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The effect of salinity on the grazing rate and survival of *Daphnia magna* females adapted to different salinities

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Abstract The cladoceran *Daphnia magna* inhabits lakes with salinities up to 10 g L^{-1}. We compared the effects of different salinities (up to 9 g L^{-1}) on the survival, specific grazing rate, and size selective feeding of *Daphnia* females adapted to fresh or saline waters (3–4 g L^{-1}). The freshwater population was more sensitive to high salinity (LC_{50} = 5.3 g L^{-1}), while the survival of the saline water population also decreased in fresh water. Freshwater population demonstrated a higher grazing rate in fresh water, while the saline water population had a higher grazing rate at the salinity above 3 g L^{-1}. A decrease in the grazing rate of the freshwater population was observed at the salinity above 4–5 g L^{-1}. Populations differed in food selectivity. The saline water population consumed particles of larger sizes than the freshwater population. The average size of phytoplankton particles grazed in fresh water was larger than in saline water. This size selective salinity-dependent grazing may be related to the dependence of the feeding efficiency of cladocerans on the viscosity of water and size of phytoplankton particles. Our results indicate that *Daphnia* populations adapted to a certain salinity can temporarily lose the ability to control phytoplankton because of salinity fluctuations.

Keywords Salinity · Grazing · Phytoplankton · Adaptation · *Daphnia*

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Introduction

Zooplankton play an important role in the functioning of aquatic ecosystems. They act as keystone grazers on phytoplankton and transfer energy to higher food web consumers (summarized by Sterner 2009). Zooplankton are able to control both the abundance and species composition of phytoplankton (e.g., Lampert et al. 1986; Levine et al. 1999). By grazing on phytoplankton, zooplankton restrain harmful algal blooms and control the transparency and quality of water (Jeppesen et al. 1999; Gerasimova and Pogozhev 2010; Plooy et al. 2017). However, by the selective feeding on certain species of phytoplankton, zooplankton can stimulate the development of toxic cyanobacteria

(Mitra and Flynn 2006; Leitao et al. 2018; Ger et al. 2019) or filamentous algae (Kasprzak and Lathrop 1997; Hambright et al. 2001), which can impair water quality.

Cladoceran *Daphnia magna* Straus is a large-bodied representative of zooplankton, which is often considered as a model organism in aquatic ecology (reviewed by Lampert 2006). Numerous studies have been carried out to investigate its feeding behavior as dependent on various factors (e.g., McMahon 1965; Watts and Young 1980) and its ability to control the phytoplankton communities differing in their composition and abundance (e.g., Dawidowicz 1990; Degans and De Meester 2002). In general, this large filter feeder is able to efficiently consume food of different sizes (e.g., Gophen and Geller 1984).

The feeding rate of zooplankton depends on many factors. The rate and the efficiency of filtration are influenced by temperature (Burns 1969), abundance, and size of food (Frost 1972), chemical composition of the medium (Lari et al. 2018), physiological state of the organism, and morphological characteristics of different populations (Stuchlík 1991; McKee 1995; Wagner and Kamjunke 2001). Salinity is one of physiologically important factors that also may affect feeding rates. The freshwater salinization due to natural and anthropogenic drivers is a worldwide problem (Dugan et al. 2017; Cañedo-Argüelles 2020). Large salinity fluctuations can cause changes in the zooplankton community associated with species composition (Gutierrez et al. 2018). Small changes of salinity may have no effect on species composition but will affect the physiology of animals, including their swimming and grazing rates (Baillieul et al. 1998).

Daphnia magna is able to survive in lakes with salinities up to 9–10 g L^{-1} (Zadereev et al. 2021b). Previous studies demonstrated that survival of *D. magna* populations adapted to specific salinity is constrained at lower or higher salinities (Arnér and Koivisto 1993). Research demonstrates that populations of *D. magna* adapted to salinity show reduced survival, growth, and reproduction in fresh water, while some clones of freshwater populations can be relatively successful in saline water (Teschner 1995).

Large-bodied zooplankton species such as *D. magna*, due to their ability to consume food of different sizes, are often considered as bioengineers that determine water quality (Degans and De Meester 2002). Thus, it is important to understand the effect of salinity on the grazing of these species. Previously, it was shown that salinity affects the swimming velocity of *D. magna* (Baillieul et al. 1998). Changes in locomotor activity can affect the feeding rate. Salinity also changes the viscosity of water, which can affect the interaction of food particles with the animals' filter screen. If the grazing by large filter feeders is one of the mechanisms to control water clarity, the negative effect of salinity on the grazing efficiency may induce the deterioration of the water quality.

Few studies are available on the effect of salinity on the grazing activity of *Daphnia*. Moreover, it is not clear whether the populations of *D. magna* adapted to various salinities differ in their grazing activity. The answers to these questions are critically important to understand the ecological effect of salinity on interactions between phyto- and zooplankton. The aim of our study was to examine in laboratory experiments the grazing activity of two *D. magna* populations differing in their salinity tolerance to the effects of various salinities. We performed a grazing experiment with water from lakes with different salinities and either standard green unicellular algae or a natural phytoplankton sample as food. We also conducted acute survival tests to assess the salinity tolerance of two *D. magna* populations pre-adapted to different salinities. We tested the following assumptions: 1) *D. magna* population adapted to moderate salinity will have higher salinity thresholds for survival than freshwater population; 2) populations of *D. magna* will show maximum feeding rates at the salinities that they have been adapted to; 3) *D.magna* will exhibit size selective feeding at different salinities.

Materials and methods

General information

We used two *Daphnia magna* populations inhabiting the same region but adapted to different salinities. Individuals of the *Daphnia*_kras population were isolated about ten years ago from Lake Krasnenkoye (54.445164°, 90.337008°, average long-term salinity 1.0–1.5 g L^{-1} (Zadereev et al. 2021b)). Since then, animals have been successfully grown in the laboratory of the Institute of Biophysics SB RAS in aged tap water (pH–7.3; total permanent hardness—62.9 mg equivalent of $CaCO_3$ L^{-1}; total content of cations (macro- and trace elements)—26.4 mg L^{-1}) with the unicellular green alga *Chlorella vulgaris* Beije as food. Samples of diverse individuals of the *Daphnia*_ut population were collected with plankton net vertical tow from Lake Utichie 3 (54.512453°, 90.463401°, average long-term salinity 3–5 g L^{-1} (Zadereev et al. 2021b)) one week before the start of experiments (June, 2020) and were kept in the lake water with the unicellular green alga *Chlorella vulgaris* as food.

Two days before the experiment, randomly selected animals from both populations were transferred into a culture medium with the non-axenic green alga *C. vulgaris* at a concentration of 200 thousand cells mL^{-1}. The culture medium volume was 20 mL per animal. Tap water aged for at least 72 h was used as a medium for the individuals of *Daphnia*_kras population, and water from Lake Utichie 3 was used as a medium for the individuals of *Daphnia*_ut population.

The grazing experiments were carried out in 50-mL vessels. Two hours before the experiment, animals were placed in a similar volume of the treatment medium filtered through a GF/F filter (Whatman). To start the experiment, the animals (15 adult *Daphnia* of the same body size per vessel) were placed into the treatment vessels. The control vessels were kept without animals.

After 5 h of grazing, the water was removed from the control and treatment vessels, and the size and fluorescence characteristics of phytoplankton were measured. The body length (L, mm) of animals from each vessel was measured under 16 × magnification. The dry weight (DW, µg) was calculated as $DW = L^{2.917} \cdot 0.094$ (Gutelmakher 1986).

Grazing on the unicellular green alga Chlorella vulgaris at different salinities (Experiment 1)

We used aged tap water mixed with the water from Lake Jirim (54.810638°, 90.429847°, average long-term salinity 6–10 g L^{-1} (Zadereev et al. 2021b)) and water from Lake Utichie 3 to create treatment media of different salinities. To remove natural phytoplankton, the lake water was filtered through GF/F filter (Whatman) before being mixed with tap water. All treatment media were aged at 23 °C for 24 h prior to the grazing experiment.

The following treatment media of different salinities were used in the experiment: tap water (salinity 0.09 g L^{-1}); tap water mixed with Lake Jirim water, 7:1 (salinity 1.0 g L^{-1}), 3:1 (salinity 1.8 g L^{-1}), 1:1 (salinity 3.5 g L^{-1}), and 1:3 (salinity 5.1 g L^{-1}); and Lake Utichie 3 water (salinity 3.1 g L^{-1}). Hereinafter, salinity refers to the total dissolved salts (TDS, g L^{-1}), calculated automatically by YSI Exo probe (YSI Inc., U.S.A.) based on measurements of the specific electrical conductivity of water.

Unicellular green alga *C. vulgaris* was used as food in this experiment. We tested two food concentrations: 280 thousand cells mL^{-1} and 430 thousand cells mL^{-1} (ca. 3.2 and 4.8 µg C mL^{-1}). Experiments with each treatment medium and with each food concentration were performed sequentially. For each treatment, 3 control vessels (without animals), 3 test vessels with 15 *Daphnia* _kras, and 3 test vessels with 15 *Daphnia* _ut were maintained at 23 °C in darkness for 5 h. After 5 h of grazing, water was removed from all vessels, and *Chlorella* content in the water from each vessel was measured with a SpectraMax M5 spectrophotometer (Molecular Devices, USA). Measurements were taken at a 470-nm fluorescence excitation wavelength and a 680-nm fluorescence absorption wavelength. These parameters corresponded to the excitation and absorption wavelengths of chlorophyll a fluorescence (Thorne et al. 1977).

In order to assess the effect of the treatment media on the survival of both populations, we performed acute toxicity tests. Twenty one-day-old juvenile females (size 0.8–0.9 mm) were placed individually into 20 mL of each treatment medium without food. Additionally, undiluted Lake Jirim water (salinity 6.5 g L^{-1}) was also tested. After 24 h and 48 h, the number of dead individuals was counted.

Grazing on natural phytoplankton at different salinities (Experiment 2)

We used water from Lake Chaloskol (54.401568°, 90.213695°, average long-term salinity 0.5–1.5 g L^{-1}), Lake Vlasyevo (54.457138°, 90.383218°, average long-term salinity 2.5–3.5 g L^{-1}), Lake Utichie 3 and Lake Bele (54.682150°, 90.228909°, average long-term salinity 8–9 g L^{-1} (Zadereev et al. 2021b)) to create treatment media with different salinities. The lake water was aged at 23 °C for 24 h prior to the grazing experiment.

The following treatments with the native phytoplankton were examined: Lake Chaloskol water (salinity 1 g L^{-1}), Lake Vlasyevo water (salinity 3.2 g L^{-1}), a 1:1 mixture of water from Lakes Vlasyevo and Utichie 3 (salinity 4.1 g L^{-1}), a 1:1 mixture of water from Lakes Bele and Utichie 3 (salinity 7 g L^{-1}), and Lake Bele water (salinity 9.2 g L^{-1}). Experiments with each treatment were performed sequentially. For each treatment, 3 control vessels (without animals), 3 test vessels with 15 *Daphnia* _kras, and 3 test vessels with 15 *Daphnia* _ut were maintained at 23 °C in darkness for 5 h. After 5 h of grazing, water was removed from all vessels, and the size and the spectral characteristics of the phytoplankton community in the water from each vessel were measured.

To determine the size and number of phytoplankton particles in the medium, we used a FlowCam flow cytometer (FluidImaging Inc., USA) with a 50-µm capillary. From each vessel, we took a 0.2 ml sample and ran it through the capillary at a flow rate of 0.04 mL per minute. The measurements were taken in the trigger mode. In the trigger mode, the FlowCam captures images of particles when the fluorescent signal, at least in one of the detection channels, exceeds the threshold (400 nm). The FlowCam was configured with an excitation 532 nm laser and two photodetectors detecting red (wavelength ≥ 650 nm, chlorophyll a) and orange (575 ± 30 nm wavelength, phycoerythrin) fluorescence. The minimal size of captured images of particles was set at 2 µm. With the FlowCam, we analyzed the concentration and volume of particles, the size distribution of particles of different diameters and volumes, the area-based average diameter, and the average particle volume (Zadereev et al. 2021a).

To determine the fluorescence characteristics of phytoplankton, we used a FluoroProbe multichannel fluorimeter (bbe Moldaenke GmbH, Germany). The total concentration of chlorophyll and the proportions of green algae and cyanobacteria in the phytoplankton were estimated; they were automatically determined by the spectrofluorimeter based on fluorescence signals associated with the chlorophyll "a", phycocyanin, and phycoerythrin excitation. The manufacturer calibrations were used. The measurements were taken in a 30-mL quartz cuvette. Each measurement was taken for several minutes. Within that time interval, up to 50 values of fluorescence signals were recorded. The average of those values was used (Zadereev et al. 2021a).

Data analysis

The survivals of *D.magna* females from different populations exposed to similar salinities in the acute toxicity test were compared using the proportion difference test. The LC_{50} values in the acute toxicity test were determined in "drc" package for R (Ritz and Streibig 2005).

To estimate the specific grazing rate, first, we calculated the average carbon content in the dry weight of algae (µg C mL^{-1}, SpectraMax measurements), the chlorophyll "a" concentration (µg Chl "a" L^{-1}, FluoroProbe measurements), and the number or volume of particles (particles mL^{-1} or mm^3 mL^{-1}, FlowCam measurements) in control vessels. Then, this value was subtracted from the corresponding value in a test vessel. The resulting value was divided by the dry weight of animals in the vessel (µg DW) and the volume of the vessel (L) and converted to 24 h. (As the duration of grazing experiments was 5 h, the value was multiplied by 4.8.)

We used previously obtained linear regression to convert fluorescence values of SpectraMax spectrophotometer into *Chlorella* cells mL^{-1} values. The number of chlorella cells was transformed into carbon units (1) by converting the number of cells into dry weight (dry weight of 1 million chlorella cells is equal to 0.0224 mg (Hu, 2014)) and (2) assuming that the carbon content of dry weight is equal to 50% (Mahlmann et al. 2008).

To assess the impact of the tested factors (Experiment 1: food concentration (2 concentrations), salinity (6 treatments), population (2 populations); Experiment 2: medium (5 types of media with different salinity and phytoplankton), population (2 populations)) on the specific grazing rate, we used three-way (Experiment 1) or two-way (Experiment 2) analysis of variance (Factorial ANOVA).

Changes in the average particle diameter, proportions of green algae and cyanobacteria in the control and test vessels after *Daphnia* grazing were assessed with two-way ANOVA (factors: medium (5 types of media with different salinity and phytoplankton), impact (3 types of impacts—control and two populations)).

In the experiment with natural phytoplankton, we calculated the average proportion of particles of different diameters (12 diameter classes in the range of diameters from 2 to 50 µm with a step of 4 µm) in control vessels. Then, the difference between the proportions of particles of each diameter class in the test and control vessels was determined: negative values characterized a decrease in the proportion of particles of a diameter class after grazing, positive values — an increase in the proportion of particles of a diameter class after grazing. Two-way analysis of variance (factors: diameter (12 size classes) and population (2 populations)) was used to estimate the effect of grazing on size distribution of particles.

We also estimated the correlations between the concentrations of chlorophyll "a" measured with FluoroProbe and the concentration of particles measured with FlowCam. All statistical calculations were performed in STATISTICA 7.0.

Results

Acute test

We observed salinity related differences in the survival of animals of two *D. magna* populations in acute toxicity tests (Table 1, Fig. 1). After 24 h of the acute test, all animals of the *Daphnia*_kras population died in water of 6.5 g L^{-1} salinity. Animals of the *Daphnia*_ut population tolerated salinity better, as at the end of the 24-h acute test, 20% of the animals were alive in the medium with the salinity of 6.5 g L^{-1}, and after 48 h, 10% of the animals survived. At the same time, the survival of animals from the *Daphnia*_ut population sharply decreased in fresh water. After 48 h of the acute test, only 40% of the animals were alive in that medium (Fig. 1).

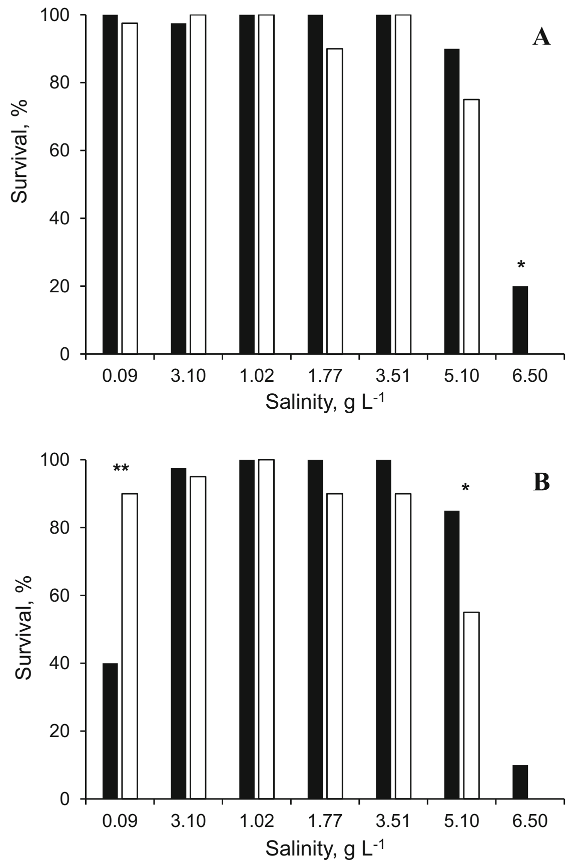

Fig. 1 Survival of *D.magna* females from populations adapted to saline water (black bars) or to fresh water (white bars) in water media of different salinities in acute 24-h (**A**) and 48-h (**B**) tests. *the difference in survival between populations is significant at $p < 0.05$, **at $p < 0.0001$ (proportions difference test)

Grazing on the unicellular green algae Chlorella vulgaris at different salinities (Experiment 1)

The specific grazing rate of *Daphnia* strongly depended on the salinity, food concentration,

Table 1 Salinity producing a 50% mortality (LC_{50}) of *Daphnia magna* females in 24 h and 48 h acute toxicity tests

		LC_{50}, g L^{-1}	SE	*t*-value	*p*-value
Daphnia_kras population	24 h	5.35	0.18	30.23	< 0.0001
	48 h	5.17	0.16	31.79	< 0.0001
Daphnia_ut population	24 h	5.93	0.03	212.69	< 0.0001
	48 h	6.26	NA	NA	NA

Table 2 The results of factorial ANOVA for the effects of salinity, food concentration, and adaptation of animals to saline water (population) on the specific grazing rate of *D. magna*

Factor	df	F	P
Population	1	10	0.003
Salinity	5	39.8	<0.000
Food concentration	1	339.1	<0.000
Population*Salinity	5	16.8	<0.000
Population*Food concentration	1	2.1	0.154
Salinity*Food concentration	5	11.7	<0.000
Population*Salinity*Food concentration	5	3.3	0.013

population, and several interactions between these factors (Table 2).

The average specific grazing rate of animals from the *Daphnia*_ut population (1.28 ± 0.02 μgC μgDW^{-1} day^{-1}) was higher than that of animals from the *Daphnia*_kras population (1.21 ± 0.02 μgC μgDW^{-1} day^{-1}). The specific grazing rate at the food concentration of 4.8 μgC mL^{-1} was higher (1.46 ± 0.02 μgC μgDW^{-1} day^{-1}) than at the food concentration of 3.2 μg C mL^{-1} (1.03 ± 0.02 μgC μgDW^{-1} day^{-1}).

Salinity significantly affected specific grazing rate, which decreased almost linearly with an increase in salinity. The maximum specific grazing rate was observed in fresh water (1.46 ± 0.03 μgC μgDW^{-1} day^{-1}) and the minimum—in water with the salinity of 5.1 gL^{-1} (0.98 ± 0.03 μgC μgDW^{-1} day^{-1}).

The interaction between the effect of salinity and population resulted in the higher specific grazing rate of the *Daphnia*_ut population compared with the *Daphnia*_kras population at high salinities. The interaction between salinity and food concentration resulted in a stronger effect of salinity on the specific grazing rates at higher food concentration.

The interaction between three studied factors (Fig. 2) was also significant. The highest specific grazing rate (1.91 ± 0.06 μgC μgDW^{-1} day^{-1}) was demonstrated by animals from the *Daphnia*_kras population under high food supply in fresh water. The lowest specific grazing rate (0.71 ± 0.06 μgC μgDW^{-1} day^{-1}) was also demonstrated by animals from the *Daphnia*_kras population at low food supply in water of the highest salinity. The specific grazing rate of animals from the *Daphnia*_ut population in

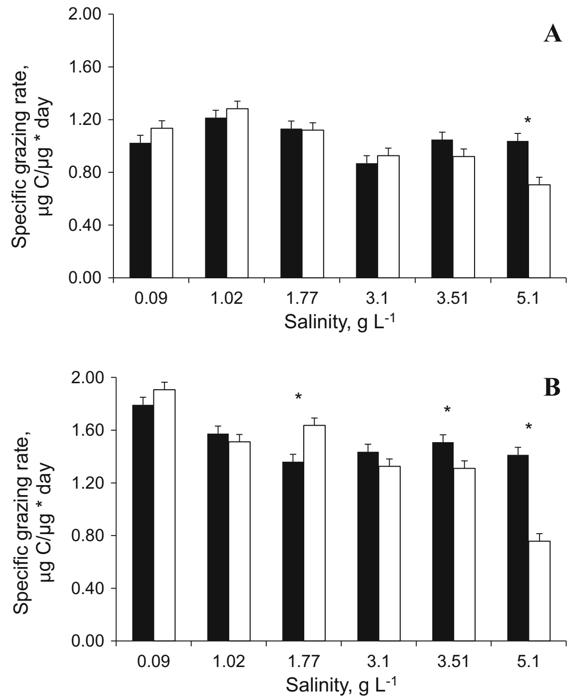

Fig. 2 Specific grazing rate of *D.magna* females from populations adapted to saline water (black bars) or to fresh water (white bars) in water media of different salinities with *C.vulgaris* as food. **A** food supply 3.2 μg C mL^{-1}, **B** food supply 4.8 μg C mL^{-1}. *the difference in specific grazing rate between populations is significant at $p < 0.01$ (post hoc LSD test)

fresh water was lower than that of animals from the *Daphnia*_kras population, but that difference was not significant. The specific grazing rate of animals from the *Daphnia*_kras population sharply decreased at high salinity (Fig. 2).

Grazing on natural phytoplankton at different salinities (Experiment 2)

Treatment media that we used in grazing experiments differed in salinity and abundance, size structure, and species composition of phytoplankton community (Table 3, Fig. 3). The highest abundance of phytoplankton particles dominated by the large cyanobacteria was observed in the water with the lowest salinity from Lake Chaloskol. The highest concentration of chlorophyll “a”, with the colonies of green algae dominating the phytoplankton, was observed in the water from Lake Vlasyevo. The most saline water from Lake Bele was characterized by phytoplankton dominated by cyanobacteria with both a relatively

Table 3 The characteristics of water from different lakes used in experiments

Lake	Water salinity, g L^{-1}	Abundance of phytoplankton particles, cells mL^{-1}	Average particle diameter, μm	Chlorophyll concentration, μg Chl "a" L^{-1}	Ratio of green algae to cyanobacteria
Chaloskol	1	50,181 ± 2054	4.36 ± 0.06	20.9 ± 0.6	0.39 ± 0.02
Vlasyevo	3.2	40,644 ± 2009	4.65 ± 0.09	33.3 ± 1.8	1.60 ± 0.23
Vlasyevo:Utichye	4.1	34,100 ± 1813	3.75 ± 0.03	14.6 ± 0.5	1.66 ± 0.07
Bele:Utichye	7	12,766 ± 2280	3.89 ± 0.15	1.3 ± 0.1	0.86 ± 0.05
Bele	9.2	21,959 ± 408	3.87 ± 0.11	4.3 ± 0.1	0.47 ± 0.02

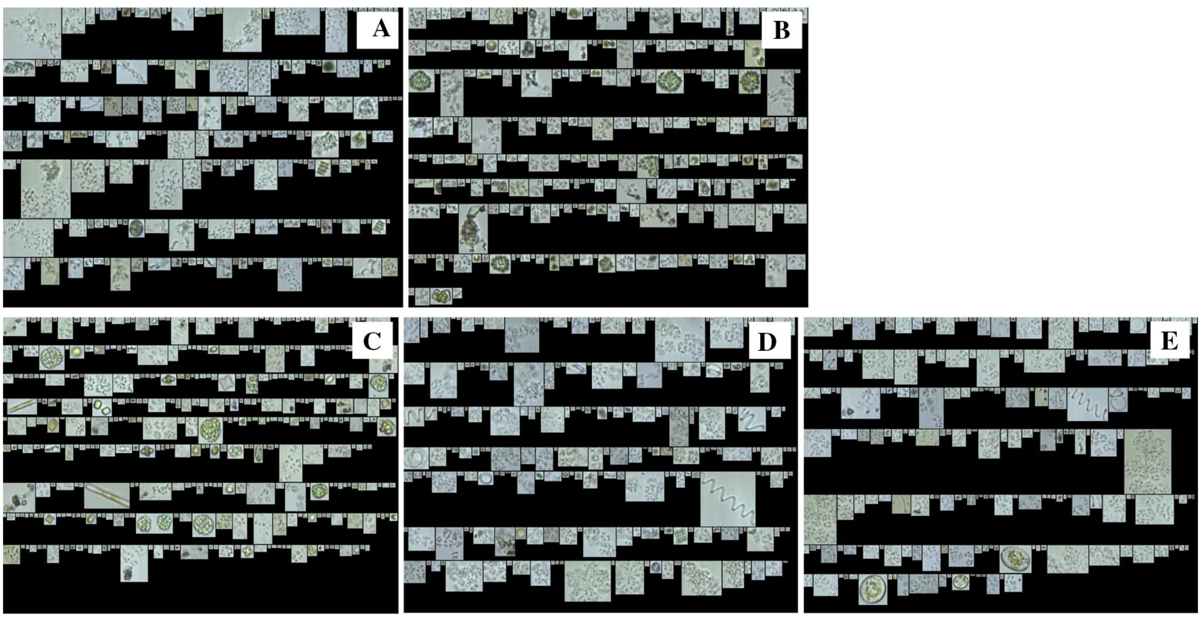

Fig. 3 An example of images of phytoplankton in the water from different lakes used in grazing experiments. Images were obtained in the trigger mode with the FlowCam flow cytometer. **A** water from Lake Chaloskol, **B** water from Lake Vlasyevo, **C** 1:1 mixture of water from Lakes Vlasyevo and Utichie 3, **D** 1:1 mixture of water from Lakes Bele and Utichie 3, **E** water from lake Bele

small number of particles and low chlorophyll "a" concentration. The water from these lakes mixed with the water from Lake Utichie 3 showed decreased abundance of phytoplankton and a change of salinity (Table 3).

We observed the difference between grazing rates and grazing selectivity of two *Daphnia* populations when using FlowCam to estimate the size characteristics and abundance of phytoplankton particles in treatment media.

The highest specific grazing rate of animals from the *Daphnia*_kras population was observed at the lowest salinity and the highest abundance of phytoplankton particles (Fig. 4). With the increase in salinity, the grazing rate of animals from the *Daphnia*_kras population decreased. By contrast, the specific grazing rate of animals from the *Daphnia*_ut population was the lowest at the minimal salinity. The grazing rate of animals from the *Daphnia*_ut population increased with the increase in salinity and was maximal at the salinity corresponding to the habitat of this population (Lake Utichie 3).

We observed changes in the average diameter of phytoplankton particles caused by *Daphnia* grazing (Fig. 5). The effect of the *Daphnia*_kras population on the size characteristics of phytoplankton (significant

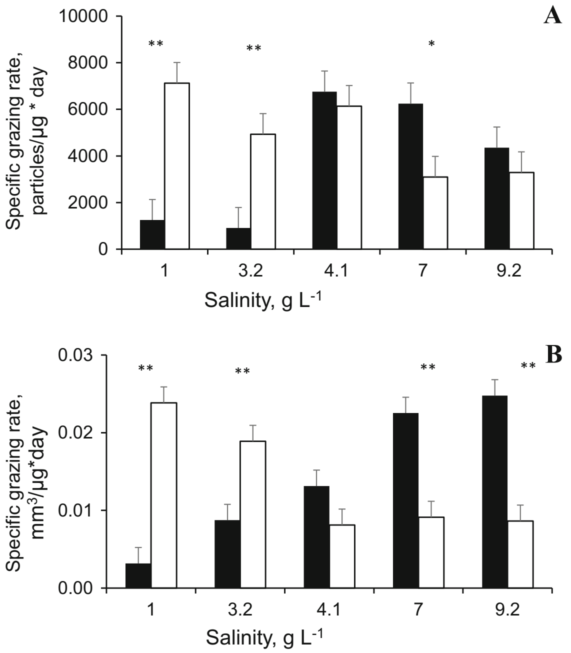

Fig. 4 Specific grazing rate of *D.magna* females from populations adapted to saline water (black bars) or to fresh water (white bars) in the water from different lakes with natural phytoplankton as food (details on the phytoplankton composition are in Table 3). **A** grazing rate expressed as daily consumption of phytoplankton particles per unit of *Daphnia* biomass, **B** grazing rate expressed as daily consumption of the volume of phytoplankton particles per unit of *Daphnia* biomass. **the difference in specific grazing rates between populations is significant at $p < 0.01$, *at $p < 0.05$ (post hoc LSD test)

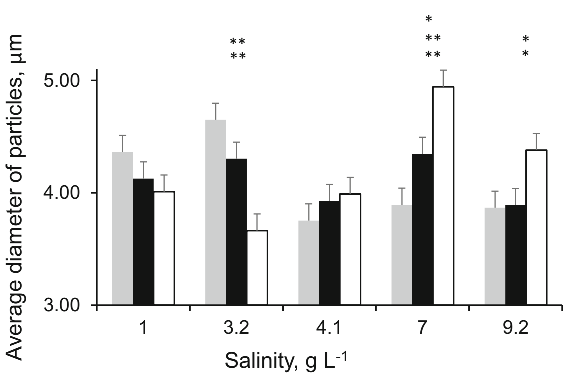

Fig. 5 Average diameter of phytoplankton particles in control vessels (gray bars) and treatment vessels with animals from the populations adapted to saline water (black bars) or to fresh water (white bars). *differences between average diameters are significant at $p < 0.05$, **t $p < 0.01$. The upper row of symbols is the difference between the control and the *Daphnia*_ut population, the middle row is the difference between the control and the *Daphnia*_kras population, and the lower row is the difference between the two *Daphnia* populations

differences in the average particle diameter between the control and three treatments) was more pronounced than that of the *Daphnia*_ut population (a significant difference between the control and one treatment).

We analyzed changes in the proportions of phytoplankton particles of different diameters in different treatments to characterize grazing selectivity of animals (Fig. 6). In the treatment with water from Lake Chaloskol, animals of both populations similarly ($p = 0.497$, ANOVA) consumed particles in the size

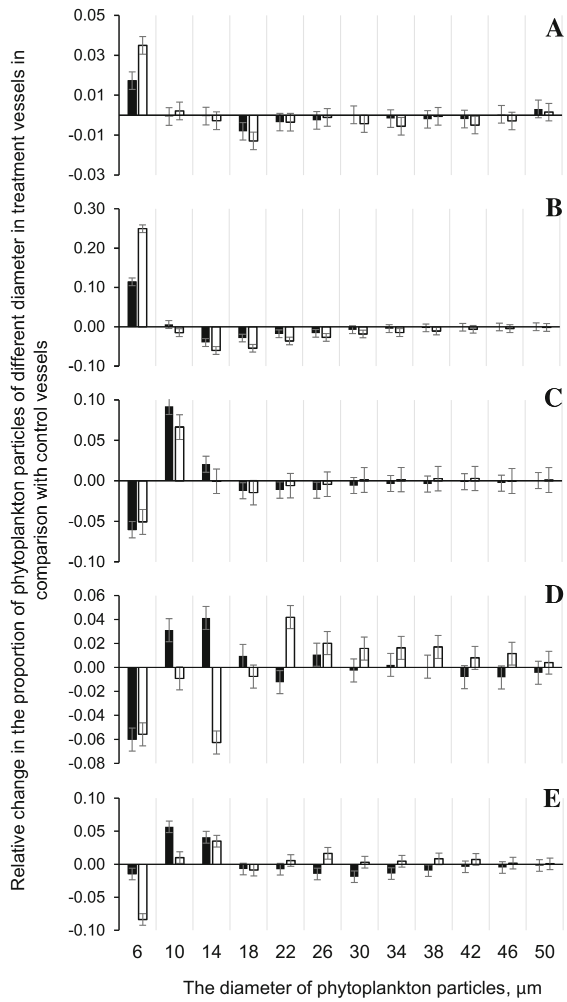

Fig. 6 The change in the proportion of phytoplankton particles of different diameters in the feeding experiment with *D.magna* females from populations adapted to saline water (black bars) or to fresh water (white bars). **A** water from Lake Chaloskol, **B** water from Lake Vlasyevo, **C** 1:1 mixture of water from Lakes Vlasyevo and Utichie 3, **D** 1:1 mixture of water from Lakes Bele and Utichie 3, **E** water from Lake Bele

range of 14–18 µm. In the treatment with water from Lake Vlasyevo, the significant difference in grazing selectivity of populations ($p < 0.0001$, ANOVA) was due to the wider range of particles consumed by the *Daphnia*_kras population (10–30 µm). There was no difference between two populations ($p = 0.987$, ANOVA) in grazing selectivity in mixed waters from Lakes Vlasyevo and Utichye. In that treatment, both populations primarily consumed particles in the size range of 2–6 µm. In the treatment with mixed waters from Lakes Bele and Utichie 3, the two populations had different grazing selectivity ($p < 0.0001$, ANOVA). The *Daphnia*_kras population consumed particles in the size range of 2–18 µm, while the *Daphnia*_ut population predominantly consumed small particles (2–6 µm). In the treatment with water from Lake Bele, the *Daphnia*_kras population consumed small particles (2–6 µm), while the *Daphnia*_ut population consumed both small (2–6 µm) and large particles (22–34 µm). This difference in grazing selectivity was significant ($p < 0.0001$, ANOVA).

We did not observe any difference between grazing rates of two *Daphnia* populations ($p > 0.05$, ANOVA) when using FluoroProbe to estimate the phytoplankton abundance by the chlorophyll "a" fluorescence (Fig. 7). The effect of treatment (water from lakes of different salinities with different phytoplankton communities) on the specific grazing rate was significant ($p < 0.001$, ANOVA). The maximal grazing rate for both populations was observed in the treatments with salinity of 3–4 g L^{-1} (Fig. 7) and the phytoplankton dominated by green algae (Table 3). The grazing rate of *Daphnia* was lower in treatments with the phytoplankton dominated by cyanobacteria. Besides, we did not find any difference between proportions of green algae and cyanobacteria in the phytoplankton community in the control and treatment vessels ($p > 0.05$, ANOVA) (Fig. 8).

Strong linear regression ($p < 0.001$, correlation analysis) (Fig. 9) was observed between the content of chlorophyll "a" in the control and treatment vessels measured with FluoroProbe and the abundance and volume of phytoplankton particles measured with FlowCam.

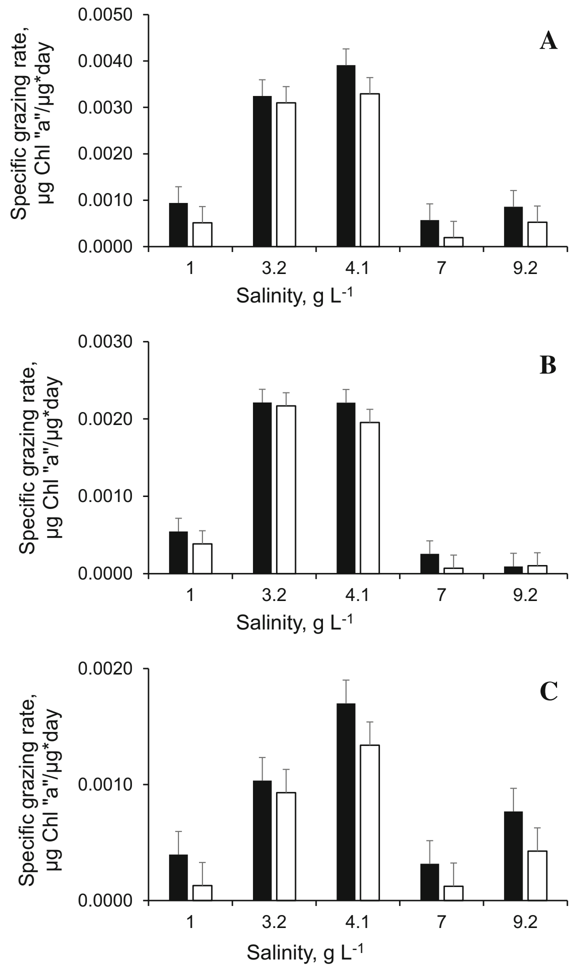

Fig. 7 Specific grazing rate expressed in units of chlorophyll "a" of *D.magna* females from populations adapted to saline water (black bars) or to fresh water (white bars) in the water from different lakes with natural phytoplankton as food. **A** total phytoplankton, **B** green algae, **C** cyanobacteria

Discussion

Daphnia magna is a widespread freshwater animal, which is found in habitats with a wide range of salinities (up to 10 g L^{-1}) (Lagerspetz 1955; Teschner 1995). In our study, we used two *D. magna* populations adapted to different salinities. These populations originally inhabited the same region. The *Daphnia*_kras population individuals were collected in Lake Krasnenkoye located 10 km away from Lake Utichie 3. These animals were kept in the laboratory in 10-L vessels in fresh water for several years, so we could expect strong selection toward freshwater tolerant clones (or clone) in this population.

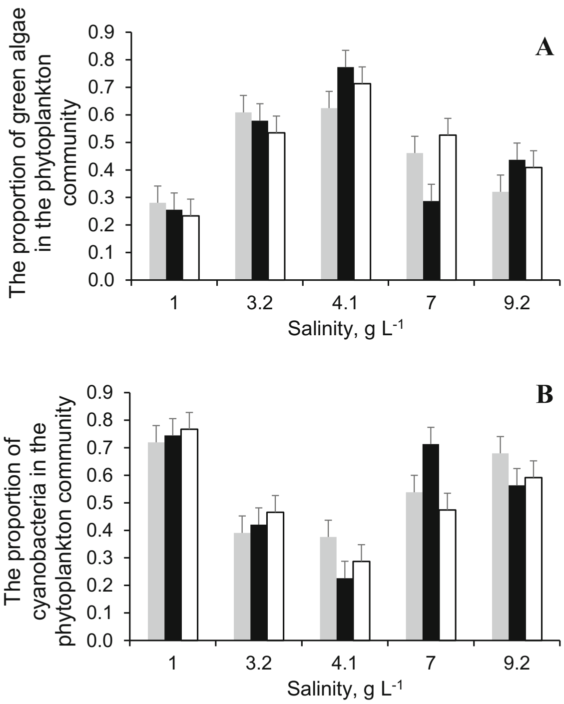

Fig. 8 Proportions of green algae (**A**) and cyanobacteria (**B**) in the phytoplankton community in the control vessels (gray bars), and in the treatment vessels with animals from *Daphnia*_ut (black bars) or *Daphnia*_kras (white bars) populations

*Daphnia*_ut population individuals were collected by vertical tow in Lake Utichie 3 one week before the experiment. As we collected animals in early June, that is about one month after ice melt, we could expect that the sample contained genetically diverse animals adapted to saline water. Salinity is a strong selection factor, which imposes stress on osmoregulation system and limits the survival of freshwater zooplankton at critical salinity, above ca. 8–10 g L^{-1} (Khlebovich 1974). Thus, we have strong evidence that in our experiments we used animals of *Daphnia magna* from the less genetically diverse *Daphnia*_kras population and the genetically diverse *Daphnia*_ut population that were adapted to different salinities. Consequently, the observed differences in grazing rate and survival of animals at different salinities are not related to variation among clones but are linked to the salinity background of the populations.

In accordance with our first hypothesis, the two populations differed in their tolerance to salinity. *Daphnia*_kras population animals were more sensitive to high salinity. At the same time, lethal effects on *Daphnia*_ut population animals were observed in fresh water. This result confirms the assumption that in natural habitats, *D. magna* can relatively easily adapt to increased salinity. However, with the increase in salinity, the population may lose its adaptability to freshwater conditions (Teschner 1995). The first hypothesis is certainly not obvious. The effect of salinity on survival and fitness of freshwater animals is not linear. For many freshwater species, there is a critical salinity above which they will die (Khlebovich 1974). Animals of particular species can be adapted to moderate (below critical) salinity but they will also die at critical salinity. In our experiments, we used *Daphnia* females adapted to fresh water and moderately saline water (3–4 g L^{-1}). It was not obvious that they will not die at similar critical salinity. Indeed, the

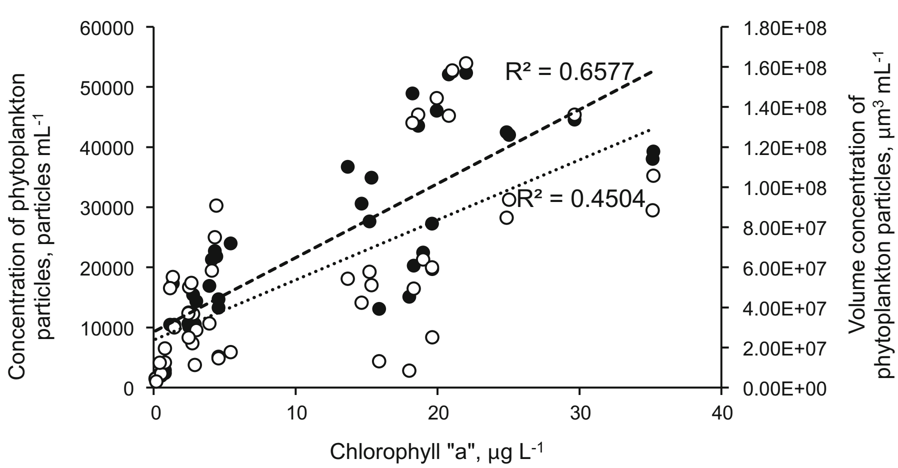

Fig. 9 Correlation between the chlorophyll "a" content in control and treatment vessels measured with FluoroProbe and concentration (black dots) and volume (white dots) of phytoplankton particles measured with FlowCam

difference in LC_{50} between animals adapted to fresh water or moderately saline water was not strong. Moreover, at the salinity equal to 3–4 g L^{-1}, the survival of adapted and non-adapted females was comparable, suggesting that there is critical salinity above which *Daphnia magna* females will die irrespective of pre-adaptation to salinity, and the effect of salinity is not linear but stepwise. Previously we obtained similar results with *Moina macrocopa* females, when abrupt decline of survival was observed above critical salinity equal to 6 g L^{-1} (Lopatina et al. 2021).

The salinity tolerance of freshwater zooplankton animals depends not only on the total amount of dissolved salts but also on their ionic composition (e.g., Derry et al. 2003). In laboratory studies, NaCl is the most often used salt to create media with different salinities. For example, assessing the sensitivity of the *D. magna* freshwater population to changes in NaCl concentration, Martínez-Jerónimo and Martínez-Jerónimo (2007) found that the value of sublethal salinity was equal to 5.48 g L^{-1} and observed the reproduction of some individuals from freshwater population at a salinity of 7 g L^{-1}. In our experiments, to create a salinity gradient, we used water from Lake Jirim. This lake is located in the same region as the lakes that were habitats for experimental *Daphnia* populations. In the acute test, we observed that in the water from Lake Jirim, at the salinity of 6.1 g L^{-1}, all animals from the freshwater *Daphnia* population died. This lake has an extremely poor zooplankton community consisting of one copepod species, one amphipod species, and several species of rotifers (Zadereev et al. 2021b). Obviously, the effect of the ionic composition on the physiological parameters of zooplankton is an issue that needs to be studied in detail. Most results of laboratory studies with the simple ionic composition of salts (mainly NaCl) cannot be directly extrapolated to natural ecosystems.

Our second hypothesis was confirmed. In the grazing experiment with unicellular green alga as food, the population adapted to saline water demonstrated a higher grazing rate in saline water compared with the freshwater population. In the grazing experiment with the natural phytoplankton, the results depended on the method we used to estimate the decline in the phytoplankton abundance. When we used FlowCam to measure the numbers and volume of phytoplankton particles, we had strong support for our hypothesis: The freshwater population showed higher grazing rate in fresh water, while the saline water population—in saline water. As we mentioned, the genetic complexity of our populations was different, with the less diverse laboratory freshwater population and the more complex natural saline water population. However, this difference was not the main reason of grazing effects observed at low or high salinity, as regardless of genetic complexity, animals from both populations demonstrated comparable grazing rates at the moderate salinity. In addition, our results with animals from freshwater population were comparable with the decrease in the feeding rate of the freshwater *Daphnia magna* population observed at salinity above 5 ppm (Baillieul et al. 1998; Queirós et al. 2019).

When we estimated grazing rates based on FluoroProbe measurements of the concentration of chlorophyll "a", we did not detect the difference in grazing rates between two populations. Both populations demonstrated comparable maximum grazing rates at salinities of 3–4 g L^{-1}. In our previous study, we demonstrated the difference between multichannel fluorimeter FluoroProbe and flow cytometer FlowCam in an ability to analyze the composition of phytoplankton (Zadereev et al. 2021a). The fluorimeter is more accurate in assessing the proportions of algae of different classes in a sample, while the flow cytometer is more suitable to estimate the total number of particles. Obviously, animals consume particles. When the feeding is selective, these particles can be of different sizes or shapes or belong to different species. Indeed, the quantitative characteristics of phytoplankton (number or volume of particles) generally correlate with chlorophyll «a» concentration (Kring et al. 2014). However, in the grazing experiments, estimates of grazing rate based on discrete measurements of the number of particles may differ from continuous measurements of chlorophyll "a". There are several explanatory reasons such as (1) the presence of particles that do not contain pigments (bacteria, detritus, and pellets, other objects in a size range comparable to unicellular and colonial phytoplankton); (2) the difference in the concentration of photosynthetic pigments in cells or colonies of different phytoplankton species. Short-term grazing experiments are designed to estimate the amount and size of consumed particles, while the estimation of the amount of consumed and assimilated organic matter requires other methods. At the same time, taking into account the ability of zooplankton to control the development of phytoplankton and consume particles suspended in water, which is the mechanism to control water clarity, a change in the number of particles is a reliable estimate for the grazing rate.

Our third hypothesis was also confirmed. The major salinity related effects on size selective feeding that we observed were as follows: (a) animals from *Daphnia* population adapted to saline water consumed larger sized particles than animals from freshwater adapted population; (b) the average size of grazed phytoplankton particles in fresh water was larger than in saline water. The variable size selectivity in treatments with different salinities and phytoplankton communities is noticeable. This selectivity depends on the food preferences of animals with different genetic background (clonal diversity), the size structure of phytoplankton community, the filtration rates of animals, and the complex interactions of phytoplankton particles of different sizes with filter screen of animals in the water of different density and viscosity.

The plausible explanation of our results is the effect of salinity on the density and viscosity of water and the corresponding changes in the interactions between filter screen of animals and food particles. The feeding process of *Daphnia* is described by two main mechanisms: mechanical sieving and direct interception (Bednarska and Dawidowicz 2007). The relative contribution of these processes to *Daphnia* feeding depends on the values of Reynolds numbers on filtering appendages. For example, for large *Daphnia* grazing on the phytoplankton community consisting of filamentous or large algae, a decrease in Reynolds numbers by changes in the filter-screen morphology or depth selection is a strategy to reduce the negative effect of food particles that are not optimal in size and shape on the filtration process (Bednarska and Dawidowicz 2007). Since the density and viscosity of water increase with salinity, this reduces the Reynolds number on filtering appendages. We can assume that the grazing of *Daphnia* in the medium containing larger phytoplankton will be more effective in saline water. Also, if this assumption is valid, populations adapted to fresh and saline waters will differ in the filter-screen morphology. To confirm this hypothesis, direct study of filter-screen morphologies is required.

With our approach of using natural water of different salinities with natural phytoplankton, it is difficult to separate the effect of salinity from the effects of abundance, size, or composition of phytoplankton on *Daphnia* feeding. We used phytoplankton communities differing in the proportion of cyanobacteria and in the number and average size of particles. At the same time, many colonies of unicellular algae of different sizes were observed in all treatment media. The proportion of small particles after grazing could increase in the medium due the physical interaction of colonies with animals. This remark indicates that the analysis of grazing intensity and preferences of zooplankton feeding on natural phytoplankton is a much more difficult task than the analysis of the results of laboratory experiments with one-sized and/or single species used as food.

Conclusion

We demonstrated that animals from the two *D. magna* populations from the same region adapted to different salinities differed in survival at higher and lower salinities, salinity at which the maximal grazing rate was observed and in the size of phytoplankton particles they grazed on. This result indicates a potential temporal loss of the ability of zooplankton to control phytoplankton in natural habitats with an increase or decrease in salinity. A fluctuation in salinity is a typical feature of many saline lakes in arid climate (Zadereev et al. 2020). Such fluctuations can be either long-term or short-term, including seasonal fluctuations. For many saline lakes, springtime is characterized by a decrease in salinity due to the melting of snow and fallout of spring precipitation in the closed watershed. By contrast, summertime typically sees an increase in salinity due to intensive evaporation and low precipitation. Such seasonal fluctuations can reduce the zooplankton grazing pressure on phytoplankton, as populations adapted to the previous salinity level will not be as efficient as grazers with changed salinity, and cause an outbreak of harmful algae blooms. This reduction in grazing pressure will probably not last for a long time, as it can be compensated by the emergence of offspring, which will be produced under new conditions. The maternal effect can be responsible for the rapid adaptation of the offspring to the new conditions (Garbutt and Little 2014). Still, the reduced survival can be the reason for lower offspring numbers. Therefore, the temporal loss of grazing control will be mediated by both reduced survival and reduced grazing rate. This assumption requires verification. In particular, it would be interesting to study seasonal fluctuations of salinity in a specific lake and track related seasonal changes in abundance of phytoplankton and grazing intensity and efficiency of zooplankton. Such research can be also performed in a mesocosm gradient experiment, taking into account the wide support of mesocosm research in many limnological laboratories (Póda and Jordán 2020).

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Data availability Data, associated metadata, and calculation tools are available from the corresponding author (egor@ibp.ru)

Code availability All used packages and used tools have been cited in the manuscript, and there is no specific code for this manuscript.

Declarations

Conflict of interest All the authors declare that there is no conflict of interests/ All the authors declare that they have no competing interests.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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