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Spatial patterns reveal strong abiotic and biotic drivers of zooplankton community composition in Lake Mývatn, Iceland

Mireia Bartrons,[1,2,]† Árni Einarsson,[3] Regina L. G. Nobre,[4] Cristina M. Herren,[1] Kyle C. Webert,[1] Sandra Brucet,[5,6] Sólveig R. Ólafsdóttir,[7] and Anthony R. Ives[1]

[1]*University of Wisconsin-Madison, Department of Zoology, Madison, Wisconsin 53706 USA*
[2]*CREAF, Cerdanyola del Vallès, Barcelona, Catalonia 08193 Spain*
[3]*Myvatn Research Station, Iceland, and University of Iceland, Faculty of Life and Environmental Sciences, Reykjavík 101 Iceland*
[4]*Universidade Federal do Rio Grande do Norte, Ecology Department, Natal-RN 59072-970 Brazil*
[5]*BETA Technological Centre (Tecnio), Aquatic Ecology Group, University of Vic–Central University of Catalonia, Vic, Catalonia 08500 Spain*
[6]*Aarhus University, Department of Bioscience, Aarhus 8000 Denmark*
[7]*Marine Research Institute, Reykjavik 101 Iceland*

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Abstract. Spatial patterns in the abundance of species are determined by local abiotic and biotic conditions, and by the movement of individuals among localities. For species distributed among discrete habitat "islands", such as zooplankton distributed among lakes, local conditions within lakes often dominate low movement rates among lakes to determine the composition of communities. Here, we ask whether the same abiotic and biotic environmental conditions can generate spatial patterns in the distribution of zooplankton within a lake where there are high horizontal movement rates. We conducted three spatial surveys of zooplankton communities in Lake Mývatn, Iceland, a moderately sized (37 km^2) shallow lake with a high outflow rate. The pelagic zooplankton community showed strong spatial structure (spatial autocorrelation), with species composition varying with spatial variation in chlorophyll-a, the abundance of *Anabaena* (cyanobacteria), lake depth, light extinction coefficient, and temperature. These factors are known from other studies to be strong drivers of among-lake variation in freshwater zooplankton communities. However, in contrast with among-lake studies, fish (stickleback) abundance had no measureable effect on the abundance or species composition of the zooplankton community, although high local stickleback abundance was associated with low zooplankton:phytoplankton biomass ratios. Finally, a parallel study of the underlying benthic crustacean community showed much finer spatial variation (spatial autocorrelation to a range $\leq$0.6 km vs. 9 km for pelagic zooplankton), suggesting that the stationary character of the benthos allows finer grained spatial patterns. Given the high flow rate of water in Mývatn (>200 m/d), the generation of spatial patterns suggests very strong effects of variation in abiotic and biotic environmental conditions on the population dynamics of zooplankton in the lake.

Key words: community composition; ecosystem dynamics; Iceland; lake; Mývatn; spatial patterns; zooplankton.

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† **E-mail:** bartrons@wisc.edu

Introduction

Understanding spatial patterns in the abundance of species and the composition of communities is a well-established goal in ecology (Clements 1916, Gleason 1926, Whittaker 1956). A central issue in understanding spatial patterns is identifying the local abiotic and biotic environmental conditions that drive them. The environmental conditions that affect freshwater zooplankton communities are particularly well studied (Pulliam 1988) and provide striking examples of the strength of local environmental drivers of community composition (Carpenter 1988, Pinel-Alloul et al. 1999). These patterns are especially clear because lakes represent discrete "islands" for zooplankton, and the low dispersal rates of zooplankton among lakes allow local environmental conditions to dominate zooplankton abundance and community composition (Havel and Shurin 2004, Kramer et al. 2008, Frisch et al. 2012). Here, we ask whether the abiotic and biotic environmental factors that drive zooplankton abundance and composition among lakes could be strong enough to generate spatial patterns in abundance and composition within a lake.

Abiotic factors driving variation in freshwater zooplankton communities among lakes include water chemistry (e.g., nutrient concentrations, pH, conductivity, and turbidity; Johannsson et al. 1991, Pourriot et al. 1994), hydrology (e.g., wind and wind induced currents; Jones et al. 1995, Lacroix and Leschermoutoue 1995, Rennella and Quirós 2006), temperature (Betsill and Vandenavyle 1994, Pinel-Alloul et al. 1999, Winder and Schindler 2004), and lake morphometry (e.g., depth, area or perimeter; Patalas and Salki 1992, Jeppesen et al. 2001, Amsinck et al. 2006). Biotic drivers can be both bottom-up factors involving resources and top-down factors such as predation (Carpenter et al. 1985, McQueen et al. 1986, Northcote 1988, Vanni 1988). These abiotic and biotic drivers are often highly variable among lakes, making it easy to identify their effects on zooplankton. In contrast, within a lake many of these environmental factors are less variable, and lakes experience horizontal water mixing which generates high dispersal of zooplankton among locations (Jeppesen et al. 2003, Havel and Shurin 2004, Kramer et al. 2008, Frisch et al. 2012). Thus, the main drivers of spatial patterns are generally thought to consist of factors affecting movement within lakes, such as wind-induced water currents and immediate weather conditions (Jones et al. 1995, Pinel-Alloul et al. 1999, George and Winfield 2000, Thackeray et al. 2004, Rinke et al. 2009). Nonetheless, it is possible for sufficiently strong abiotic and/or biotic gradients to generate spatial patterns in zooplankton composition within large lakes or among isolated basins (Stansfield et al. 1997, Pinel-Alloul et al. 1999, Levesque et al. 2010, Davidson et al. 2011, 2013). Whether spatial gradients in environmental factors can drive large differences in abundance and community composition in smaller well-mixed lakes, however, has not been shown.

We investigated spatial patterns in the zooplankton community of Lake Mývatn, Iceland, a moderately sized (37 km^2) lake whose high throughflow (flushing rate of ~30 d), shallow depth (maximum 4 m), and windy weather make it subject to strong horizontal mixing. Despite the strong mixing, Mývatn exhibits pronounced abiotic and biotic environmental gradients (Einarsson et al. 2004). Mývatn is fed by both hot and cold springs that establish temperature and nutrient gradients (Fig. 1). Furthermore, because it is shallow, most of the primary productivity is benthic, and variation in depth (and hence light penetration) leads potentially to variation in nutrient uptake or release from the benthos. Also, the phytoplankton community varies spatially in biomass and composition, likely driven by differential population growth rates of phytoplankton species caused by the presence of particular species and environmental conditions in different locations. Finally, fish abundances vary among regions in the lake. Because these gradients are largely orthogonal (see *Results*), we hoped that they would allow us to determine whether abiotic and biotic drivers are important in determining zooplankton community structure and, if so, identify those drivers that have the largest effects.

Our study consisted of three transect surveys of 30–31 sites conducted in the summer of 2012, separated by 23 and 11 days; in the short summer of Iceland, the surveys spanned from early to middle-late seasonal succession of zooplankton in Mývatn (Adalsteinsson 1979*b*). In addition to sampling zooplankton, we also sampled abiotic

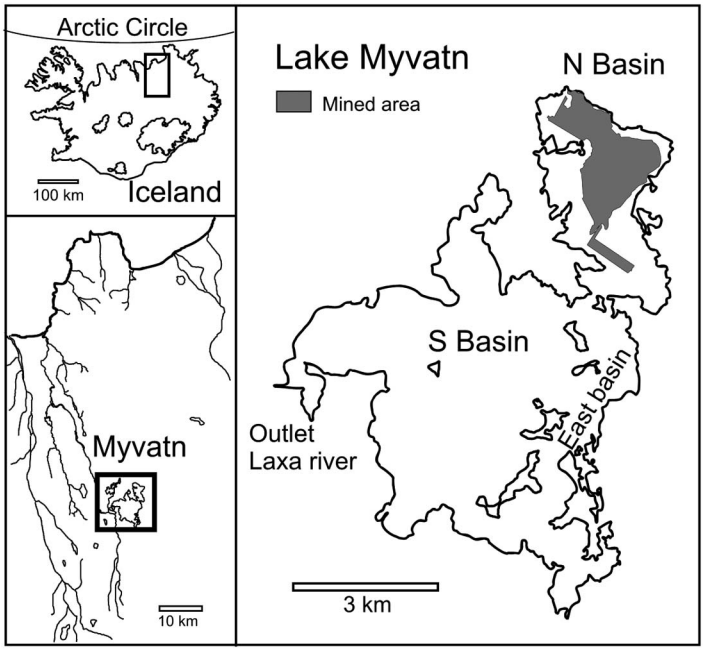

Fig. 1. Map of Mývatn (after Einarsson et al. 2004).

(nutrient concentrations, pH, conductivity, temperature, light extinction coefficient, turbidity, dissolved oxygen, depth, distance from the outlet) and biotic (phytoplankton, chlorophyll-a, phycocyanin) variables, and we used trapping data from June and August to estimate fish abundances. To compare pelagic spatial patterns in zooplankton with the community associated with a stationary substrate, during the second transect survey we sampled the benthos at nine sites for crustaceans, and abiotic and biotic variables. The timing of the three transect surveys provided contrasts in the environmental setting of possible spatial patterns in the lake: the first survey occurred in early seasonal succession when phytoplankton and zooplankton abundances were low; the second survey occurred following a long windy period with concomitant horizontal mixing; and the third survey occurred at high growing season following relative calm. Our overall goal was to use these surveys to ask whether there are spatial patterns in the distribution of zooplankton within Mývatn, and if so, whether they are driven by the same abiotic and biotic drivers that are known elsewhere to generate variation in zooplankton community composition among freshwater lakes.

Material and Methods

Study site

Mývatn is a shallow eutrophic lake in northeast Iceland (65°4′ N, 17°0′ W, 278 m a.s.l.) subject to a oceanic, subarctic climate, and often high winds (Einarsson 1979). The lake is physically divided into two main basins, with significant variation in the chemical composition and temperature of the artesian springs feeding each basin (Ólafsson 1979, Dickman et al. 1993, Einarsson et al. 2004). Most of the South Basin (28.2 km^2) is 2.5–4 m deep (mean depth of the sites sampled in the South Basin was 2.3 ± 0.6 m), with benthic substrate that is covered largely by epiphytic diatoms, free-floating green algae filaments of Cladophorales, and chironomid (midge) larval tubes, mainly of the species *Chironomus islandicus* (Kieffer) and *Tanytarsus gracilentus* (Holmgren). The southeastern part of the South Basin is influenced by inflowing cold spring water. The smaller North Basin (8.5 km^2) is 1–2.5 m deep and is mainly covered by macrophytes (mean depth of the sites sampled in the North Basin was 1.4 ± 0.5 m); some areas of this basin have been dredged for diatomite mining, which increased depth to a maximum of

5.5 m, leaving a muddy substrate with no vegetation. The North Basin is partly fed by warm springs (up to 30°C; Ólafsson 1979) and outflows into the South Basin. The discharge of water is 20.9 m^3/s from the South Basin at the outlet and 7.1 m^3/s from the North Basin to the South Basin (Ólafsson 1979).

The water column is vertically mixed during the summer (Ólafsson 1979). External loading of phosphorus, nitrogen, and silica is estimated to be 1.5, 1.4 and 340 g m^{-2} $year^{-1}$, respectively, and nitrogen fixation by cyanobacteria and internal loading from sediments is important in the total nutrient budget (Ólafsson 1979). Resuspension of sediments occurs frequently in this shallow lake with no trees on the shoreline, and is estimated to be three times more common in the North than the South Basin (Jóhannesson and Birkisson 1991).

Biotic communities

Only two crustacean species that are considered primarily planktonic are regularly found in Mývatn, *Daphnia longispina* (Müll.) and *Cyclops* cf. *abyssorum* Sars, but the tychoplanktonic *Chydorus sphaericus* Müll. is common in some years (Adalsteinsson 1979*b*). Large rotifers dominate the lake in spring, being replaced by small rotifers in early summer (Adalsteinsson 1979*b*). In Transect 1 (2 July), we only counted the large rotifer *Asplanchna* Gosse, although we also counted the small rotifer *Keratella* Bory de St. Vincent, in Transects 2 and 3. The benthic cladoceran community is dominated by *Eurycercus lamellatus* (Müll.), *Alona rectangula* Sars, *Alona affinis* (Leydig), *Alona quadrangularis* (Müll.), *Alonella nana* (Baird), *Acroperus harpae* (Baird), and *Chydorus sphaericus* Müll.

Diatoms, especially *Fragilaria construens* (Ehrnb.) Grun, occur everywhere in the lake. In 2012 the two other common phytoplankton groups were the cyanobacteria *Anabaena flos-aquae* (Lyngb.) Bréb. and the green alga *Oocystis* spp.; these two groups negatively covaried throughout the lake and therefore were the main drivers of spatial patterns in the phytoplankton community. Chrysophyceans, mostly dominated by colonies of different flagellate cells, occurred at low abundance early in the season, but increased as the summer progressed (Fig. 2).

In Mývatn, three fish species are found; Arctic char (*Salvelinus alpinus* (L.)), brown trout (*Salmo trutta* L.), and three-spined stickleback (*Gasterosteus aculeatus* L.) (Adalsteinsson 1979*a*). Sticklebacks are the most abundant, show spatial segregation (Millet et al. 2013), and mostly feed in the benthos on chironomid larvae, cladocerans, and *Cyclops* (Adalsteinsson 1979*a*, Gislason et al. 1998). Therefore, we focused on sticklebacks as possible drivers of zooplankton and epibenthic communities.

Sampling and analyses

Three transects were performed consisting of 30–31 sites located at 500–600 m intervals. The transects originated in the cold springs in the southeast of the South Basin, ran to the outlet of the South Basin (west), and then back through the outlet of the North Basin towards the warm springs that feed it (Fig. 2). Transect 1 was performed on 2 July during the clear phase of the lake. Transect 2 was performed on 25 July after a period with rain and very strong winds; during the 23 days prior to sampling, eight days had average wind speeds >5 m/s (which is sufficient to completely mix the water column at most sites; Ólafsson 1979), with gusts exceeding 10 m/s on 11 days. Transect 3 was performed on 5 August following calm conditions and after pelagic communities were well developed. Stations were selected to capture the maximum environmental variability within the lake, and to sample the most representative areas of the lake in less than one day.

At each site, measurements of turbidity, conductivity and phycocyanin (a photosynthetic pigment found in Cyanobacteria) were made at a depth of 1 m using a Hydrolab water quality multiprobe (model DS5X with self-cleaning turbidity sensor); values were taken every minute for 10 minutes and averaged. Vertical profiles of temperature, DO, pH, and light were made at each station at 0.5-m intervals using a handheld optical DO meter (model YSI Professional ODO), a portable pH/Conductivity multiparameter meter (Thermo Scientific Orion 4-Star Plus), and a LI-COR light meter (LI-250A). Integrated vertical tows of the whole water column for the analysis of zooplankton and phytoplankton community composition, and chlorophyll-a (Chl-a) were made at each station with a Plexiglas cylinder (length 100 cm, diam-

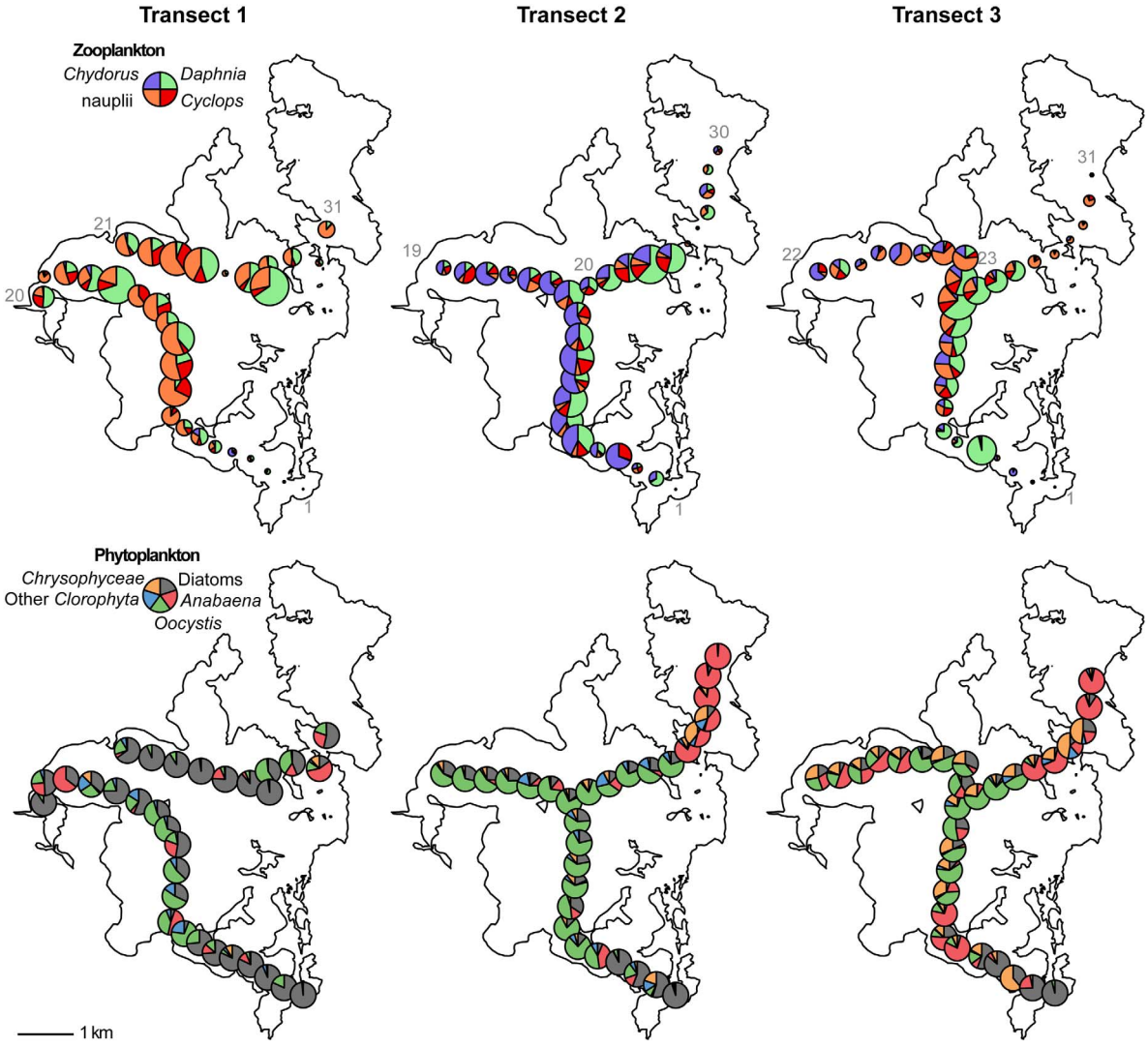

Fig. 2. Spatial distributions of zooplankton abundance (number/L) and phytoplankton proportion (%) in Mývatn during the three transects. Distances between sites are about 500 m. The size of the circle denotes the total abundance of the zooplankton community in relation to the other stations of the transect. The number of the stations appears in grey.

eter 3.6 cm; Ramberg 1976) which was used to sample water at 1-m vertical increments to within 1 m from the benthos.

Zooplankton sampling and processing were done according to the methods of Edmondson and Litt (1982). Briefly, zooplankton samples were integrated over the whole water column, with two or three vertical water tows made for each sample depending on depth to equalize the total volume of water sampled. The pooled sample of 15 L was filtered through 63-μm mesh size and counted in entirety under a binocular microscope. Every other site (i.e., the odd-numbered stations 1, 3, . . .) on the transect was sampled twice independently using the same procedure in order to estimate sampling variability within sites.

Samples for phytoplankton community composition, Chl-a, and nutrients were taken using the same protocol as zooplankton using a separate 15-L integrated water sample. The relative abundance of phytoplankton, identified

to species or genus, was estimated by the Utermöhl method after fixation with Lugol's acid solution (Sournia 1978). At least 400 individuals were counted from each sample to achieve counting accuracies of 90% (Lund et al. 1958). Relative abundances of phytoplankton were converted to carbon biomass using the conversions of Reynolds (2006).

Water for Chl-a analysis was filtered through a 47-mm Whatman glass fiber filter (GF/F) and extracted in 100% methanol for 24 h in the dark at −20°C. Following extraction, Chl-a concentrations were measured fluorometrically with acid correction (0.1 N HCl) by the method of Welschmeyer (1994) using an AquaFluor Handheld Fluorometer (Turner Designs). To determine zooplankton:phytoplankton biomass ratios, Chl-a was converted to phytoplankton dry weight (DW) using a Chl-a:C ratio of 1:30 and a DW:C ratio of 2.2 (Jeppesen et al. 1994). Zooplankton biomass was based on Adalsteinsson (1979*b*) who estimated species-specific volumes from the geometric configurations of the organisms.

Total and dissolved nutrients (total phosphorus TP, orthophosphate PO_4-P, total nitrogen TN, nitrate + nitrite, ammonium nitrogen NH_4-N, and silica SiO_2-Si) samples were collected in 250-mL low-density polyethylene bottles washed with dilute hydrochloric acid prior to each sampling. Total nitrogen and phosphorus concentrations were obtained after UV-digestion of the samples. Concentrations of dissolved nutrients were determined using a Seal 3 channel autoanalyzer, as described in Grasshoff (1970) but using deionized water for blank and standards. Except for phosphate, methods were modified from Murphy and Riley 1962). Silicate samples were diluted before measurement. The estimated analytical uncertainties are ±0.2 μM for NO_3-N and SiO_2-Si, ±0.03 μM for PO_4-P and ±0.3 μM for NH_4-N.

Sticklebacks were sampled from 11 sites across the lake during the breeding season (late June) and again in mid-August, 2012, as part of the stickleback annual long-term monitoring of the lake (Gudmundsson 1996, Einarsson et al. 2004). Five unbaited minnow traps (Dynamic Aqua-Supply, Surrey, BC, Canada; mesh size 3.2 mm) per site were set out in two 12-h bouts over a 24-h period, and the number of captures was counted. The 11 sites were grouped into four zones based upon historic sampling patterns that showed high correlations in catch among traps within the same zones and an order of magnitude difference in CPUE (catch per unit effort) between different zones (Gislason et al. 1998). Genetic studies showed spatial phenotypic and subtle genetic differentiation between the four zones as well (Millet et al. 2013). Stickleback abundances were assigned to transect sample sites according to their location among the four zones (see map in Gislason et al. 1998) and according to each stickleback sampling season (late June stickleback sampling was used for Transect 1 and mid-August sampling for Transects 2 and 3).

Benthic crustaceans and rotifers were collected using an activity trap that contained a set of six jars mounted with inverted funnels. The activity trap was based on a prototype introduced by Whiteside and Williams (1975) which was modified by Örnólfsdóttir and Einarsson (2004) for use in Mývatn. Benthic samples were obtained from nine sites of Transect 2 (25 July) separated by about 1 km in the South Basin. Three sampling jars were integrated to produce three independent samples per site. The two jars that were integrated were located close to each other on the sampling rack and 40 cm from the next nearest set of two jars. The nine benthic sites corresponded to the pelagic sampling sites 1, 3, 5, 7, 9, 11, 13, 15, 17 from Transect 2. During the benthic zooplankton sampling, we also obtained samples for benthic Chl-a, sediment characteristics (rocks, bare sediment, sediment with sparse chironomid tubes, sediment with >50% chironomid tubes, sediment with *Cladophora*, sediment with macrophytes), organic content, and abundance of chironomids. Chironomids were collected using a Kajak gravity core. Top layers of 10-cm thickness were sliced from the sediment cores from which chironomids were counted and identified to subfamily/tribe.

Statistical analyses

We used multilevel models, MLMs (Gelman and Hill 2007), to quantify simultaneously the composition of zooplankton communities and the abundance of the constituent species (Jackson et al. 2012). When applied using predictor (independent) variables, this approach makes it possible to assess the effects of abiotic and biotic drivers on community composition and abun-

dances, while taking into account spatial correlation in the residuals. When applied without predictor variables, this approach gives a test for spatial autocorrelation in community composition and species abundances.

A formal statement of the model for n species regressed against m predictor variables distributed among p sites is

$$\begin{aligned}
\log Y_q &= a_{\text{spp}[q]} + b_{1,\text{spp}[q]} x_{1,\text{site}[q]} + \cdots \\
&\quad + b_{m,\text{spp}[q]} x_{m,\text{site}[q]} + \varepsilon_q \\
a_{\text{spp}[q]} &= \alpha + c_{\text{spp}[q]} \\
b_{i,\text{spp}[q]} &= \beta_i + e_{i,\text{spp}[q]} \\
c &\sim \text{Gaussian}(0, \sigma^2_{\text{species}}) \\
e_i &\sim \text{Gaussian}(0, \sigma_i^2 \text{slope}) \\
\varepsilon &\sim \text{Gaussian}(0, \sigma^2 \Sigma) \qquad (1)
\end{aligned}$$

where

$$\Sigma = \begin{pmatrix} 1 & (1-g)e^{d[1,2]/r} & (1-g)e^{d[1,p]/r} \\ (1-g)e^{d[2,1]/r} & 1 & (1-g)e^{d[2,p]/r} \\ & & \ddots \\ (1-g)e^{d[p,1]/r} & (1-g)e^{d[p,2]/r} & 1 \end{pmatrix}.$$

This model performs a regression of the log abundance of n species, log Y, on the m predictor variables, x_i, simultaneously for all species; thus, log Y_q is the log abundance of a given species at a given site, with q denoting the species-site datum. The function spp[q] maps the datum q onto one of the corresponding n species, and the function site[q] maps the datum q onto one of the corresponding m sites. From this nomenclature, it follows that the n values of the coefficient $a_{\text{spp}[q]}$ give the mean abundances (intercepts) for each of the n species. The values of $a_{\text{spp}[q]}$ are treated as a random variable in the model; they are modeled with a "fixed effect" α giving the mean among all species and a "random effect" $c_{\text{spp}[q]}$ assumed to be normally distributed with mean 0 and variance $\sigma^2_{\text{species}}$. Similarly, the response of species to predictor variable x_i, $b_{i,\text{spp}[q]}$ is composed of a fixed effect β_i giving the mean response of all species to predictor variable x_i and a random effect $e_{i,\text{spp}[q]}$ giving deviation from the mean response of each of the n species which has variance ${\sigma_i}^2_{\text{slope}}$. Finally, the residual variation ε_q incorporates spatial autocorrelation in the covariance matrix $\sigma^2\Sigma$ that depends on the Euclidean distance $d[k, l]$ between sites k and l ($k, l = 1, \ldots, p$). Parameter r is the "range" that scales the distance between sites at which there is spatial autocorrelation among residuals, and parameter g is the "nugget" that scales the nonspatial variance in the residuals; parameters r and g are estimated during the fitting process.

The abiotic variables we tested were turbidity, pH, conductivity, temperature, light extinction coefficient, DO, lake depth, distance from the outlet of the South Basin, and latitude and longitude. The biotic variables were Chl-a and pelagic phycocyanin concentrations, proportion of all the phytoplankton that is *Oocystis* and proportion that is *Anabaena*, and stickleback density. All variables were transformed if needed to minimize skew. We excluded from the analyses those variables that were closely correlated to one another, so all abiotic and biotic variable listed above had pairwise correlations <0.7 (see Appendix: Table A1 for a complete list of variables). Because abundances of some species at some sites were zero, we added 0.5 to all abundances Y_q before taking the logarithm. For analyses of benthic communities, we included the same variables as the pelagic communities, and in addition benthic Chl-a, proportion of the benthos that is *Nostoc,* chironomid abundance, and organic content. For the analysis comparing pelagic and benthic communities, the response variable log Y_q was standardized (mean 0 and variance 1) to facilitate comparison of regression coefficients. We checked for normality and homogeneity of residuals by visual inspection of residuals plotted against fitted values.

This analysis simultaneously provides information about abiotic and biotic drivers of the community composition and the responses of individual species to these drivers (Jackson et al. 2012). Species-specific differences in responses to predictor variables are quantified by the coefficients $b_{i,\text{spp}[q]}$. Furthermore, the statistical significance of the variance terms ${\sigma_i}^2_{\text{slope}}$ gives a statistical test for whether predictor variable i plays a role in explaining variation in community composition; if different species respond differently to a given predictor variable (${\sigma_i}^2_{\text{slope}} > 0$), then the composition of the community must

vary with this variable. Finally, spatial autocorrelation is included on top of responses to predictor variables in the term ε_q. Thus, the single analysis reveals species-specific sensitivities to abiotic and biotic variables, the importance for these variables for community composition, and the spatial autocorrelation that is not explained by the included predictor variables. We performed these analyses with a linear mixed model on log-transformed data, rather than attempt a generalized linear model, because linear models applied to log-transformed count data can often give more reliable tests for the statistical significance of regression coefficients than generalized linear models (Ives 2015).

In addition to analyzing all species together, we estimated spatial autocorrelation for each species separately using both equation 1 and calculating Moran's I (Moran 1950). Using Eq. 1, these analyses were performed excluding predictor variables x_i, so the spatial correlation given by the range r was determined solely by distances between sites.

Data were analyzed using the package *lme4* (Bates et al. 2014) in R v. 3.1.0 (R Development Core Team 2014), and Moran's I was calculated using functions in the R package *ape* (Paradis et al. 2004). The maps were generated using the R packages *rgdal* (projection of latitude/longitude coordinates; Bivand et al. 2014), *maptools* (read in data from a shapefile and plot the map; Bivand and Lewin-Koh 2014), and *mapplots* (add the plot pie charts to the map; Gerritsen 2013). Code is provided in the Supplement.

Results

Community patterns

Daphnia longispina and *Cyclops abyssorum* were the two crustacean species with highest abundance in Mývatn in summer 2012 (mean abundance for *D. longispina*, 6.7, 11.6 and 13.6 individuals/L in Transects 1–3, respectively, and for *C. abyssorum*, 3.0, 4.7, 3.0 individuals/L; Fig. 2; Appendix: Table A2). *Chydorus sphaericus* had highest abundance in Transect 2 (25 July) following the prolonged period of strong wind (mean abundance: 0.3, 12 and 5 individuals/L in Transects 1–3, respectively). Simultaneously, *Cyclops* nauplii abundance decreased in Transect 2. The rotifer *Keratella*, which was only counted in Transects 2 and 3, was particularly abundant (mean abundance: 51and 43 individuals/L in Transect 2 and 3, respectively) and dominated the zooplankton community in the North Basin. Almost no zooplankton were found in the southeastern part of the South Basin where water temperatures were low due to inflow from cold springs (ca. 6°C).

In Transects 2 and 3, two zooplankton samples were taken in every other site to assess measurement error. Within-site (among replicate) variance relative to the total variance was 0.092 and 0.015 for Transect 2 and 3, respectively.

In the benthos sampling during Transect 2, *Cyclops abyssorum* had highest activity-abundance (286 CPUE; number individuals/net; Fig. 3, Appendix: Table A3), and it almost completely dominated the clear, cold southeast part of the South Basin. Small cladocerans (cladocerans other than *Daphnia longispina*) were also abundant, especially *Macrothrix hirsuticornis* Norman et Brady and *Alona* spp. (*rectangula*, *affinis*, and *quadrangularis*) that had activity-abundances of 229 and 175 CPUE, respectively.

Spatial structure

We performed initial analyses to document possible spatial structure in the pelagic and epibenthic communities. Spatial structure was assessed for all species as a group using the multilevel model (Eq. 1) deployed without predictor variables. For zooplankton communities, the estimates of the ranges r were 6.88, 2.55, and 5.52 km for Transects 1–3, respectively, demonstrating statistically significant (all $P < 0.001$) spatial autocorrelations on the scale of several kilometers. The nuggets g were 0.21, 0.33, and 0.05, demonstrating additional statistically significant (all $P < 0.001$) variation at a scale smaller than the minimum distance between sites (0.5 km). A measure of the unexplained autocorrelated "regional" variance is one minus the nugget g, $1 - g$, multiplied by the residual variance σ^2 (Eq. 1), which was 0.75, 0.61, and 1.74 for Transects 1–3, respectively. Because these analyses were performed on all zooplankton species together, they give a synoptic view of spatial structure for the zooplankton community.

We analyzed spatial autocorrelation for individual species using both the multilevel model without predictor variables and Moran's I.

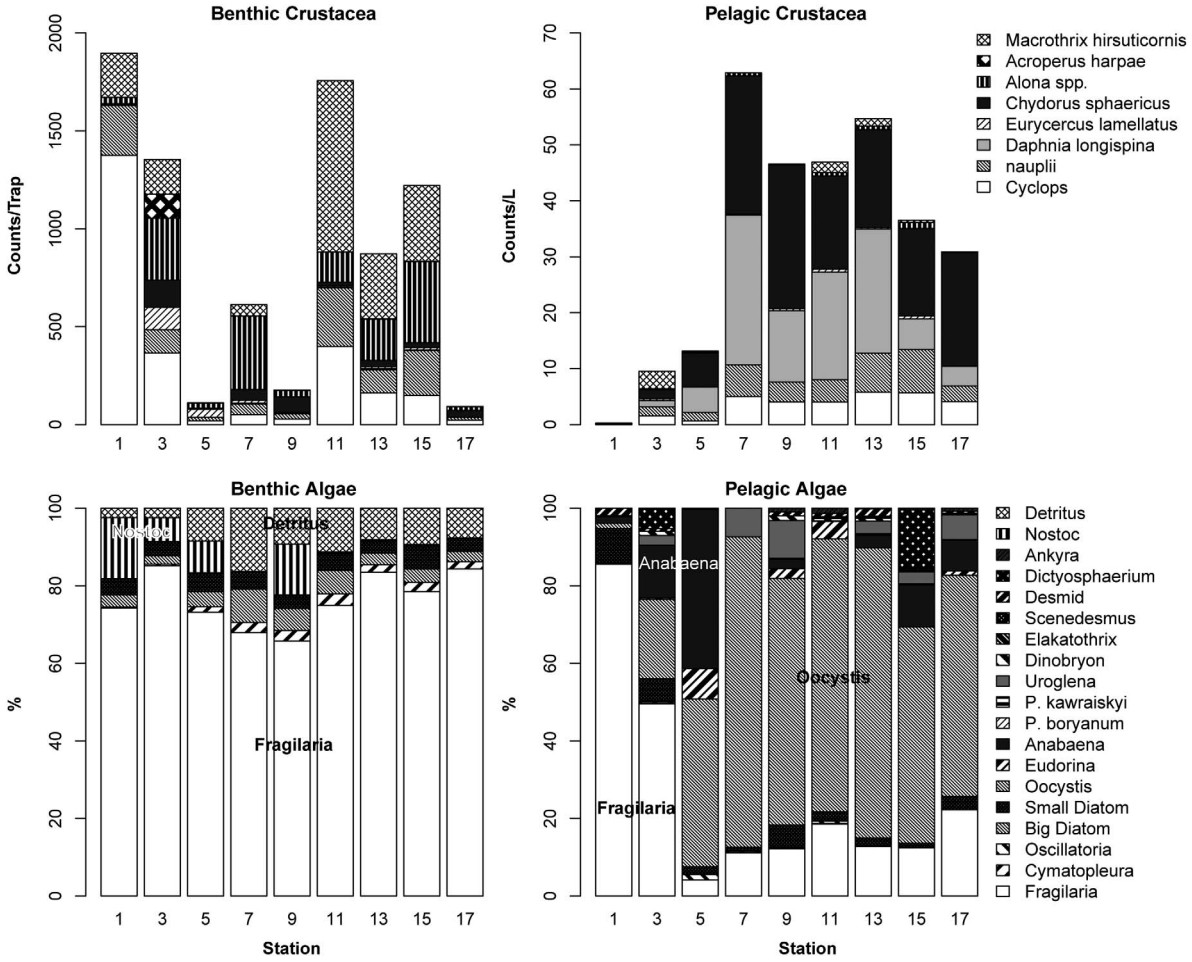

Fig. 3. Benthic crustacean abundance (mean catch per unit effort given as the number individuals/net, n = 2) in stations 1, 3, 5, 7, 9, 11, 13, 15 and 17 of Transect 2 (25 July 2012) in comparison to pelagic crustacean (number/L), and benthic and pelagic algae composition (%).

Spatial autocorrelation was found for *Asplanchna*, *Keratella*, *Cyclops abyssorum* adults and copepodites, and nauplii, *Daphnia longispina*, and *Chydorus sphaericus*, with all of these taxa showing significant spatial autocorrelation in Transect 3, and many showing significance in one or both of the other transects (Appendix: Table A4). Moran's I was more likely to identify spatial autocorrelation as statistically significant than Eq. 1, although this apparent increase in statistical power was slight.

We also performed a direct comparison for spatial structure between zooplankton and epibenthic communities by limiting the number of pelagic sites to those corresponding to the benthic sites that were sampled during Transect 2. When pooling samples to give a single value per benthic site, comparable to the single samples per pelagic site, spatial correlation in community composition occurred at a finer spatial scale for the benthic community, with the range *r* estimated as 0.61 km versus 9.0 km for the pelagic samples (Table 1).

Abiotic and biotic variables

We used the multilevel model (Eq. 1) to investigate abiotic and biotic variables as drivers of spatial variation in zooplankton community composition (Table 2). In these analyses, log abundances of all species were included, and random effects indicated differences among species in how they respond to the drivers. The

Table 1. Environmental determinants of benthic community structure, and comparison of spatial autocorrelation with the pelagic community during Transect 2 (25 July). Benthic data were analyzed using both 3 samples per site, and pooling to give one sample per site. The full model (Eq. 1) included abiotic (turbidity, nutrient concentrations, pH, conductivity, temperature, light extinction coefficient, DO, depth, distance from the outlet, latitude and longitude) and biotic (phytoplankton and benthic algae community composition, fish densities, benthic and pelagic Chl-a, pelagic, phycocyanin, benthic chironomid abundance) variables. Variables were removed to give the model with the lowest AIC. Similar analyses were performed without predictor variables to estimate spatial autocorrelation in community composition, performing analyses with both 3 samples and pooled samples per site. For comparison, the model without predictor variables was analyzed for the pelagic communities at the same sites as the benthic samples. 95% confidence intervals are presented in parentheses for the range, *r*, and nugget, *g*, when they are significant. †P < 0.1, *P < 0.05, ***P < 0.001.

	Benthic				Pelagic	
Model	Full		Spatial		Spatial	
Coefficients	Fixed	Random	Fixed	Random	Fixed	Random
Species	1.46*	1.63	1.44*	1.60	0.07	0.11
Species/Site		1.29		–		–
Pelagic Chl-a (log μg/L)	−0.49*					
Nostoc (%)	−0.52*					
Residual variance		0.67		1.53		1.52
Range (km)	0.0036		0.61*** (0.32–1.16)		9.01*** (3.24–25.1)	
Nugget	0.07		0.14*** (0.09–9.22)		0.10† (0.03–0.28)	

best-fitting models (best AIC) contained only a small subset of the total predictor variables (Appendix: Table A1) and included random effects for Chl-a and proportion *Anabaena* (Transect 1); depth, Chl-a and proportion *Anabaena* (Transect 2); and Chl-a and proportion *Oocystis* (Transect 3). Thus, Chl-a and the makeup of the phytoplankton community (proportion *Anabaena* or *Oocystis*) were consistent biotic predictors of differences among zooplankton in their spatial distributions. In Transects 2 and 3, *Anabaena* and *Oocystis* were the two dominant phytoplankton throughout much of the lake outside the southeast corner of the South Basin; thus, the phytoplankton communities at different sites could be roughly categorized as *Anabaena* dominated or *Oocystis* dominated, with the correlation between logit proportion *Anabaena* and logit proportion *Oocystis* −0.77 and −0.36 in Transects 2 and 3, respectively. Because Transect 1 did not have sample sites into the North Basin (a storm blew in), we also performed the same analyses but removing all samples from the North Basin; the qualitative results were not changed, suggesting that the results were not sensitive to differences in sample locations among transects.

In addition to these biotic and abiotic drivers which had different effects on different zooplankton taxa, there were also negative fixed effects for temperature and positive fixed effects for light extinction coefficient which affected all zooplankton taxa in the same way; higher abundances of all zooplankton species were found at lower temperature and lower water clarity. After accounting for these abiotic and biotic drivers, there was still residual spatial variation (range $r = 7.7$, 1.02, and 3.6 km for Transects 1–3), thereby implying that the observed spatial variation in zooplankton was not completely explained by these variables. Furthermore, the autocorrelated component of the residual variances, given by $(1 - g)\sigma^2$ (Eq. 1), were 0.69, 0.13, and 0.71 for Transects 1–3. Comparing to the autocorrelated components of the model without environmental variables, these represent decreases of 8% (0.69 vs. 0.75), 79% (0.13 vs. 0.61), and 59% (0.71 vs. 1.74). These values imply that in Transects 2 and 3, the environmental variables we measured explained more than half of the spatial autocorrelation in the abundances of zooplankton. Nonetheless, in all transects there were factors other than the environmental variables we measured that were additionally responsible for the spatial autocorrelation of zooplankton abundances.

These statistical analyses also provide information about the responses of individual species to the abiotic and biotic variables (Table 3). We

Table 2. Multilevel model (Eq. 1) for the effects of abiotic and biotic variables on the composition of zooplankton communities during Transect 1 (2 July), Transect 2 (25 July), and Transect 3 (5 August). Fixed and random effects are included for predictor variables that were included in the lowest-AIC models, selecting from abiotic variables (turbidity, nutrients nitrate, phosphate, ammonia, total nitrogen, total phosphorus, silica, N:P, pH, conductivity, temperature, light extinction coefficient, dissolved oxygen (DO), lake depth, distance from the outlet, and latitude and longitude) and biotic variables (Chl-a, phycocyanin, proportion of the phytoplankton that is *Oocystis* and proportion *Anabaena*, chironomid abundance, and stickleback densities). 95% confidence intervals are presented in parentheses for the range, *r*, and nugget, *g*, when they are significant.

Variable	Transect 1		Transect 2		Transect 3	
	Fixed	Random	Fixed	Random	Fixed	Random
Species	−0.04	0.03	0.75·	1.32	0.44	1.00
Temperature (exp °C)	...	...	−0.13*	...	−0.17*	...
Depth (m)	0.09·	...	0.13	0.23**	...	...
Light extinction coefficient (k)	0.07*	...	0.09·	...	0.04	...
Chl-a (log μg/L)	0.12*	0.07	0.24**	0.22**	0.30***	0.15
Prop. Oocystis (logit)	−0.08*	...	...	...	0.15	0.41***
Prop. Anabaena (logit)	−0.11*	0.11*	−0.13·	0.16*	...	...
Residual		0.93		0.65		0.90
Range (km)	7.70*** (3.65–16.2)		1.02* (0.21–4.88)		3.60*** (1.16–10.9)	
Nugget	0.20*** (0.11–0.33)		0.70		0.12** (0.05–0.27)	

focused on those variables with random effects included in the model, implying that different species responded differently to these variables. The large crustaceans *Cyclops abyssorum* and *Daphnia longispina* responded negatively to the proportion *Anabaena* and positively to the proportion of *Oocystis*, whereas the reverse was generally true for the small crustaceans. Similarly, *Keratella* responded negatively to *Anabaena* and positively to *Oocystis*, whereas the reverse was true for *Asplanchna*. Thus, high concentrations of "palatable" phytoplankton favor *Cyclops abyssorum*, *Daphnia longispina*, and *Asplanchna*, whereas dominance by *Anabaena* appears to favor smaller cladocerans and *Keratella*. Finally, depth was a driver of differences in zooplankton community composition in Transect 2, with greater depth favoring large crustaceans *Cyclops abyssorum* and *Daphnia longispina*, and less depth generally favoring small crustaceans and rotifers.

We analyzed the benthic samples from Transect 2 to identify possible abiotic and biotic drivers of the epibenthic community composition. The analysis could not identify abiotic or biotic drivers that were responsible for variation in community composition among sites; none of the predictor variables had random effects that were included in the model. Nonetheless, both pelagic Chl-a and the proportion of *Nostoc* in the benthic samples had negative fixed effects on the log abundances of epibenthic taxa as a group, implying that these variables reduced the abundances on average for all taxa in the epibenthic community.

Bottom-up and top-down control

The results of the multilevel model (Table 2) suggest that the main determinants of zooplankton community composition are characteristics of the lower trophic level: Chl-a and the makeup of the phytoplankton community. Furthermore, in all three transects there was a statistically significant decrease in phytoplankton biomass with increasing zooplankton biomass ($r^2 = 0.17$, $P = 0.02$; $r^2 = 0.45$, $P < 0.001$; $r^2 = 0.37$, $P < 0.001$, in Transects 1–3, respectively; Fig. 4), implying high consumption of phytoplankton by zooplankton. These results suggest that zooplankton community composition is determined primarily by bottom-up forces.

Sticklebacks varied in abundance within Mývatn, having high densities in the North Basin and very low densities in the southeast part of the South Basin. Nonetheless, there was no statistical evidence that they affected spatial variation in zooplankton species composition; sticklebacks were not included in any of the best-fitting multilevel models (Table 2). Furthermore, the zooplankton:phytoplankton biomass ratio for the lake was on average 1, 16, and 11 for Transects 1–3 (ratio calculated using average species biomass). These values are characteristic

Table 3. Coefficients from the multilevel model (Eq. 1) giving species-specific responses to Transect 1: Chl-a and proportion *Anabaena*; Transect 2: Depth, Chl-a, and proportion *Anabaena*; and Transect 3: Chl-a and proportion *Oocystis*. Values are the species-specific random effect plus the estimate for fixed effects.

	Transect 1		Transect 2			Transect 3	
Species	Chl-a	*Anabaena*	Depth	Chl-a	*Anabaena*	Chl-a	*Oocystis*
Rotifera							
Asplanchna	−0.01	0.02	−0.13	−0.12	0.13	0.05	−0.36
Keratella			−0.33	−0.12	−0.07	0.00	0.25
Copepoda							
Cyclops abyssorum	0.07	−0.14	0.08	0.16	−0.23	0.07	0.30
Nauplii	0.06	−0.02	0.11	0.16	0.09	0.12	−0.20
Cladocera							
Daphnia longispina	0.01	−0.20	0.36	0.35	−0.04	0.17	1.03
Eurycercus lamellatus	−0.02	0.07	−0.13	−0.10	0.06	−0.13	−0.16
Alona spp.	−0.02	0.07	−0.06	−0.11	0.13	−0.05	−0.24
Chydorus sphaericus	−0.03	0.03	0.24	0.19	−0.18	0.12	−0.05
Acroperus harpae	−0.03	0.06	−0.16	−0.23	0.07	−0.14	−0.17
Macrothrix hirsuticornis	0.01	0.05	0.02	−0.19	0.05	−0.08	−0.26
Simocephalus vetulus	−0.02	0.06				−0.14	−0.14

of temperate-zone lakes with little top-down regulation by fish predators (Jeppesen et al. 2003).

Although there is no evidence that sticklebacks affected the species composition of the zooplankton community, the zooplankton:phytoplankton biomass ratio was inversely related to stickleback abundance, except in the cold southeast part of the South Basin and the connecting area between the North and South basin of Transect 2 (Fig. 4). We suspect that the low pelagic biomass of zooplankton in the southeast part of the South Basin is primarily due to physical conditions (temperature < 6°C and phytoplankton productivity < 0.5 μg Chl-a/L) rather than absence of sticklebacks. Nonetheless, even with this region excluded, areas with high stickleback abundance generally had low zooplankton biomass ($r^2 = 0.05$, $P = 0.2$; $r^2 = 0.16$, $P < 0.05$; $r^2 = 0.16$, $P < 0.05$, in Transects 1–3, respectively; Fig. 4). This suggests that there is top-down control of zooplankton biomass, although this does not affect zooplankton species composition.

Discussion

The zooplankton community in Mývatn showed strong spatial structure despite the fast flow rate (>250 m/d) and horizontal mixing due to high winds. The degree of spatial variation differed among taxa and transects, but spatial differences in abundances could reach one and two orders of magnitude for some crustacean and rotifer taxa, respectively. Overall, evidence points to bottom-up forces determining the composition of the zooplankton community. Sites with lower phytoplankton biomass had higher zooplankton biomass, with these sites dominated by *D. longispina* and *C. abyssorum*. These large crustaceans, along with the rotifer *Keratella*, were also associated with either high relative abundance of *Oocystis* (a palatable green algae) or low relative abundance of *Anabaena* (an unpalatable cyanobacteria) in the phytoplankton community. These patterns in the zooplankton community were found in all three transects, but were less evident after a period of prolonged strong wind events before Transect 2 when the primarily epibenthic species *C. sphaericus* reached high abundance (Fig. 2). The presence of spatial patterns in all three transects, even after the windy period before Transect 2, suggests that the bottom-up biotic drivers of zooplankton community composition are sufficiently strong to overcome the high flow rate and horizontal mixing within a lake.

The biotic factors driving spatial patterns in zooplankton community composition in Mývatn are among the most common factors driving large-scale spatial heterogeneity of freshwater zooplankton across lakes (e.g., Pinell-Alloul et al. 1995). Chl-a had positive effects on *D. longispina* and *C. abyssorum*, and was associated with higher total zooplankton abundance in all transects. However, it had negative effects on rotifers and small cladocerans. In among-lake

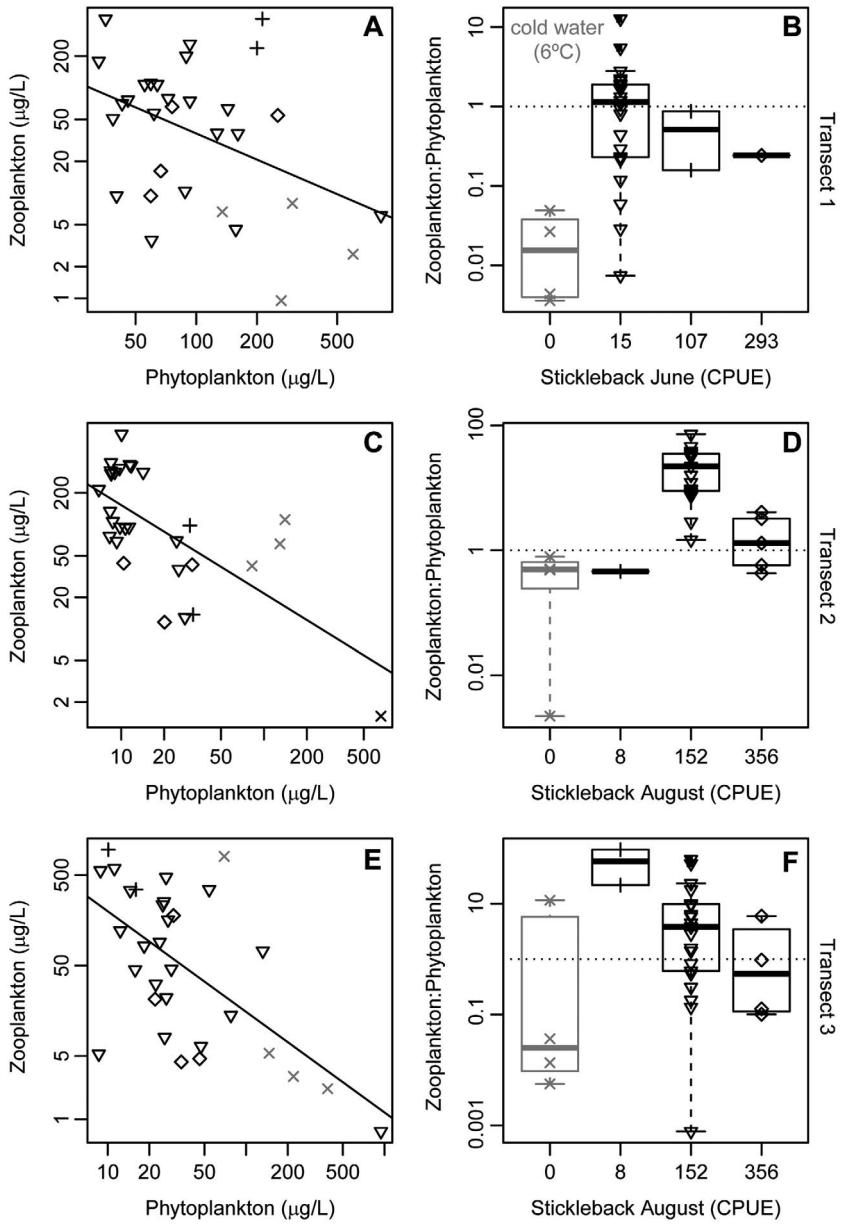

Fig. 4. (A, C, E) Zooplankton and phytoplankton biomass (µg/L) relationships, and (B, D, F) zooplankton:phytoplankton biomass ratio with stickleback abundance (CPUE; number individuals/net) for Transects 1–3 (rows). Stations from the south-east corner of the South Basin, where water temperatures are roughly 6°C, are shown in gray, stations from the rest of the South Basin in black triangles; stations in the transition zone between the South and the North Basin in x; and stations in the North Basin in diamonds.

comparative studies, higher productivity is associated with dominance by large-bodied cladocerans, which are superior competitors to smaller-bodied taxa provided fish predation is low (Romanovsky and Feniova 1985, Gliwicz 1990). In Mývatn, large-bodied crustaceans were associated with *Oocystis*, whereas small-bodied crustaceans and rotifers were associated with *Anabaena*. Cyanobacteria are often associated with lower abundance of larger herbivorous

zooplankton, because they have low nutritional value (Muller-Navarra et al. 2000), because they physically interfere with the zooplankton feeding apparatus (Webster and Peters 1978, DeMott 1989), or because they produce toxins (Sarnelle et al. 2010). These effects are less severe for rotifers and small-bodied cladocerans (e.g., Sommer et al. 1986, DeMott 1989), and hence numerous studies show an association between cyanobacteria and rotifers or small-bodied cladocerans either across lakes or within lakes through time (Fulton and Paerl 1988, Bednarska 2006). Thus, the main drivers of zooplankton community composition in Mývatn, Chl-a and the relative abundance of unpalatable or palatable phytoplankton, have been shown to be important drivers of variation in zooplankton community composition among lakes.

Top-down fish predation is also a common driver of among-lake variation in zooplankton community composition; generally, lakes with high fish predation contain small-bodied crustacean species, because large-bodied species are more vulnerable to predation (Brooks and Dodson 1965, Jeppesen et al. 2004, Brucet et al. 2010). However, in Mývatn, we found no evidence that stickleback density changed zooplankton species composition. This might be due to high movement rates of sticklebacks within the lake. Nonetheless, high stickleback density was associated with a low zooplankton:phytoplankton biomass ratio, suggesting that top-down effects may partially determine the biomass of zooplankton (Adalsteinsson 1979*a*).

Despite the strong bottom-up effects on zooplankton community composition, after factoring out statistically significance environmental variables there was still spatial autocorrelation in the residual variation on the order of 2.5–7 km (Table 2); the inclusion of environment variables reduced the autocorrelated component of the residual variation by 8%, 79%, and 59% in Transects 1–3, respectively. This suggests either that there are important but unmeasured environmental variables that are spatially autocorrelated, or that water movement has caused mixing among adjacent areas which are subject to different abiotic and biotic drivers. Because the rate of zooplankton population response to temporal changes in environmental conditions is limited by their population growth rates, there will likely be temporal lags in the zooplankton community response to abiotic and biotic drivers. In moving water, temporal lags can generate spatial autocorrelations (lags in space) that are not immediately explained by the local site conditions.

In comparing the spatial autocorrelation structure of zooplankton and epibenthic communities, the spatial extent of autocorrelations in the pelagic zone (9 km) were much greater than in the benthos ($\leq$0.6 km) (Table 1). This suggests that finer-grained spatial patterns can develop in the stationary substrate of the benthos. Studies comparing spatial patterns in plankton and benthos are scarce. A previous study on the spatial distribution of benthic invertebrates showed a high degree of similarity in the fauna occurring at sites 12 km apart which was attributed to the uniformity of the sediment (Darlington 1977). A particular problem in comparing pelagic vs. benthic spatial correlations in the literature is that the composition of the fauna in these two zones typically differs considerably. In the case of Mývatn, however, we found the same species in both zones, although differing in relative abundances. The contrasting extent of spatial structure we found for pelagic and benthic community composition implicates the importance of substrate, rather than taxonomic makeup of the zooplankton species, in determining spatial patterns.

The strength of the bottom-up forces driving zooplankton community composition can be very roughly inferred by estimating the rate of water flow in Mývatn and comparing this to the possible population growth rates of the zooplankton. The discharge rate from the South Basin is 20.9 m^3/s, and its volume is 67.86 10^6 m^3. These give a water turnover rate of 37 d, which in turn translates roughly into a flow rate of 200 m/d. Windy periods will likely generate flow rates of similar or even greater magnitude when integrated over the water column (Kjaran et al. 2004). Taking the dominant zooplankton, *D. longispina*, variation in abundance among sites can be characterized by the ratio of the density from the five highest sites to the density from the 5 lowest sites, which are 158, 122, and 1096 for Transects 1–3, respectively. These differences in densities occur over a distance of 5 km (Fig. 2). For these differences to be generated given a

water movement rate of 200 m/d, the difference between the intrinsic rates of increase of *D. longispina* between low and high density sites would have to be 0.20, 0.19, and 0.28 for Transects 1–3, while these values would have to be 0.41, 0.38, and 0.56 with a flow rate of 400 m/d. These rough values are mostly within the range of possible intrinsic rates of increase for *D. longispina*, with peak values from the literature ranging from 0.27 to 0.47 depending on the study (Lundstedt and Brett 1991, Ojala et al. 1995, Antunes et al. 2003, 2004). Furthermore, the intrinsic rate of increase depends strongly on food type, food abundance, and temperature (Lundstedt and Brett 1991, Brett 1993, Ojala et al. 1995, Lair and Picard 2000, Antunes et al. 2003, 2004, Gladyshev et al. 2006). We could not find similar literature on zooplankton less-well studied than *D. longispina*, although we suspect numbers that are similar. Therefore, the spatial patterns we observed could conceivably be generated by spatial variation in zooplankton population growth. Of course, these are very coarse calculations that do not account for horizontal mixing, initial colonization of water entering the lake, potential stickleback predation, etc. Nonetheless, they suggest large spatial differences in zooplankton population growth, and hence strong bottom-up forces, underlying variation in zooplankton community composition.

Our results show that zooplankton community composition in Mývatn has strong spatial patterns that are apparently driven by bottom-up forces. Productivity (Chl-a) and the composition of the phytoplankton community, particularly the abundance of cyanobacteria, are well-known drivers of among-lake variation in zooplankton communities, and we have shown they are also important within Mývatn. Nonetheless, our finding that any consistent spatial patterns arise in the zooplankton community is remarkable given the very short water turnover times and the horizontal mixing in this windy environment. The bottom-up effects must be strong.

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Supplemental Material

Appendix

Table A1. Abiotic and biotic variables analyzed.

Variable	Transect 1		Transect 2		Transect 3	
	Mean	Range	Mean	Range	Mean	Range
Depth (m)	2	1–3	2	1–3	2†	1–3
Water column						
Temperature (°C)	14.3	8.7–16.0	11.7	6.2–13.3	14.9	7.2–17.4
Light extinction k	0.4	0.1–0.6	0.8	0.2–1.7	0.7	0.2–1.7
Turbidity	8.9	0–4.3	1.8	0–4.4	2.0	0–24.6
O_2sat (%)	120	88–141	98	79–129	113	79–155
DO (mg/L)	12.3	10.3–15.3	10.6†	9.0–13.7	11.4	9.6–15.0
pH	9.8	9.4–10.1	9.3†	8.3–10.4	9.5	8.6–9.8
Conductivity	188†	135–288	190†	133–285	190†	131–295
Nitrate (µmol/L)	0.3	0.1–1.7	0.2	0–2.9	0.3	0.1–2.8
Phosphate (µmol/L)	0.7	0.2–1.6	1.3	0.2–2.2	1.4	0.2–2.6
TN (µmol/L)	4.3	3.2–5.3	3.3	1.6–4.6	4.6	2.3–6.4
TP (µmol/L)	1.0	0.5–1.8	1.9	0.5–3.0	1.9	0.4–3.4
NH4 (µmol/L)	1.3	0.5–4.2	0.9	0.3–1.8	0.6	0.3–1.0
Silica (µmol/L)	147	43–360	160	65–402	155	90–318
NP (%)	4.8	2–11	2.6	1–8	3	1–11
Chl-a (µug/L)	0.85	0.08–2.01	5.05	0.10–9.47	2.81	0.07–7.66
Phycocyanine (µg/L)	0.04	0.002–0.16	0.01†	0.004–0.04	0.01†	0.004–0.03
Oocystis (%)	22	0–71	43†	0–84	27	0–76
Anabaena (%)	10	0–63	20	0–98	29	0–89
Nostoc (%)	...	...	5	0–16	...	...
Chironomids (N)	...	...	16	4–34	...	...
Organic content (%)	...	...	27	16–33	...	...
Stickleback (number)	80	0–324	112	0–324	102	0–324
Benthos						
Chl-a (µg/L)	...	...	6717	824–13953	...	...
Nostoc (%)	...	...	5	0–16	...	...
Chironomids (N)	...	...	16	4–34	...	...
Organic content (%)	...	...	27	16–33	...	...

† Measured variables excluded in the analyses due to pairwise Spearman correlation coefficients with other variables >0.7.

Table A2. Pelagic zooplankton abundance (number per L) in Lake Mývatn during Transect 1 (2 July), Transect 2 (25 July), and Transect 3 (5 August). *Keratella* was only measured in Transects 2 and 3.

Species	Transect 1		Transect 2		Transect 3	
	Mean	Range	Mean	Range	Mean	Range
Rotifera						
Asplanchna	0.8	0–7.7	0.2	0–1	0.9	0–6
Keratella	...	...	50.5	1–99	42.9	0–122
Copepoda						
Cyclops abyssorum	3.1	0–14.1	4.7	0–12	3.0	0–11
Nauplii	8.7	0–25.1	3.0	0–8	8.5	0–30
Cladocera						
Daphnia longispina	6.7	0.07–34.6	11.6	0–54	13.6	0–72
Eurycercus lamellatus	0.009	0–0.2	0.2	0–1	0.03	0–0.3
Alona spp.	0.008	0–0.1	0.2	0–1	0.1	0–1
Chydorus sphaericus	0.3	0–1.7	12.1	0–33	5.3	0.1–16
Acroperus harpae	0.02	0–0.3	0.1	0–2	0.01	0–0.2
Macrothrix hirsuticornis	0.1	0–0.7	0.4	0–3	0.1	0–1
Simocephalus vetulus	0.02	0–0.3	...	...	0.02	0–0.3

Table A3. Benthic zooplankton abundance (number per jar, with nine replicates pooled per site) in Lake Mývatn during Transect 2 (25 July).

Species	Mean	Range
Rotifera		
Asplanchna	1	1–4
Keratella	...	...
Copepoda		
Cyclops abyssorum	286	20–1376
Nauplii	126	14–298
Cladocera		
Daphnia longispina	2	0.3–7
Eurycercus lamellatus	23	1–114
Alona spp.	175	18–413
Chydorus sphaericus	44	5–139
Acroperus harpae	15	0.3–122
Macrothrix hirsuticornis	229	1–875
Simocephalus vetulus	0	0–0

Table A4. Spatial correlation structure for pelagic zooplankton species during Transect 1 (2 July), Transect 2 (25 July), and Transect 3 (5 August).

	Transect 1			Transect 2			Transect 3		
Species	Range	Nugget	I	Range	Nugget	I	Range	Nugget	I
Asplanchna	724*	0.0002	0.10**	0.003	0.05	−0.007	469	0.002	0.06*
Keratella	...	...	...	321	0.67	−0.02	3424***	0.00003	0.26***
Cyclops abyssorum	1205***	0.0005	0.20***	1253*	0.25	0.16***	1669***	0.00003	0.23***
Nauplii	1778***	0.001	0.27***	872*	0.12	0.12**	3721***	0.09	0.30***
Daphnia longispina	332	0.03	0.07*	678*	0.003	0.10**	1734***	0.15	0.18***
Eurycercus lamellatus	29	0.12	−0.04	381	0.52	0.08*	133	0.11	−0.005
Alona spp.	47	0.11	−0.06	45	0.12	−0.01	3	0.003	0.01
Chydorus sphaericus	598	0.28	0.05*	2884***	0.19	0.24***	3729***	0.01	0.26***
Acroperus harpae	15	0.13	−0.05	276	0.007	0.005*	29	0.11	−0.05
Macrothrix hirsuticornis	287	0.002	−0.01	371	0.01	0.04	287	0.002	0.01
Simocephalus vetulus	35	0.12	−0.04	27	0.15		8	0.13	−0.04

SUPPLEMENT

R code and scripts for computing multilevel models with spatial autocorrelation for zooplankton spatial distribution data (*Ecological Archives*, http://dx.doi.org/10.1890/ES14-00392.1.sm).