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PRIMARY RESEARCH PAPER

Role of predation in biological communities in naturally eutrophic sub-Arctic Lake Mývatn, Iceland

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Abstract Effects of fish predation on consumers tend to be particularly strong in oligotrophic Arctic and sub-Arctic lakes. However, it remains unclear whether the fish influence the trophic structure and dynamics of naturally eutrophic lakes in these cold environments with simple food web structures. To study this, we conducted a 3-month in situ-controlled experiment in sub-Arctic Lake Mývatn, Iceland. We used the planktivorous fish three-spined sticklebacks (*Gasterosteus aculeatus*) as the main top predator. The cladocerans *Eurycercus lamellatus* and *Acroperus harpae* were significantly associated with fishless enclosures, whereas the rotifers *Polyarthra* sp. and *Filinia terminalis* were significantly associated with the fish enclosures. Fish predation led to a significant increase in phytoplankton biomass and a reduction in the zooplankton:phytoplankton biomass ratio, the mean zooplankton length and cladoceran mean biomass. Fish effects might have been stronger if a bloom of *Anabaena* in August had not overridden potential cascading effects. We argue that both top-down and bottom-up forces are important for structuring the communities in the lake. Our results suggest that Arctic and sub-Arctic lakes may undergo important changes in trophic dynamics if they get warmer

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and more nutrient rich as expected with the global climate change.

Introduction

The relative importance of predator and resource control in lakes has been extensively debated, and while some argue that top-down control is strongest in eutrophic lakes (Leibold, 1989; Sarnelle, 1992; Jeppesen et al., 1997), others claim it to be most profound in oligotrophic lakes (McQueen et al., 1986; Brett & Goldman, 1996). Based on data from 466 lakes covering a 500-fold variation in total phosphorus (TP) concentrations, Jeppesen et al. (2003) concluded that predation on large-bodied zooplankton showed a U-shape relationship with TP, being lowest at intermediate TP. Their data also suggested that the high predation in oligotrophic lakes does not cascade down to the phytoplankton level as otherwise observed in hypertrophic lakes and attributed this to strong nutrient limitation of phytoplankton (Jeppesen et al., 2003). Lakes in the Arctic and sub-Arctic are most often oligotrophic, poor in species and have simple food web structures (Rigler, 1975; Stross et al., 1980; Hobbie, 1984; Hobson & Welch, 1995). In these lakes, as well as in alpine oligotrophic lakes, fish predation effects on consumers tend to be particularly strong in the pelagic, affecting zooplankton (Anderson, 1971, 1972; O'Brien, 1975; Gliwicz et al., 2003; Jeppesen et al., 2003) and benthos, with subsequent impact on the macroinvertebrate community (Knapp et al., 2001; Jeppesen et al., 2003), but with little effect on phytoplankton biomass expressed as chlorophyll *a* (Jeppesen et al., 2003). However, not all Arctic and sub-Arctic lakes are oligotrophic. In areas with a naturally high loading of nutrients, such as areas with past or present volcanic activities, lakes may become mesotrophic or eutrophic. It remains unclear whether the fish influence the trophic structure and dynamics of naturally eutrophic lakes in these cold environments with simple food web structures in the same way and with equally strong cascading effects as in temperate and more species-rich lakes. Clarifying this question is

important because these lakes are expected to experience an increase in the abundance of small-sized planktivorous fishes due to climate change (Christoffersen et al., 2008; Cheung et al., 2013; Gonzalez et al., 2014) and become more nutrient rich with warmer temperatures, increased vegetation cover and precipitation/runoff (Hobbie et al., 1999; Michelutti et al., 2005).

Lake Mývatn in Iceland is an example of a natural eutrophic lake receiving nutrient-rich inlet water (Jónasson, 1979; Einarsson et al., 2004). The biota in this lake shows strong and relatively regular fluctuations without any evident correlation with external factors (Einarsson et al., 2004). The most prominent fluctuations are those of the chironomid *Tanytarsus gracilentus* Holmgren, 1883, which according to Ives et al. (2008) and Einarsson et al. (2004) are driven by interactions between the species and its sediment resources. According to Einarsson et al. (2004), these interactions might trigger fluctuations in other invertebrate communities due to the large impact of *T. gracilentus* on the benthic environment of this detritus-driven ecosystem. It has been argued that temporal variations in epibenthic chironomids and cladocerans translate into variable production of vertebrate predators (i.e. Arctic charr, *Salvelinus alpinus* L., 1758, and various duck species), body condition and mortality of fish and sometimes varying return rates of migrating adult ducks (Einarsson et al., 2004). This bottom-up perception has been somewhat modified by Einarsson (2010) who argued that also top-down control might play a role in structuring the ecosystem. This would align with observations made in oligotrophic Greenland lakes showing strong fish predation effects on zooplankton and the tadpole shrimp *Lepidurus arcticus* Pallas, 1793 (Jeppesen et al., 2001, 2003), however with weak effects on the phytoplankton (Jeppesen et al., 2003). As in Greenland, Icelandic Lake Mývatn hosts Arctic charr and three-spined stickleback (*G. aculeatus* L., 1758), but also brown trout (*Salmo trutta* L., 1758) occurs (Adalsteinsson, 1979). Sticklebacks are the most abundant species showing spatial segregation (Millet et al., 2013) and feeding mostly in the benthos on chironomid larvae, cladocerans and cyclopoid copepods (Adalsteinsson, 1979; Gislason et al. 1998). The fish populations also exhibit strong interannual variations, apparently influenced by changes in the benthic invertebrate communities (Gislason et al., 1998; Einarsson et al., 2004).

However, we still do not know to what extent these changes in fish populations cascade down to the plankton.

Bartrons et al. (2015) conducted spatial surveys of zooplankton communities in Lake Mývatn and found that the pelagic zooplankton community showed strong spatial variation, with species composition varying with spatial variation in chlorophyll *a*, the abundance of *Anabaena* Bory de Saint-Vincent ex Bornet & Flahault (cyanobacteria), lake depth, the light extinction coefficient and temperature. However, in the same study, stickleback abundance apparently had no measureable effect on the abundance or species composition of the zooplankton community, although high local abundances were associated with low zooplankton:phytoplankton biomass ratios. Thus, Bartrons et al. (2015) suggest that there is some top-down control of the zooplankton biomass but without any evident cascading effects on phytoplankton community structure. To get further insight into the role of fish predation in the trophic cascade of naturally eutrophic cold lakes, we conducted a 2-month in situ-controlled experiment in Lake Mývatn using sticklebacks as top predators. Based on the evidence from oligotrophic lakes in Greenland (Jeppesen et al., 2003), we hypothesised that sticklebacks would have a strong effect on the abundance and relative composition of zooplankton and macroinvertebrates; however, whether changes in the invertebrate community would cascade down to the primary producers in these cold species-poor lakes seemed less certain than in eutrophic temperate lakes.

Methods

Study site

Lake Mývatn (37 km^2) is divided into two main basins, the North Basin (8.5 km^2) and the South Basin (28.2 km^2) (Jónasson, 1979). Extensive areas in the South Basin are between 3 and 4 m deep, and maximum depth is about 4 m. Water enters the lake almost exclusively from springs along its eastern shore. Most of the springs are about 5°C, but springs in the North Basin are warmer (up to 23°C) (Ólafsson, 1979). The average duration of ice cover is about 190 days (Rist, 1979).

Experimental design

The experiment was conducted in the western part of the South Basin (Fig. 1). Six enclosures with a diameter of 1.2 m were established from 28 May to 31 August 2014. The sampling started on the 23 June and ended on the 20 August (i.e. total of 61 days). The average water level in the enclosures was 0.8 m, and each enclosure had a water volume of approximately 1 m^3. The enclosures were kept open to the sediment and consisted of a clear polyethylene tube, which was attached to a plastic hoop at the top and wrapped around a metal cylinder forced into the sediment. The plastic tube was suspended approximately 30 cm above the surface between four poles using elastic connectors. During filling, a net (1 mm mesh size) was held underneath the bottom of each enclosure to prevent fish from entering. The net was removed again when the enclosures had reached the sediment. The experiment followed a 2 × 3 design with two fish treatments (with fish and without fish) and three replicates for each treatment that were set randomly. The three-spined sticklebacks were caught with tramp nets in an area close to the mesocosms and added to half of the enclosures on the 20th of June. Only medium-sized fish (average 5.5 cm) were used in the experiment. Four fish were used for each enclosure. An earlier mark-recapture study undertaken in the North Basin showed fish densities to range between
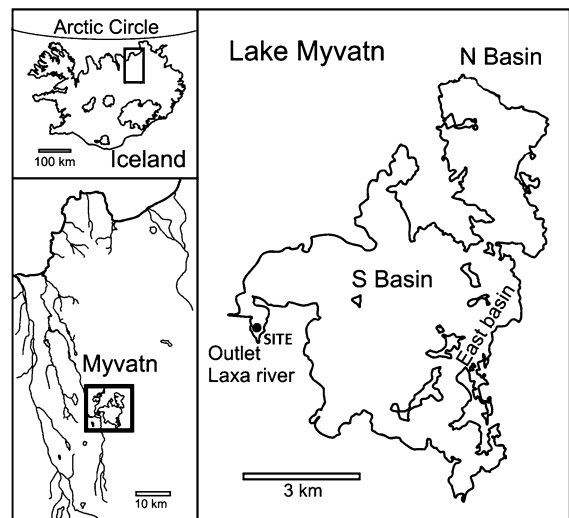

Fig. 1 Map of the study site (Lake Mývatn, Iceland) and location of the mesocosms

100 and 200 fish m^{-2}, most individuals caught being young-of-the-year. In the South Basin, stickleback densities ranged between 0.3 and 2.5 individuals m^{-2}, and about half were 1-year-old fish and the other half young-of-the-year (Gislason et al., 1998). So, the abundances found in our study were within the lower range of earlier findings. To obtain similar initial communities, a zooplankton mix from the same area of the lake was inoculated to all the enclosures on the 5th of June.

Sample collection

Periodical samplings (i.e. approximately every 14 days) began on 23 June (fifteen days after zooplankton addition and 3 days after fish addition). Physical parameters—temperature (°C), pH, conductivity (µS/cm) and dissolved oxygen (%)—were determined using a Hanna multi-parametrical device, while turbidity was estimated with a Secchi disc (m). Water samples were taken with a 1-m-long core sampler (diameter 6 cm), which collected water from the surface to just above the sediment.

For every enclosure, the water (10–12 l) collected from three different spots within each module was mixed in a barrel, and an 8 l subsample was filtered through a 50 mm mesh filter for zooplankton analysis, and the residue was immediately fixed in acid Lugol's solution (4%). From the same barrel, 1 l water was stored in a plastic bottle for water chemistry analysis, including TP (µg/l), soluble phosphorous (PO$_4$, µg/l), total nitrogen (TN, µg/l) and ammonium (NH$_4$, µg/l). TP was determined as molybdate-reactive phosphorous (Murphy & Riley, 1962) following persulfate digestion and TN as nitrite after potassium persulfate digestion (Solorzano & Sharp, 1980). Two litres of water were collected in brown bottles for laboratory chlorophyll-a (chl a) filtration using funnel filters on the same day as the sampling. Filters were immediately frozen for further laboratory analysis. Chl a was determined spectrophotometrically after acetone extraction (Lin et al., 2005). Phytoplankton samples were kept in glass bottles and fixed in acid Lugol's solution (4%). Invertebrate samplings were conducted on artificial leaves tied to a string (Brucet et al., 2012) and suspended on the surface of the enclosure (hereafter epiphytic macroinvertebrates). An artificial leave string was carefully removed from the enclosure using a core sampler and subsequently washed and filtered on

a 250 µm mesh size net. Macroinvertebrates were preserved in 70% of alcohol. Benthic macroinvertebrates were collected from the sediment (upper 5 cm) using Kajak corers with a diameter of 5.2 cm at three different locations in each enclosure. We took three cores per enclosure to capture spatial variability and merged them into a single sample. Thus, the total number of samples per each measured variable was 30 (1 sample per enclosure × 6 enclosures (3 with fish and 3 without fish) × 5 sampling dates).

Phytoplankton organisms (including cyanobacteria) were counted using an inverted microscope (Zeiss Axiovert A1) at 400 × after sedimentation in a 30 ml settling chamber (Throndsen, 1995). Biomass (biovolume) was calculated based on the linear dimensions of the cells measured under the microscope using appropriate geometric formulae (Sun & Liu, 2003). At least 100 individuals of the most abundant zooplankton taxa were counted and all zooplankton taxa were identified to species level (except some Rotifera that were identified to genus level). The whole sample was analysed so as not to overlook rare species. Copepods were separated into nauplii, copepodites and adults. Biomass dry weight estimations were obtained from the allometric relationship between the weight and the length of the body (Dumont et al., 1975; Bottrell et al. 1976; McCauley, 1984). For Rotifera, biomass dry weight was calculated by converting biovolume into dry weight (Ruttner-Kolisko, 1977; Malley, 1989). Rotifera biomass was estimated from measurements of the principal diameters of the organisms (Malley, 1989). We measured up to 25 individuals of each taxon, whenever possible. We also calculated the phytoplankton and zooplankton biomass ratio as a surrogate of the strength of the trophic interactions (i.e. effect of zooplankton on phytoplankton). Macroinvertebrates were identified to the lowest possible taxonomic resolution (i.e. genus/species level for all taxa except Oligochaeta, Hydracarina and Dolichopodidae) following Andersen et al. (2013) for Chironomidae and Tachet et al. (2000) for the remaining invertebrates. The chironomids *Cricotopus* van der Wulp, 1874+*Orthocladius* van der Wulp, 1874 were grouped together due to their complex taxonomy.

Data analysis

All statistical analyses were performed in R (R Core Team, 2015). The indicator taxa of each treatment

group were identified using IndVal analysis (Dufrêne & Legendre, 1997). The analysis assigned each taxon to a most probable group (fish, no fish) based on its relative abundance and relative frequency, and provided an indicator value (IV, varying between 0 and 1) and an alpha value obtained by Monte Carlo permutations (9,999 runs). Treatments were combined using the "multipart" function in the R package "indicspecies" (De Cáceres et al., 2010). Normality was checked performing the Shapiro–Wilk test of normality. In the cases where normality was not met, data were log-transformed. Linear mixed effect models (LMM), lmer function in the R package lme4 (Bates et al., 2014), were used to assess the effect of treatment (i.e. fish addition) on the different measured variables, while taking into account the fact that the samples were inter-dependent (i.e. each enclosure was sampled on five different dates). As random effects, we had intercepts for sampling dates and the enclosure position. P values were obtained by likelihood ratio tests of the full model with treatment and sampling date as fixed effects against the model without treatment as fixed effect (Winter, 2013). The same approach was followed to assess the effect of time; t tests, which are best suited for low sample sizes (de Winter, 2013), were used to test if one of the groups (fish, no fish) had a significantly larger mean than the other for each analysed variable at each sampling date. Given the high risk of Type I error associated with our multiple comparisons, we applied the Benjamini-Hochberg correction, which is especially recommended when having a large number of correlated tests, to our P values (Benjamini & Hochberg, 2000; Benjamini & Yekutieli, 2001; Narum, 2006).

Results

According to INDVAL analysis (performed separately for zooplankton and aquatic macroinvertebrates), four zooplankton species were significantly associated with one of the treatments (i.e. fish absence vs. fish presence). Thus, the cladocerans *Eurycercus lamellatus* Müller, 1776 (IV = 0.70, P value = 0.04) and *Acroperus harpae* Baird, 1834 (IV = 0.70, P value = 0.04) were associated with fishless enclosures, whereas the rotifers *Polyarthra* sp. Ehrenberg, 1834 (IV = 0.86, P value = 0.03) and *Filinia terminalis* Plate, 1886 (IV = 0.58, P value = 0.03) were

associated with the fish enclosures. No macroinvertebrates were significantly associated with any of the treatments.

According to LMM, fish addition led to a significant increase in phytoplankton biomass ($\chi2 = 7.81$; P value = 0.0181) and significant decreases in the zooplankton:phytoplankton ratio ($\chi2 = 6.43$; P value = 0.0405), mean zooplankton length ($\chi2 = 8.17$; P value = 0.0182) and cladoceran mean biomass ($\chi2 = 8.71$; P value = 0.0148). When analysing each sampling date separately, only two variables showed significant differences between treatments (Figs. 2 and 3)—the zooplankton:phytoplankton biomass ratio (day 16, $t = -3.32$, P value = 0.019) and cladoceran mean biomass (day 16, $t = -2.90$, P value = 0.028), both being reduced by fish addition. There was also a strongly significant temporal variation (i.e. $P < 0.005$ in all cases) in soluble phosphorous, total phosphorous, ammonium, total nitrogen, chlorophyll *a*, biomass of cyanobacteria and total phytoplankton, zooplankton:phytoplankton biomass ratio, benthic invertebrates and *T. gracilentus* (Supplementary material). Furthermore, it is important to notice the increase in cyanobacteria with time, from a mean value of 25 ± 22 μm³/l for days 1, 16 and 30 to 9958 ± 3998 μm³/l for days 44 and 58 (Fig. 2).

Discussion

Our experiment indicates that top-down forces play a role at structuring food webs in the naturally eutrophic Lake Mývatn. However, their importance changes over the summer and differs among the different trophic levels. In spite of using a conservative statistical approach (i.e. P value correction), we detected that fish addition led to a significant increase in phytoplankton biomass and significant decrease in the zooplankton:phytoplankton biomass ratio, mean zooplankton length and cladoceran mean biomass. Moreover, the zooplankton:phytoplankton ratio and cladoceran mean biomass decreased significantly 16 days after fish addition. Additionally, there were differences in species composition between treatments: two species of benthic cladocerans were associated with the fishless enclosures, whereas two pelagic rotifers were more abundant in the fish enclosures. Fish addition could probably have led to a stronger top-down effect if *Anabaena* had not
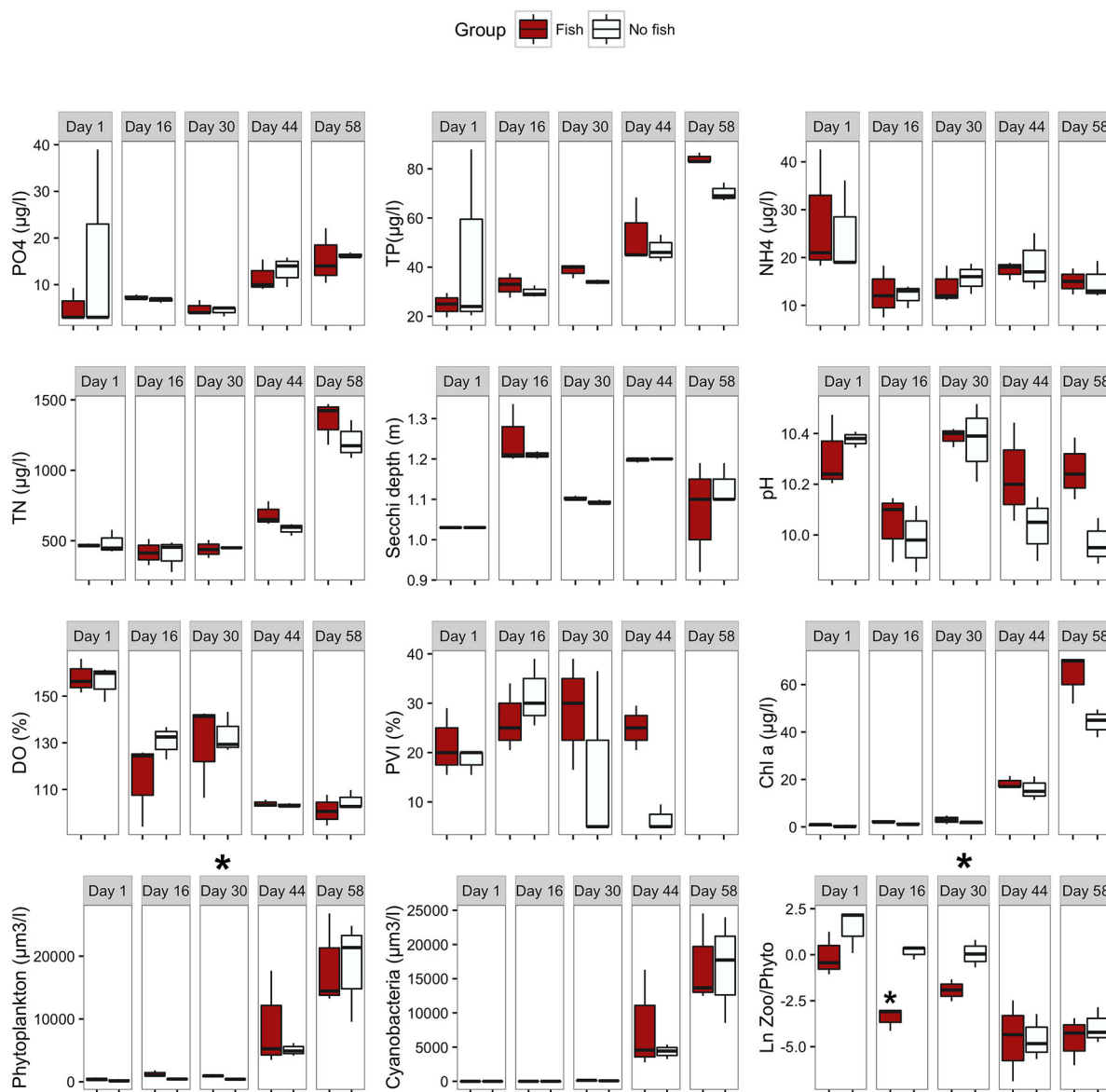
Fig. 2 Variations in different water chemistry parameters, primary production and zooplankton:phytoplankton ratio (as an indicator of top-down control) with treatment (i.e. fish addition) and along time (*5 sampling dates* 1, 16, 30, 44 and 58 days after fish addition). Significant overall effects of fish addition (if present) are shown on top of each graph. Additionally, significant differences are shown for each sampling date on top of the fish addition box. * = $0.05 < P$ value < 0.01. *DO* dissolved oxygen, *PVI* perpendicular vegetation index (at the end of the study poor water transparency in the fish enclosures prevented estimates). $n = 30$ (1 sample per enclosure × 6 enclosures (3 with fish and 3 without fish) × 5 sampling dates)

bloomed around day 44, clearly overriding the possible cascading effects of fish addition. While the top–down effects during the first month are reflected in the higher phytoplankton biomass and the lower zooplankton:phytoplankton biomass ratio in the fish enclosures, the occurrence of *Anabaena* blooms led to a reduction of the zooplankton:phytoplankton biomass ratio in both the enclosures with and without fish. At the start of the second month of the experiment, cyanobacteria dominated the phytoplankton community in both the fish (relative biomass for days 44 and 58 = $87.61 \pm 3.67\%$) and the fishless enclosures (relative biomass for days 44 and 58 = $89.54 \pm 3.18\%$), indicating that the blooming
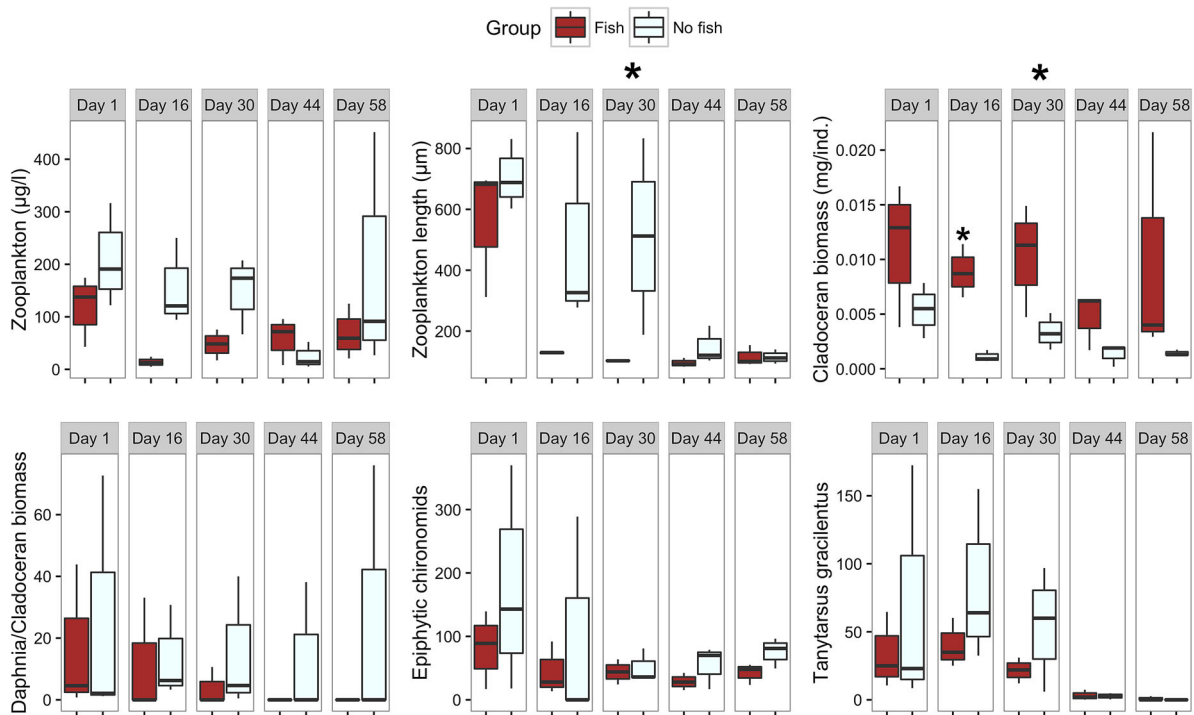
Fig. 3 Variation of different biological variables with treatment (i.e. fish addition) and along time (*5 sampling dates 1*, *16*, *30*, *44* and *58* days after fish addition). Significant overall effects of fish addition (if present) are shown on top of each graph. Additionally, significant differences are shown for each sampling date on top of the fish addition box. * = 0.05 < *P* value < 0.01. *n* = 30 (1 sample per enclosure × 6 enclosures (3 with fish and 3 without fish) × 5

sampling dates). Given their relative abundance and their reported importance as structuring forces of the aquatic food web of Mývatn, the epiphytic chironomids *Cricotopus+Orthocladius* (mean relative abundance on the plants = 53%) and *Psectrocladius sordidellus* Zetterstedt, 1838 (mean relative abundance on the plants = 42%) and the benthic chironomid *Tanytarsus gracilentus* (mean relative abundance in the sediment = 63%) were analysed separately

was not caused by a cascading effect. TP and TN increased slightly in the fish enclosures, but this increase was overall not significant and ammonium and phosphate were not affected at all, which suggests that top–down effects only cascaded weakly to the nutrient level.

Two species of benthic cladocerans, the large-bodied *E. lamellatus* and the medium-sized *A. harpae*, were associated with the fishless enclosures, whereas two pelagic rotifers, *Polyarthra* sp. and *Filinia terminalis*, were more abundant in the fish enclosures. Benthic crustaceans have already been reported to be among the preferred food items by sticklebacks in Lake Mývatn (Adalsteinsson, 1979). Probably, size-selective predation (Brooks & Dodson, 1965) of sticklebacks on large cladocerans led to the observed dominance of small rotifers in the fish enclosures. The size-selective predation by sticklebacks was also reflected in the lower mean zooplankton length and

individual biomass of cladocerans in the fish enclosures. This suggests that fish could have a stronger link with the zooplankton community than previously suggested by Einarsson et al. (2004), who argued that changes in cladoceran (including *E. lamellatus*) abundances were mainly driven by changes in the abundances of *T. gracilentus*, which digests the sediment and modifies it by forming dense mats of tubes and silk strands. Epiphytic and benthic macroinvertebrates were not significantly affected by fish predation, but their density in the fish enclosures was half of that in the fishless enclosures until day 30. Gislason et al. (1998) reported very low abundances of *T. gracilentus* in the stomach of sticklebacks in Lake Mývatn, suggesting that this is not an important prey for them. The abundances of benthic macroinvertebrates and *T. gracilentus* (which clearly dominated the benthic assemblage) decreased significantly with time, being remarkably low in both sets of enclosures when

Anabaena bloomed (day 44). In Lake Mývatn, *T. gracilentus* has 1–2-week mating periods (Jónsson et al., 1986), the first in May and the second (up to ten times more important in terms of emerging adults) in late July and early August (corresponding to days 30 and 44 of our study, respectively). Thus, the overall decline in *T. gracilentus* larvae that we registered by the end of the study is most likely related to their emergence as adults.

We recorded a notable influence of *Anabaena* on the trophic structure of the lake. Our results partly agree with those of a recent study conducted in Lake Mývatn (Bartrons et al., 2015), showing that *Anabaena* blooms are one of the main drivers of the spatial patterns in the zooplankton community composition of the lake. However, Bartrons et al. (2015) found that stickleback density had no measureable effect on the abundance or species composition of the zooplankton community along several areas of the lake on the contary, in our study, stickleback addition did have a significant effect on the zooplankton/phytoplankton biomass ratio, the mean zooplankton length and the cladoceran mean biomass, as well as on the composition of species. This could be related to the fact that we directly manipulated fish presence/absence under similar experimental conditions, whereas Bartrons et al. (2015) used data from field surveys with variable stickleback densities. *Anabaena* is a cyanobacteria that occurs regularly in Lake Mývatn in summer, particularly in years with low chironomid abundance (Einarsson et al., 2004). Cyanobacteria are often associated with lower abundances of larger herbivorous zooplankton due to their low nutritional value (Müller-Navarra et al., 2000), either because they physically interfere with the zooplankton feeding apparatus (Webster & Peters, 1978; DeMott, 1989) or because they produce toxins (Knapp et al., 2001). These effects are less severe for rotifers and small-bodied cladocerans (e.g. Sommer et al., 1986; DeMott, 1989). Accordingly, the blooming of the unpalatable *Anabaena* led to a remarkable decrease in large-sized zooplankton, such as *Daphnia longispina* Müller, 1776 (mean biomass = 13.45 µg/l before the bloom and 2.96 µg/l after the bloom), and by the end of the experiment, it overshadowed the effects of fish predation. This negative association between *Daphnia* and *Anabaena* blooms has been observed previously in Lake Mývatn (Einarsson et al., 2004). These blooms have been registered frequently, and they are thought to be associated with low *N:P* ratios,

naturally high P-values in the spring water and the ability of *Anabaena* to grow at low availability of *N* (Jónasson & Adalsteinsson, 1979). Our results support this hypothesis. Both phosphorous and nitrogen concentrations increased significantly with time. The mean *N:P* ratio was 13.98 ± 1.72, and the mean TN concentration increased from 0.45 mg l^{-1} before the bloom to 0.63 mg l^{-1} on day 44 and 1.21 mg l^{-1} on day 58, probably as a result of the fixing of atmospheric *N* by *Anabaena* (see Allen & Arnon, 1955). While much debate is still ongoing about the possible effects of cyanobacterial blooms in lakes and the coping strategies that could be developed by zooplankton (Ger et al., 2016), our study clearly shows that *Anabaena* blooms have the potential to interfere with top-down effects in shallow lakes. This interference can be expected to be stronger in cold lakes (e.g. Arctic lakes) where the selection of tolerance and defensive traits in zooplankton is lower than in warm (e.g. tropical) lakes (Ger et al., 2016).

Overall, we conclude that an increase in the density of sticklebacks in Lake Mývatn (as an example of a naturally eutrophic lake) had a cascading effect on the pelagic food web leading to higher phytoplankton biomass, although a late summer bloom of *Anabaena* bloom counteracted the fish effects. The potential effects of increased stickleback densities in naturally eutrophic lakes like Lake Mývatn deserve further study, especially considering the marked changes in fish community structure (i.e. a higher dominance of small planktivorous fish) expected to occur with the ongoing global warming (Jeppesen et al., 2012; Emmrich et al., 2014). Within this context, our results can be applied to other shallow lakes in the sub-Arctic since this region is expected to become warmer and more nutrient enriched (Hobbie et al., 1999; Michelutti et al., 2005; Jeppesen et al., unpubl. results).

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