does not have any inflow nor outflow and because of the irregular precipitation irregularly dries up.

The bedrock consists of gravel and sand rich in calcium (Zwoliński et al., 2007). There is also gypsum and anhydrite which could enrich the water with the HCO_3^- , SO_4^{2-} and Ca^{2+} ions (Mazurek et al., 2012).

1.3.2 Blue lake

This lake is a typical kettle or pothole lake (Kalff, 2002). Its maximum depth is 6 meters, and it has one inflow and one outflow. In winter there a 130 cm thick layer of ice but there is liquid water below. It belongs to the category of cold monomictic lakes because it's temperature usually does not exceed 6 °C, and the lake is therefore being mixed during the whole season without ice. The bedrock consists primarily of palaeozoic sediments rich in calcium.

As well as in Ebba, there are no fish in this lake and the only predator is again *Lepidurus arcticus*. It is, however, benthic and therefore does not usually hunt in the pelagic zone. Because of this, there is expected to be lower predation rate. The zooplankton in this lake is represented by *Daphnia middendorffiana*, *Cyclops sp. X* and to a very limited extent by *Macrothrix hirsuticornis*. Phytoplankton consists of the same groups as in Ebba lake except for *Euglena* which was not recorded here.

1.4 Tadpole shrimp *Lepidurus arcticus*

This is a species of tadpole shrimp inhabiting Norway, Russia, Iceland, Finland, Sweden, Greenland, Kuril islands and Svalbard (Grzimek et al., 2003). It lives in the benthos of cold lakes (4–7 °C), and it is a top aquatic consumer with a wide food spectrum, and it is a predator of *Daphnia pulex* and *Daphnia middendorffiana* (Crook & Greenwood, 1978; Christoffersen, 2001). It is an ecosystem engineer and it is presumed to be the main driver of the ecological variety of *Daphnia* in our studied lakes.

This tadpole shrimp has two main predators on Svalbard – arctic tern (*Sterna paradisaea*) and purple sandpiper (*Calidris maritima*) (Lakka, 2015). Another important predator is the tadpole shrimp itself as it is cannibalistic (Arnold, 1966). *Lepidurus* survives winter using resistant eggs which it produces in autumn, and they hatch in spring. At the beginning of spring, it is possible that it feeds on the carcasses of the individuals frozen at the end of the previous season (Lakka, 2015).

1.5 Plankton

In the studied lakes there were seven species of zooplankton, two of which were *Rotifera*, four were *Cladocera* and one species of *Cyclopoida*.

1.5.1 *Daphnia middendorffiana*

In the studied lakes the dominant species is probably *Daphnia middendorffiana* as described by Fischer (1851). However, there is some discussion whether it is *D. middendorffiana* or *D. pulex* (Mergeay et al., 2008). These two species are nearly impossible to differentiate without a genetic analysis because of their morphological similarity (Mergeay et al., 2008; Wilhelm, Hardie, McNaught, & Clare, 1998). For the purpose of this thesis, the species is going to be identified as *D. middendorffiana*.

It is a species in the order of *Cladocera* which is one of the main groups of freshwater zooplankton. *Cladocera* have a strong carapace consisting of chitin (Kalf, 2002). They have two pairs of antennae, the second one of which is noticeably larger and is used for movement. They feed by filtering live matter and detritus by pulsating their limbs.

They reproduce mainly asexually by producing parthenogenetic eggs from which females hatch. When the condition deteriorates, haploid males are born, and sexual reproduction occurs. This results in strong resistant eggs called *ephippia* which can last in the sediment for a very long time.

Cladocera generally require high amounts of phosphorus and calcium as their bodies contain a lot of these elements (Hessen & Rukke, 2000).

1.5.2 Other *Cladocera*

Macrothrix hirsuticornis is the largest species of its genus growing up to 0.9 mm. The abdomen is covered by a large number of small hairs (Norman & Brady, 1867). It is usually found in low abundancies and its populations are relatively stable. It is a benthic species, yet here it is found in the whole water column.

Acroperus cf. angustatus is a very flexible species found commonly in lakes in Norway and Svalbard, both slightly acidic and slightly basic. It is found in the lithoral zone both between water plants and on bare bottoms. It is found in shallow and deep lakes alike, and it is typical by its stripes (Sinev, 2009).

Chydorus sphaericus is a cosmopolitan species found in various habitats (Jiang, 1979). It is most commonly found in shallow and medium deep lakes (Nevalainen, 2012). Although it is a benthic species, in eutrophic systems it can become pelagic and attach itself to filamentous phytoplankton.

1.5.3 *Cyclops sp. X*

This is a species in the order of *Cyclopoidea*, and it was first recognized in 2015 (Krajíček et al., 2016). It is widely distributed in most of Europe, it was, however, mistakenly identified as *C. strenuus* (Bosselmann, 1974). Nevertheless, to this day it has not been described.

Its body consists of cephalothorax and abdomen to which a furca is attached. *Cyclops* is gonochoristic and sexually dimorphic. Both sexes have a long second pair of antennae but the one of males is specialized for grabbing on to females. The eggs are attached to the female's abdomen in pairs from which a simple unsegmented larva called nauplius hatches.

1.6 Ecological interactions

In the context of this study two main interactions are the most important. One of them is invertebrate predation by the tadpole shrimp on zooplankton, the other one is competition both interspecific and intraspecific.

1.6.1 Predation

It is presumed that in our studied lakes invertebrate predation is one of the main building blocks of the food web. Also, the predation rate is one of the main attributes in which the studied lakes differ. Both lakes are fishless and both contain the invertebrate predator (the tadpole

shrimp). However, its abundance in both lakes differs as well as the ability to control the zooplankton population due to the mobility of this typically benthic organism.

The prey can defend itself against this kind of predation in various ways (Lampert & Sommer, 1997). The prey can change the shape or constitution of its body to prevent the predator from ingesting it. It can also change its ecological behaviour, for example it can mature sooner and reproduce at a faster rate. Zooplankton can also prefer to produce resistant sexual eggs (ephippia) as opposed to producing the more common parthenogenetic eggs. Using the ephippia it can migrate both in space (by traveling to new localities without a predator) and time (by receding to sediment and waiting for better conditions) (Yurista, 2002).

1.6.2 Competition

Another important interaction is competition. The studied lakes have very limited resources which several present populations have to share (Begon, Townsend, & Harper, 2006; Hassell & Tilman, 2006). Ecology differentiates several kinds of competition.

One of them is interference which is an aggressive interaction in which one side physically harms the other or they hurt each other. The individuals are wounded or they are prevented from accessing a resource (Barton, Sanders, & Gordon, 2006; Hassell & Tilman, 2006). The interaction between *Daphnia* and *Rotifera* could be characterized as interference as *Daphnia* wound *Rotifera* by ingestion and the following rejection which then prevents the *Rotifera* from reproducing (Diéguez & Gilbert, 2011). In the studied lakes there might also appear interspecific interference between the tadpole shrimps as they are cannibalistic (Lakka, 2015).

Another kind of competition is exploitation. This interaction is indirect. The interacting species compete for the same resources and by consuming them they limit each other (Hassell & Tilman, 2006). Exploitation can also be intraspecific especially in such a highly competitive environment such as arctic lakes. This can also influence the abundance and the ability to grow and reproduce (Allan, 1973).

1.7 Goals and aims

This study was conducted in order to show the differences in the dynamics and the interspecific interactions of zooplankton in Arctic lakes with emphasis on the differences between a shallow and a deep lake which differ both in the predation rate and the nutrient availability. There are also differences in the species constitution which causes different interactions in the lakes. The main object of the study is *Daphnia* which was chosen because it

is the dominant species and because it has been considered a model organism for a long time (Lampert, 2011). For this reason, its ecology has been investigated thoroughly and our conclusions can be generalized.

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Lepidurus arcticus as the main driver of ecological and morphological variation of *Daphnia middendorffiana* in Arctic lakes

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Abstract

The Arctic lakes in this study are a highly competitive ecosystem and they differ in several key attributes such as depth, available nutrients or the species composition. In both lakes, however, the dominant zooplankton species is *Daphnia middendorffiana* and in both lakes the main predator is *Lepidurus arcticus*. The predation rate in both lakes is presumed to differ because of the benthic nature of *Lepidurus* and the pelagic nature of *Daphnia*, which means that in the shallow lake they share the same space while in the deep one they rarely meet. In the presence of the invertebrate predator, *Daphnia* seems to change its ecological behaviour, its size, fecundity and also its morphology. In both of the studied lakes, there were three distinct cohorts during the season. *Daphnia* appears to outcompete other zooplankton species in both lakes. In the shallow lake, *Daphnia* responds to the higher predation by increasing its egg ratio while in the deep lake such reaction is missing. *Daphnia* also seems to adjust its body size and shape (head:body ratio) as a response to higher predation. The abiotic factors such as low temperature or lack of nutrients affect the ecology of both lakes to a certain extent.

Key words: trophic interactions, zooplankton, arctic lakes, trophic structure, *Lepidurus arcticus*, *Daphnia middendorffiana*

1 Introduction

The area of the high Arctic hosts many different important and interesting ecosystems such as arctic lakes which contain very simplified food webs allowing detailed ecological studies. In the studied lakes only three trophic levels can be found – primary producers (phytoplankton), herbivores (zooplankton, mainly *Daphnia middendorffiana*) and an invertebrate predator (*Lepidurus arcticus*).

This study was conducted in the archipelago Svalbard, namely the island Spitsbergen in and near the Petuniabukta bay. Svalbard had been fully covered by the glacier of the last ice age and has been being uncovered ever since as the glacier has been receding (Birks et al., 2004; Rachlewicz, Szczucínski, & Ewertowski, 2007). Although the archipelago is located in the high Arctic, its climate is somewhat milder than other areas in similar altitudes due to the North Atlantic Current making the annual average temperature -5 to -6 °C (Bernardová & Košnar, 2012; Birks et al., 2004; Ingólfsson, 2008). However, the area is still extreme as there is little precipitation, little nutrients and there are great differences between summer and winter.

There have been several studies recently dealing with the dynamics of different kinds of populations in the Arctic fishless lakes. Cazzanelli et al. (2012) studied *D. middendorffiana* in Greenland and found that the amount of phytoplankton in the water column is not enough to support the observed population of zooplankton in Arctic lakes. The solution to this problem is the fact that *Daphnia* in these conditions feed on benthic mats either by direct grazing or by disturbing the material by swimming into it, letting the pelagic bacteria feed on it and then feed on the bacteria. Rautio & Vincent (2006) in Canada showed that in shallow lakes this is even easier because the benthic material gets disturbed by the wind-induced mixing as opposed to the deeper lakes where the potential disturbance can only be caused by the zooplankton itself.

Woods et al. (2003) have proven that Arctic ecto-therms are accustomed to colder conditions by higher enzymatic activity and related RNA productivity. This is reflected in higher phosphorus demand because RNA is such a phosphorus-rich molecule. In another study it was shown that when *Daphnia pulex* from Arctic localities and the same species from temperate localities are put together in an environment with the same temperature and phosphorus levels, the Arctic individuals thrive compared to their temperate counterparts. This might be due to the natural selection of individuals with a higher growth rate in polar lakes (Hessen et al., 2004). However, Van Geest et al. (2007) conducted a study monitoring the population dynamics in lakes completely without a predator. The zooplankton community in

these lakes would therefore be limited only by the available resources (bottom-up control). The results show that the amount of phosphorus in the environment has no significant role in the population development when comparing similar lakes in similar localities differing mainly by the phosphorus level.

In both our studied lakes, there is expected to be a high level of competition among the zooplankton. They are both presumed to differ in the level of predation by *Lepidurus*. Both the competition and the predation are expected to shape the population dynamics. The zooplankton community consists of 4 species of *Cladocerans*, 1 species of *Cyclopoidae* and 2 species of *Rotifera* which are all competing for similar resources. Additionally, according to Devetter & Sed'a (2006) there is also a possibility that the present *Cyclops* could be a predator of the present *Rotifera*. Also, *Daphnia* may harm the *Rotifera* population by accidental ingestion and the following rejection (Diéguez & Gilbert, 2011). The present *Cladocerans* may respond to the invertebrate predation by *Lepidurus* by altering their bodies (Petrušek et al., 2009) or by adjusting their reproductive cycle. In a study conducted by Yurista (2002), *D. middendorffiana* in the highly competitive Arctic lakes prefers producing ephippia rather than parthenogenetic neonates.

The main goal of this study is to compare the dynamics of the populations of both of these lakes, including the correlation between the trophic levels and the changes of the environment throughout the season as well as the relationships between the trophic levels themselves. Another part of the study is assuming the fecundity of the zooplankton based on the resources, the competition between the present species and the level of predation. These are all presumed to be different in each studied lake as they differ in depth and resources which are factors believed to have a great influence on the whole population (Rautio & Vincent, 2006; Yurista, 2002). We also focus on the ecological and physiological responses of studied communities.

2 Methods

2.1 Study area

This study focuses on two lakes in the area of Billefjorden, Svalbard. Both lakes are around 10 000 years old as their origin probably dates to the end of the last ice age. The east coast of the Petuniabukta bay consists of arctic wetlands with shallow tundra lakes which were created by the glacial-isostatic adjustment when the marine terraces were formed (Saulnier-Talbot et al., 2003). One of these lakes which has no inflow nor outflow is called Ebba. It is a lake in near proximity of the glacier Ebbabreen (78°42' N, 16°36' E) and in this case, it represents a shallow lake. On the other hand, Blue lake, which is near the Pyramiden settlement (78°38' N, 16°07' E) represents a deep lake. It is a kettle lake formed by a glacier, and it has one main inflow and one outflow (Kalff, 2002). The area of both lakes was deglaciaded 10–7 thousand years ago. The lakes were chosen for several main attributes – they both lack a vertebrate predator, there is almost identical zooplankton composition, and the main difference between them is their depth.

attribute	Ebba lake	Blue lake
depth	max 0.5 m	max 5.0 m
origin	marine terrace	glacier
winter	frozen	water bellow ice
Predator (<i>L. arcticus</i>)	omnipresent	scarcely

Tab. 1 Comparison of the two lakes.

2.2 Sampling

For zooplankton sampling in Blue lake, a quantitative and closing Apstein plankton net with 200 µm mash and 40 cm mouth diameter was used. Sampling was done 5 times irregularly during summer season from April to September. Sampling on Blue lake in June have not been done because of massive but unstable ice cover. In April, holes had to be drilled in the ice layer which was 130 cm thick. For each sampling date, there were three random samples of the upper 2,5 m of the water column and three random samples of the bottom 5–2.5 m. Additional sampling was done by a plankton net with 40 µm mash to determine the presence of *Rotifera*.

For Ebba lake, a different method was used. Five random spots were chosen from which 10 liters of water were taken by a 1-liter beacon and filtered through a plankton net with 40 µm mash. This sampling was done 5 times between June and August as before.

All of the samples were then fixated by sucrose formaldehyde (Haney & Hall, 1973) to prevent the zooplankton (namely *Daphnia*) from ejecting their eggs. These were then transported to a lab for analysis.

In both lakes, the phytoplankton was sampled by submerging a 1.5-liter PET bottle below the water surface. This was then concentrated by sedimentation and preserved by 4% formaldehyde. Such sample represents the whole column because the whole lake is well mixed by the wind. Chemical samples were taken to 0.5 L PET bottle as well.

2.3 Analysis

There were two ways of analyzing the zooplankton. The sample contained less than a 1000 individuals, the total sample was counted under a microscope with a 200 magnitude in Sedgewick-Rafter counting chamber. More abundant samples were diluted, well mixed and 3 accurate subsamples were counted. Counts were converted back to 1 L volume in lake First 30 individuals of each species were also measured for length using a measuring eyepiece. Three dimensions were measured (Fig. 1).

Phytoplankton was analyzed by putting a 1 ml drop on a slide and counted under a dissecting microscope. Chemical analyses have been done using standardized methods in the lab of Hydrobiological Institute, Biology Centre AS CR.

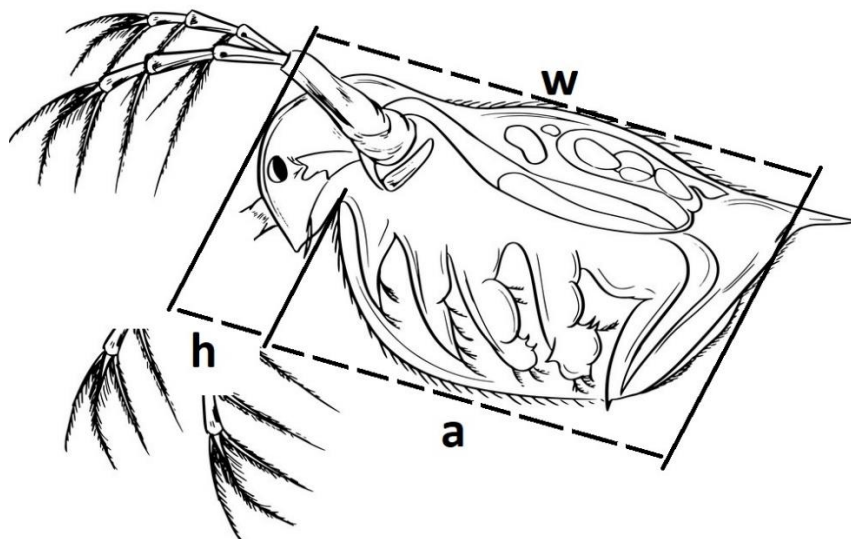


Fig. 1 Measured dimensions of *Daphnia* in this study. w = full body length, a = length of abdomen, h = length of abdomen (VectorStock.com, 2019). Edited.

For statistical analysis and graphs we used SigmaPlot version 14.0, from Systat Software, Inc., San Jose California USA, www.systatsoftware.com.

3 Results

In both lakes *Daphnia middendorffiana*, *Cyclops sp. X*, *Macrothrix hirsuticornis*, *Notholca foliacea*, and *Lepidurus arcticus* were found. In Ebba lake three additional species were found, namely *Acroperus cf. angustatus*, *Chydorus sphaericus* and *Polyarthra dolichoptera*. *Daphnia* is the dominant species of zooplankton in both lakes.

In Blue lake, the second most abundant was *Cyclops*. *Macrothrix* was extremely rare, it was found in only one sample. Although *Lepidurus* should be benthic, several individuals were found in the pelagic zone as well. In Ebba lake, *Chydorus* was the second most abundant species followed closely by *Macrothrix* and *Acroperus*. *Notholca* and *Polyarthra* were present mostly in July. *Cyclops* was represented rather scarcely.

Lake	pH	Conductivity	DOC	POC	P(dis)
	-	μS/cm	mg/l	mg/l	μg/l
Blue	7.5 ± 0.1	144.5±29.1	1.74±0.27	2.48±1.68	3.5±0.6
Ebba	8.0±0.2	233.8±22.6	7.11±2.08	2.52±0.38	13.5±9.0

Tab. 2 Chemical analysis of the lakes done simultaneously with the zooplankton and phytoplankton sampling. Mean ± standard deviation. DOC = dissolved organic carbon, POC = particulated organic carbon, P(dis) = dissolved phosphorus (Kopáček & Hejzlar, 1993)

As visible in Tab. 2, Ebba lake has slightly higher pH whereas Blue lake has neutral pH. The pH in both lakes is stable throughout the whole season. Conductivity in Ebba is almost twice as high as in Blue lake. Levels of dissolved organic carbon (DOC), particulate organic carbon (POC) and phosphorus (P) are relatively low in Blue lake during the whole season; in Ebba, however, the amount of DOC and P gradually grows until it peaks by the end of the season as shown in Fig. 2. This is then followed by the lake drying up.

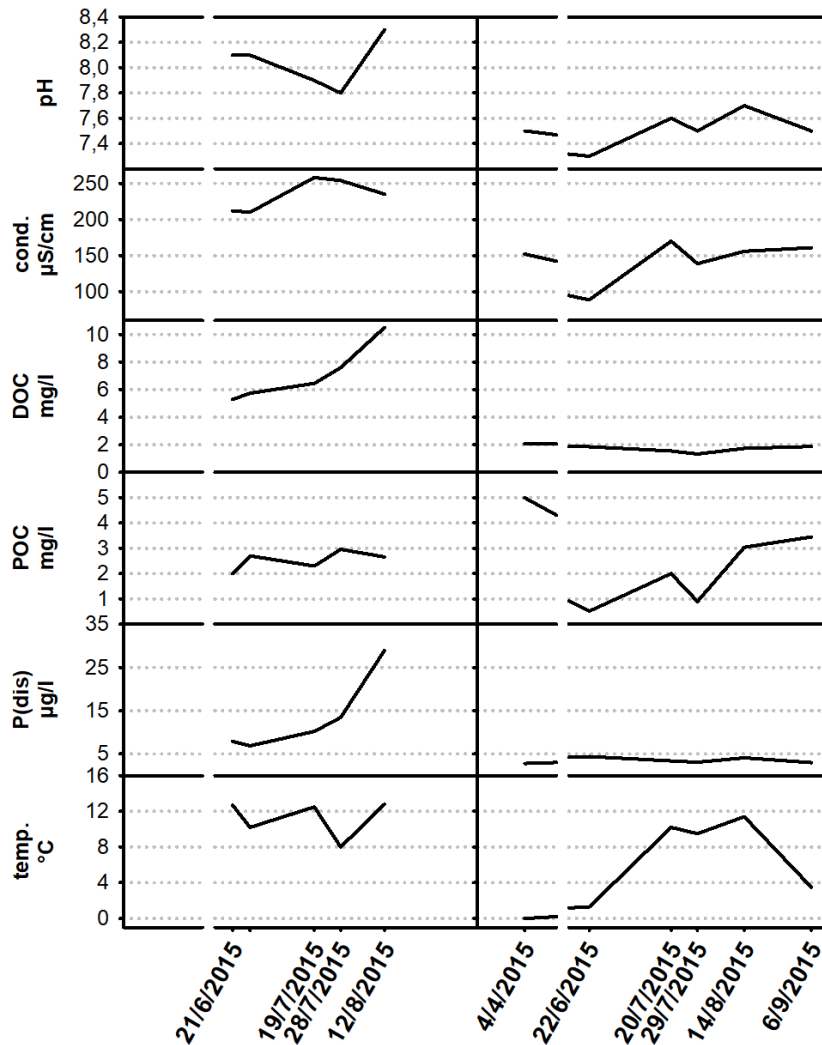


Fig. 2 Abiotic conditions of both lakes. Graphs of each attribute are scaled equally between the lakes. DOC = dissolved organic carbon, POC = particulated organic carbon, P(dis) = dissolved phosphorus (Kopáček & Hejzlar, 1993). Comparison of Ebba (left) and Blue lake (right).

3.1 Size, fertility, and the predator

In June, there are two generations of *Daphnia* in Ebba, the older one being more abundant and around 1000–1400 μm long and the younger one being 700–900 μm long. By the end of the month the older generation grows to 2000–2500 μm , the younger one reaches 1200–1800 μm and a new generation is born with sizes of 500–700 μm . At this time *Lepidurus* is present, but it is the same size as the older generation of *Daphnia*.

In July the youngest generation becomes more diversified as its size varies from 800 to 1500 μm and there is no longer any clear distinction between the two older generations which now vary between 2200 and 3100 μm . During this time *Lepidurus* becomes large enough to become a predator and the number of *Daphnia* drops significantly. At the same time, the egg

ratio of *Daphnia* reaches its maximum (Fig. 3). At this time the smallest *Daphnia* producing partenogenetic eggs is 2500 μm long. By the end of the month the older cohort does not grow in size anymore while the younger one reaches 1200–1800 μm and the smallest individuals producing eggs are now 2400 μm long. In August there is no clear distinction between the cohorts anymore as there is a continuous spectrum of individuals ranging from 800 to 2500 μm . The most represented sizes were 1100, 1800 and 2200 μm . There was also a small cohort of 2800 μm individuals. The smallest individuals producing eggs are 1840 μm long.

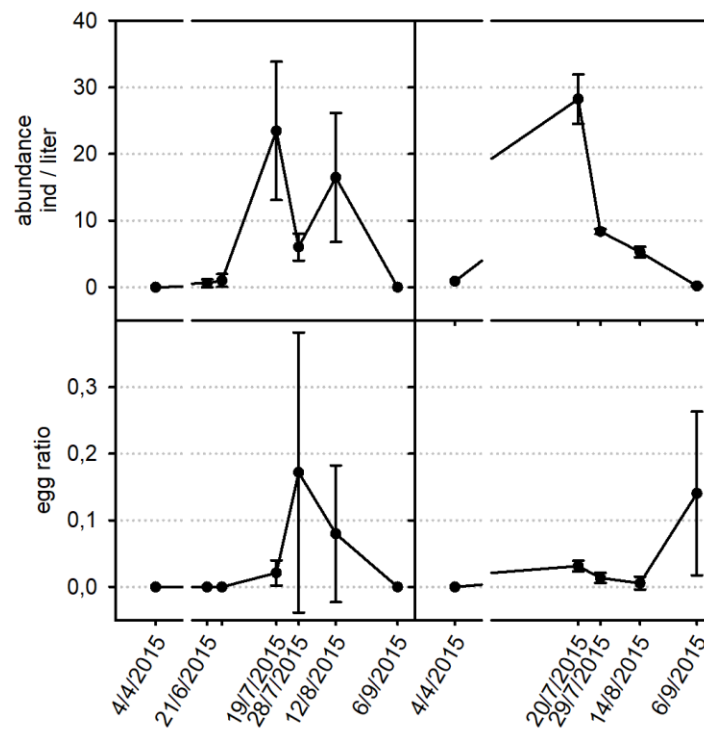


Fig. 3 The abundance of *D. middendorffiana* (top) compared to its egg ratio (bottom) throughout the season. Comparison of Ebba (left) and Blue lake (right). Error bars = SD

In Blue lake, there are two major cohorts in April (Fig. 4). Unfortunately, due to the floating ice, there is missing data in May and June. In July there is one small cohort of older *Daphnia* of sizes varying between 2300 and 2700 μm and one large cohort of sizes between 800 and 1500 μm . At this time the present *Lepidurus* is already large enough to hunt *Daphnia* but as mentioned previously, it is a benthic species and therefore should not affect the population very much. At this point, the smallest recorded individual producing eggs is 2420 μm long. One week later the younger individuals grow to 900–1600 μm accompanied by a wide spectrum of individuals varying between 1700 and 3900 μm with no distinct cohorts. Here the smallest individual producing eggs was 1040 μm long. In August two cohorts form one more abundant with sizes between 1000 and 1900 μm , the other less abundant with sizes between

2000 and 2500 μm . There was also a small number of individuals 3600 μm long. No eggbearing *Daphnia* were recorded here. In September there are three distinct cohorts, the oldest varying between 2600 and 3000 μm , the younger varying between 1500 and 2500 μm and the youngest varying between 600 and 1300 μm .

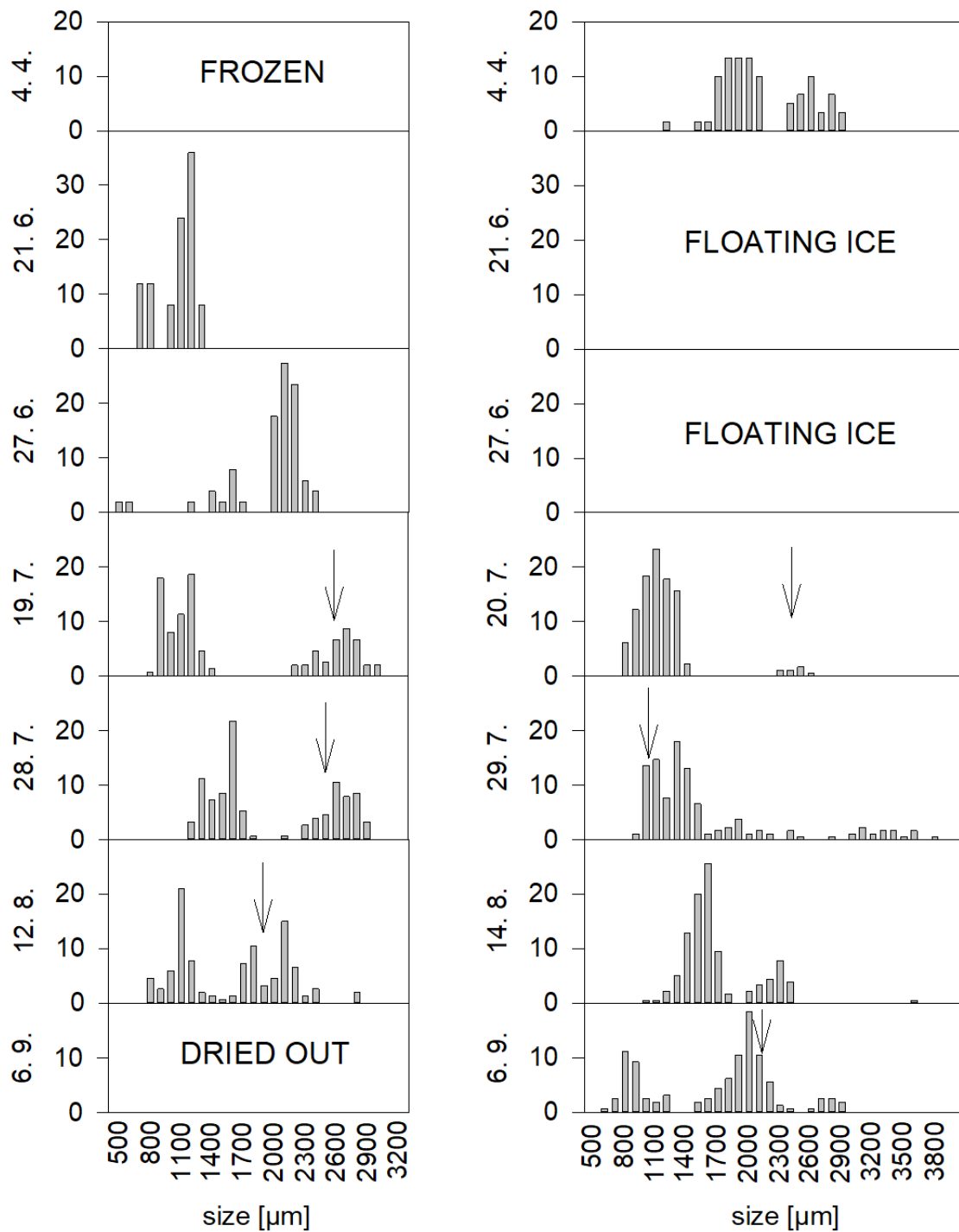


Fig. 4 Comparison of sizes in both lakes throughout the season. Arrows show the youngest fertile individual. Comparison of Ebba (left) and Blue lake (right).

A noticeable pattern is seen in the head:body ratio where the head and abdomen (h and a respectively in Fig. 1) have been measured and compared (Fig. 5). When fitted to linear regression the head:body ratio increases in Ebba during the season significantly ($p < 0.0001$, $R^2 = 0,1274$). In Blue lake, on the other, hand the same ratio significantly declines ($p = 0.03$, $R^2 = 0.01$).

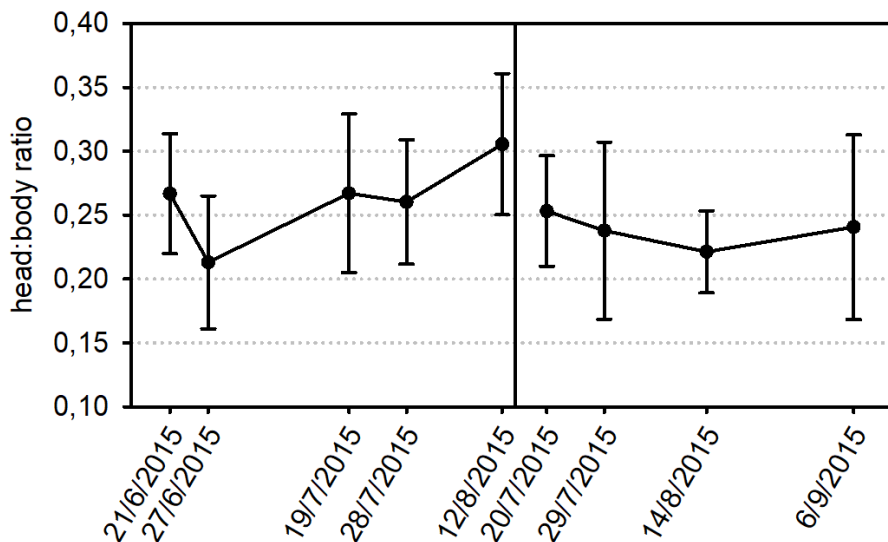


Fig. 5 Comparison of the changes in the head:body ratio in both lakes throughout the season (Ebba on the left, Blue lake on the right). Error bars = SD

3.2 Seasonal dynamics

As Ebba was frozen until May, it is assumed that the number of all the species were zero. At the end of June, *Chydorus*, *Acroperus*, and *Macrothrix* were more or less as abundant as *Daphnia* (Fig. 6). There was also a number of *Lepidurus* at the same time. They were, however, very small, almost the same size as the individuals of *Daphnia* and could not therefore prey on them. In mid-July there was a significant decline in the abundance of *Acroperus* and *Macrothrix* and significant growth in the *Chydorus* population as well as a slight growth in the population of *Daphnia*. At this point, the number of *Lepidurus* in the lake dropped, and their size increased to be 3 times the size of the largest *Daphnia*. By the end of July, the population of *Chydorus* started gradually declining while the population of *Daphnia* dropped significantly. This was probably compensated by the sudden increase of egg ratio as in August the population grew again while *Chydorus* maintained a relatively stable, significantly less abundant population. The other two species decreased rather quickly with *Macrothrix* becoming almost undetectable and *Acroperus* disappearing from the record completely. The record stops in September because the lake dried out.

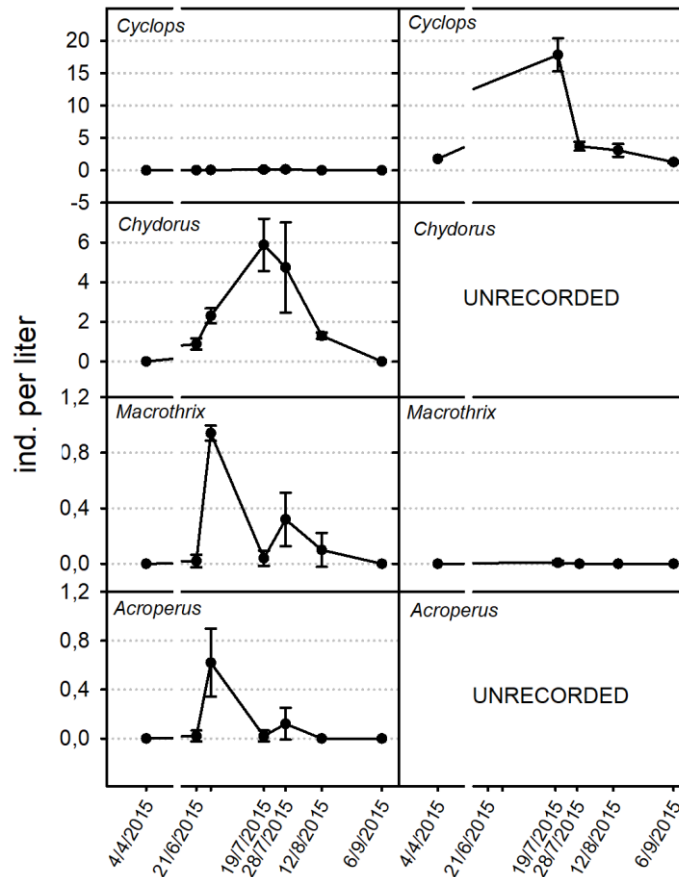


Fig. 6 Abundance of the zooplankton species in both lakes (Ebba left, Blue lake right). Graphs of each species are scaled equally between the lakes. Error bars = SD

Because Blue lake is deeper, the samples could have been collected even in April by drilling a hole in the ice. However, in May and June, the ice partially melted which made the sampling impossible. There were two dominant species with very similar patterns of their seasonal dynamics – *D. middendorffiana* and *Cyclops. sp. X*. Such *Cyclops* belongs to *C. strenuus sensu lato*, but form a unique species which is however not described yet (Fott and Krajiček in prep.). In the second half of July, both species reach their peak, *Daphnia* being the dominant one. By the end of the month, though, both *Daphnia* and *Cyclops* experienced a significant drop in their numbers to less than a half. *Daphnia* responded to this fairly slowly by increasing its egg ratio more than a month later in September.

3.3 Phytoplankton as a food source for zooplankton

Daphnia as the most effective filter-feeder is the most important consumer of phytoplankton. In Ebba lake the abundance of *Daphnia* and *Cyanobacteria* appear to be direct responses to each other (Fig. 7). At the beginning of the season, there is a high abundance of

Cyanobacteria, when *Daphnia* becomes more active, the number of *Cyanobacteria* drops. In the second half of July, there is a significant increase in the number *Daphnia* and at the same time there is a drop in the *Cyanobacteria* abundance. This is quickly followed by a decrease in the *Daphnia* abundance accompanied by the increase in the *Cyanobacteria* abundance. Similar pattern occurs with *Bacillariophyceae*.

There is a similar pattern with other groups of phytoplankton and other species of zooplankton as well. There is a high abundance of *Dinophyta*, *Chrysophyceae*, and *Xanthophyceae* at the beginning of the season (June) followed by a sudden decline when the numbers of *Daphnia*, *Acroperus*, *Chydorus*, and *Macrothrix* start growing. These groups of phytoplankton, however, remain scarce until the end of the season. *Acroperus*, *Chydorus* and *Macrothrix* decline in abundance while the number of *Daphnia* then continues growing. In this period the number of *Daphnia* suddenly drops again while *Chydorus* reaches its peak. *Daphnia* then starts increasing again as *Chlorophyta*, *Streptophyta*, *Chrysophyceae*, *Cryptophyceae*, and *Euglena* become more abundant. In Blue lake almost all groups of phytoplankton mentioned previously were present (except for *Euglena*). However, only *Cyanobacteria* and *Chlorophyta* were present in higher numbers. As mentioned previously, in this lake there were two dominant species of zooplankton – *Daphnia* and *Cyclops*. They both have a very similar dynamic. In April they were present and alive, although they were really scarce. In July there was a peak in both *Daphnia* and *Cyclops* accompanied by a drop in *Cyanobacteria* which were fairly abundant since June. When the zooplankton decreased, there was an increase in *Chlorophyta*.

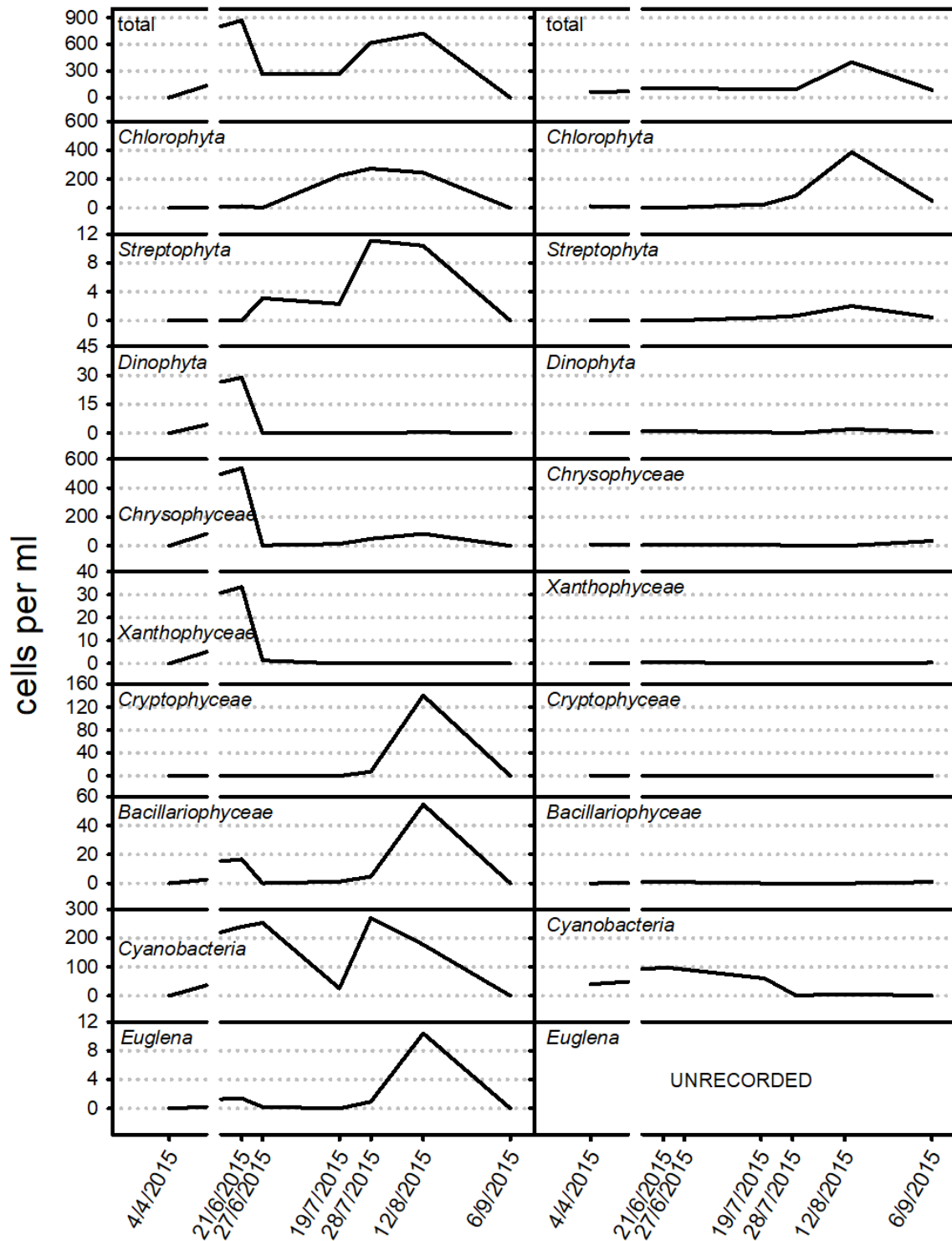


Fig. 7 Phytoplankton abundance in both lakes (Ebba left, Blue lake right). Graphs of each group are scaled equally between the lakes.

4 Discussion

Our results show significant differences between the dynamics of the two studied lakes. Although the zooplankton forms swarms especially in shallow lakes (Freund et al., 2002), repeated sampling evens out the potential irregularities. In both the shallow and the deep lake the dominant species was *Daphnia middendorffiana* even though the dynamics differ as well as the interactions within the aquatic communities which differ as well.

In Ebba, there is almost an equilibrium between the four species of *Cladocerans* at the beginning of the season which changes during the season and the populations become more variable. *Cyclops* appears in this community as well, but it remains scarce and appears unable to reproduce effectively. In Blue lake, on the other hand, *Daphnia* and *Cyclops* share a similar strategy throughout the season. They both have a significant head start compared to their counterparts in Ebba, because there are individuals alive in April already, whereas in Ebba the first generation appears in June. After their peak, they both decline rapidly and continue to do so until the end of the season. *Acroperus* and *Chydorus* were not recorded in this lake at all and *Macrothrix* was extremely rare. The absence of *Acroperus* and *Macrothrix* could be explained by their benthic nature and therefore being more vulnerable to predation by *Lepidurus* as mentioned by Jeppesen et al., (2001). However, the absence of *Chydorus* in this case is against the presumptions made by the same study where it is said that because it is a pelagic species, *Lepidurus* should have a lesser effect on it and it should therefore be more abundant. Nevertheless, there could also be different explanations for its absence such as high competition or lack of suitable nutrition.

In both lakes, the top predator is *Lepidurus arcticus*. At the beginning of the season, it is too small to prey on the zooplankton, but as soon as the individuals mature enough they have a significant impact on the community. It was presumed that in the shallow lake this effect would be stronger while in the deep lake the zooplankton population would not be affected thanks to the benthic nature of *Lepidurus* (Crook & Greenwood, 1978). As it turns out, *Lepidurus* is able to swim several meters into the pelagic zone and could potentially have certain impact on the zooplankton community.

In Ebba, *Daphnia* responds to the sudden rise in predation by increasing its egg ratio (Fig. 4). For most of the season, the individuals produce very little parthenogenetic eggs (less than 0.05), however, when the predator starts hunting the *Daphnia*, their egg ratio rises up to almost 0.20. During the whole season, there were only two sexually produced ephippia found.

This raises a question – when do the *Daphnia* reproduce sexually? They should produce ephippia in order to maintain the population over winter, yet this was not observed. The other species were not observed to produce any eggs, neither parthenogenetic, nor sexual. Palazzo et al., (2008) discuss that *Cladocera* could be forced to produce ephippia in unusual periods because of the stress of the environment. Alekseev & Lampert (2001) also claim that ephippia are usually produced shortly after the algal peak. For this reason, it is possible that the production of ephippia occurred in between our sampling or after. Nevertheless, another possibility is that ephippia were produced after our sampling as the sexual activity can be induced by the shorter photoperiod (Stross, 1969) which in Svalbard occurs after August.

In Blue lake, the egg ratio in *Daphnia* remains below 0.05 throughout almost the whole season, and it is not affected by the predation rate. More than a month after the population starts declining the egg ratio rises up to almost 0.20. However, these are still parthenogenetic eggs, and there were no sexual ephippia observed in this lake. Because the lake does not freeze in its whole volume, it is possible that the zooplankton survives winter via parthenogenesis. It is also possible that the ephippial eggs were produced in between the sampling and could not therefore be recorded as their production might have been induced by the algal peak in spring (Alekseev & Lampert, 2001).

Although the fecundity appears to be influenced by the predation in both lakes similarly, size differs. In Ebba the *Daphnia* reach the maximum of 2900 μm , whereas in Blue lake they grow up to 3800 μm . This seems to contradict the expectations that *Daphnia* would defend itself from the omnipresent predator by increasing its size (Tollrian, 1995). However, this might be influenced by temperature which might affect the ability of *Daphnia* to induce this kind of defence (Hebert, Grewe, & Nov, 2007) as the temperature in both lakes differs significantly. The difference could therefore be caused by *Lepidurus* killing off the largest individuals. There could also be a certain correlation between higher mortality of *Daphnia* and higher doses of UV light in the shallow lake (Luecke & O'Brien, 1983), or perhaps the UV-induced pigmentation is so energetically demanding that the individuals do not have the energy to grow larger.

There is a significant shift in the head:body ratio of *Daphnia* in both lakes. Interestingly in each lake, the dependence is different, but in both lakes it is significant. While in Ebba the ratio increases further into the season, in Blue lake the ratio decreases. According to Pijanowska (1990) the ratio should be stable throughout the life of each individual and it should vary between generations. This is contradicted by Hanazato & Ooi (1992) who found that the size

of the so-called helmet varies between each instar of an individual when exposed to a predator. In the present study, however, it is only the head:body ratio, not the shape of the head. No helmets were found. Dodson (1989) found a similar dependence where the head:body ratio increased in the presence of an invertebrate predator. None of these studies, however, offer any explanation of the declining head:body ratio in Blue lake where it should be stable. This phenomenon could be explained by a different abiotic attribute, e.g. temperature (Tollrian, 1990).

In Ebba, there is an apparent connection between the period of the presence of *Lepidurus* and the size (age) when *Daphnia* produce their first parthenogenetic eggs. The longer the *Lepidurus* appears in the record, the progressively smaller the *Daphnia* producing their first egg appears – at the beginning it is 2500 μm , at the end it is 1840 μm . This is in line with the findings of Boersma, De Meester, & Spaak (1999) who claim that *Daphnia magna* tends to produce fewer parthenogenetic eggs at smaller sizes. In Blue lake, on the other hand, this connection is not so obvious as the size of smallest *Daphnia* drops significantly from 2420 μm to 1040 μm only to rise up to 2060 μm . This might unfortunately be caused by imperfect fixation as in most cases there were freely floating eggs and no eggs in *Daphnia* themselves in our samples. This is also the reason it was impossible to model the fecundity of individual cohorts.

A very interesting pattern appears to be in the phytoplankton/zooplankton relationship. In both lakes it seems that certain groups of phytoplankton are quite abundant at the beginning of the season when zooplankton is rather scarce. As soon as zooplankton reaches certain abundance, phytoplankton drops probably being grazed by the zooplankton. Then the zooplankton drops as well. Interestingly, this also coincides with the increased predation and it cannot therefore be decided whether the drop in zooplankton is caused by the drop in phytoplankton (bottom-up), by the increase in predation (top-down) or the combination of both. It can be, however, inferred that the drop in phytoplankton is caused by the increase in zooplankton. The removal of certain phytoplankton groups leaves a vacant niche which is gradually filled by other groups. This is very similar in both lakes, they only differ in the zooplankton species and the phytoplankton groups involved.

Interestingly, our data show that there might be a certain connection between the abundance of *Cyclops* and the present species of *Rotifera*. In Ebba, *Cyclops* is probably outcompeted by the *Cladocerans* as it is really rare throughout the season. In this lake both *Notholca* and *Polyarthra* are present, *Notholca* reaches its peak in July, *Polyarthra* in August. In Blue lake,

on the other hand, *Cyclops* is the second dominant species. Coincidentally, *Polyarthra* is not found at all in this lake and *Notholca* is proven to be present, but in really small numbers. This shows that *Cyclops* might be the main driver in the *Rotifera* distribution (Devetter & Sed'a, 2006; Sarma, Nandini, & Dumont, 1998).

The correlation to the abiotic factors is far less obvious. The abundance of *Daphnia* in Ebba seems to be correlated with the temperature (Burns, 1969). This is not true in Blue lake. The rising concentration of phosphorus might be the reason why *Daphnia* in Ebba recovers from the predation-induced drop rather quickly as opposed to in Blue lake where the phosphorus levels stayed relatively low the whole season and *Daphnia* does not recover from the drop at all. This might be caused by the high dependence of *Daphnia* on phosphorus (Hessen & Rukke, 2000) which could be a stronger factor than temperature.

In conclusion, we have shown that there are differences in the population dynamics of the deep and the shallow lake such as different species composition both in zooplankton and phytoplankton, varying abiotic factors or the extent of ecological interactions like predation. The morphological response of *Daphnia middendorffiana* in both lakes differs significantly. However, there are also similarities in the interspecies and trophic interactions such as high competition and lack of nutrition. This paper should serve as a starting point for further and more thorough research as well as contribute to our knowledge of the Arctic ecosystems.

Acknowledgements

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